TAXONOMY AND SYSTEMATICS OF SELECTED MARINE SOFT-BOTTOM FAN-WORMS (POLYCHAETA : SABELLIDAE : SABELLINAE)

Sabine J. Cochrane

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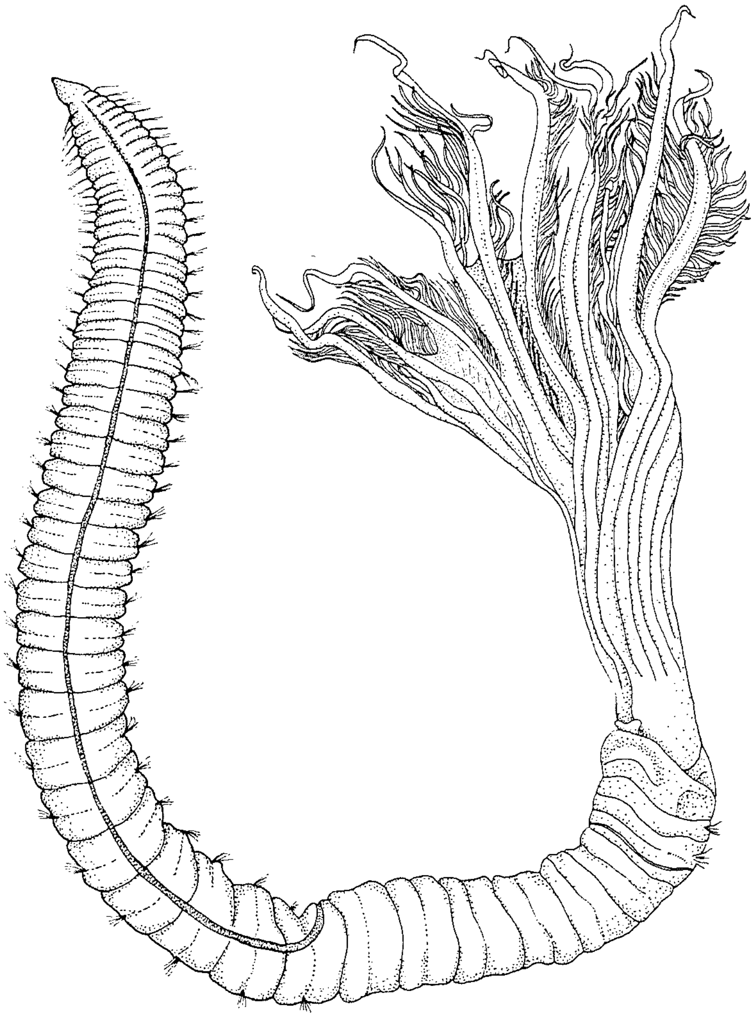
Taxonomy and systematics of selected marine soft-bottom fan-worms

(Polychaeta: Sabellidae: Sabellinae)



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05.05.2000
A thesis submitted in fulfilment of the requirements of the University of St. Andrews
for the degree of Doctor of Philosophy

University of St. Andrews, Scotland/ Akvaplan-niva, Polar Environmental Centre, Tromsø, Norway

Declarations

(i) I, Sabine J. Cochrane, hereby certify that this thesis, which is approximately 67 000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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(ii) I was admitted as a research student in September 1992 and as a candidate for the degree of PhD in September 1992; the higher study for which this is a record was carried out in Tromsø, Norway, under supervision from the University of St. Andrews between 1992 and 1999.

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Abstract

The main descriptive characters of sabellid polychaetes are presented. Easily misunderstood morphological features are clarified by a series of schematic drawings. The importance of scale is emphasised and some aspects of population ecology and reproduction are addressed.

An introduction to *Euchone* Malmgren (Polychaeta: Sabellidae: Sabellinae) is given and the diagnostic character is discussed. A new taxon, *Euchone x*, is described from the North Sea and Northern Norwegian Sea. *Jasmineira candela* Grube from the Adriatic Sea is redescribed and *Jasmineira oculata* Langerhans from Atlantic waters is reinstated. Some little-known records of *Chone* in Northern Atlantic waters are presented and one anomalous taxon is described.

A historical overview of sabellid systematics is given. Because the binomial system of taxonomic nomenclature still used today was devised more than a century before evolutionary thinking, finds of organisms that do not 'fit' into the traditional systematic hierarchy are not unexpected. An introduction to phylogenetic systematics is given and some current issues are discussed. The concept of phylogenetic taxonomy is introduced. Phylogenetic analyses were carried out of taxa mainly within *Euchone* with some members of *Chone*, *Jasmineira* and *Amphicorina*. *Euchone sensu* Malmgren is revealed as being an artificial taxon. Five taxa previously assigned to *Euchone* are recognised as a discrete sister group to *Chone*, *Euchone* and *Jasmineira*. The data set is further used to demonstrate how phylogenetic taxonomy might be applied to the study group of organisms.

Some behavioural observations were made on captive live specimens of *Euchone x* and the ecological implications are discussed. Some observations are provided on its reproduction and an enigmatic parasitic organism found within the radiolar crown is investigated.

Although several important aspects of the taxonomy of the group were resolved, there remain many future challenges in the taxonomy and systematics of soft-bottom sabellin fan worms.

Foreword

Why sabellin polychaetes?

The choice of selected soft-bottom Sabellinae (Polychaeta: Sabellidae) as the main subject-matter of the present thesis was an almost unconscious decision. At the time, through employment in environmental monitoring, first with SEAS Ltd., Scotland and later Akvaplan-niva in Tromsø, Northern Norway, we were confronted with large numbers of specimens, the likes of which I had never seen before. These turned out to be extremely small sabellins, requiring some inventive methods for close anatomical study. However, the more literature I read on the subject, and the more proficient I became in examining the material to hand, the less able I was to place specimens within discrete taxonomic categories. In fact, I was no longer able to distinguish between certain taxa at all, nor to decide where mere individual variation ended and another taxon began. This applied to identification attempts to the level of both species and higher taxa. It became a case of 'double or quits' and, obstinately, I chose the former approach.

An interest in these problematic sabellins thus developed out of the sheer frustration of being unable to place specimens into proper taxonomic and systematic categories. Frustration led to despair and eventually to the realisation that soft-bottom sabellin polychaetes were deserving of more attention than they generally have received in both the taxonomic and ecological literature. After failing to find a suitable expert on the tiny sabellins found in our sampling areas, I embarked on the task myself in 1991, with the naïve enthusiasm of the beginner. In 1999, I am merely able to state that I have uncovered more enigmas than I have solved, raised more questions than I have answered and indicated more issues for further research than I have carried out. I still cannot distinguish for certain between the sabellin 'genera' that aroused my interest in the beginning of this study. The difference is that it no longer matters.

As a consequence, I am no longer ashamed of the series of hopeless misidentifications and vague records of "Sabellidae indet." which adorn the commercial survey reports to which I have contributed. It so conspires that many of the specimens concerned belong to taxa that either have been ignored or overlooked in the literature or to species new to science. It also appears that assigning soft-bottom sabellins into a tidy 'filing system' of genera is a futile quest. The current diagnoses of several of the genera concerned do not encompass all the species assigned to them. The descriptive characters within the organisms concerned vary to such a large degree that it is not uncommon to find species showing affiliation to more than one genus.

Central to an interest in taxonomy and systematics is the study of relationships between organisms. In this context, the concept of discrete genera becomes of minor importance. In terms of applied environmental monitoring and 'biodiversity' mapping studies, it is of value to list the lowest identifiable taxa present in a particular area, which usually refers to species. Thus, the present study focuses on revealing some of the relationships between selected soft-bottom sabellin polychaetes, describing new and little-known species and a discussion of some relevant systematic and ecological issues.

Aims

The overall aims of the present study are to review the major milestones in the development of taxonomy and systematics and to contribute further knowledge of selected sabellid polychaetes. Using specimens obtained locally, supplemented by museum holdings, it is aimed to provide taxonomic descriptions of certain Atlantic soft-bottom species which commonly are mis-identified or are new to science. The principles of phylogenetic systematics are outlined, discussed and applied to a selected area of the Sabellidae. Using an existing phylogenetic tree of the Sabellidae, the relationships between a restricted group of related taxa are further clarified. The principles of phylogenetic taxonomy are discussed in the context of the present work. Further, it is aimed to discuss the logic of traditional versus phylogenetic taxonomy in a research and applied context. Finally some aspects of the behaviour and ecology of a new taxon common in Atlantic waters will be addressed.

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To Arran, Hannah and Anneke, in apology for my constant absence from their lives.

"There is no such word as impossible. It might be very difficult, but it's not impossible".

Brass band conductor George Annan, Perth, Scotland. c.1979

Sources of material

Specimens

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INTRODUCTION

"So it cometh often to pass, that mean and small things discover great, better than great can discover the small."

Francis Bacon (1561-1626)

1 Introduction to the Sabellidae

1.1 Scope

The present section first and foremost aims to provide a basic understanding of sabellid morphology, for readers not specialised in this group. In addition, an attempt has been made to clarify certain features which are subject to misinterpretation both in the literature and during specimen examination. Neither the anatomical features covered, nor the examples given, are comprehensive but have been selected as being most informative for the present purpose. The extensive use of drawings found in the literature on the Sabellidae is deliberate, allowing features illustrated in published descriptions to be compared and contrasted in the context of general sabellid morphology. In the captions, the word ‘from’, as in “illustration from ….”, refers to a drawing reproduced directly from the literature, in unchanged form. On the other hand, ‘after’ refers to a drawing essentially unchanged from its original publication, but which may have been re-traced for clarity (for example omitting detail superfluous to the present purpose) or had some of the original labelling removed for simplicity. Where significant changes have been made, these are referred to as “modified after”. Original drawings and images of study material are indicated as such.

The lack of scale bars in the illustrations presented in this introductory chapter also is deliberate because of the great variation in size between sabellid polychaetes. The degree to which size affects the morphology is not consistent; some taxa of similar size possess very different features and conversely, other taxa of very different body sizes may possess remarkably similar features, differing only in scale. Therefore, for a general overview of sabellid morphology, size indications are inappropriate.

At the risk of oversimplification, a series of schematic drawings has been created to illustrate certain general, but important, features and concepts, around which there is or has been a certain amount of confusion in the literature. In this way, eventual misinterpretation of features discussed in the subsequent chapters is avoided.

A glossary of the key terms used throughout this thesis is given in Section 1.5. Note that the term 'chaetae', as adopted by Knight-Jones & Perkins (1998), is used throughout to refer to the bristles of sabellid polychaetes, as opposed to the common usage of the term 'setae' (e.g. Fauchald 1977; Knight-Jones & Fordy 1979; Knight-Jones 1981; Fitzhugh 1989). The latter term is considered more reminiscent of that applied to the Crustacea (e.g. Sars 1890), which are of a very different structure. Thus, the term chaetae is retained and likewise, the derivations 'chaetiger', 'chaetigerous', 'notochaetae' and 'neurochaetae' are used.

Further details on the morphology of the Sabellidae, as well as diagnoses of the higher taxa given as examples, are found in Fitzhugh (1989). Other key general reference works include Hartmann-Schröder (1996), Knight-Jones (1990), Hobson & Banse (1981), Day (1967), Ushakov (1955) and Fauvel (1927). A wealth of information on *Chone* Krøyer and *Euchone* Malmgren is found in Banse (1970, 1972).

For simplicity, in Chapter 1, the traditional usage of species is retained. A further discussion of the species concept is given in Chapter 3.

1.2 Basic sabellid morphology

1.2.1 Basic body plan

Members of the polychaete family Sabellidae are most easily recognised by the presence of a radiolar crown at the anterior end, comprising a number of plume-like filaments, adorned with bilateral 'fringes', the pinnules. The radiolar crown is not unique to the Sabellidae, but, unlike the related family Serpulidae, sabellids (with one exception) occupy mud or mucous tubes rather than the calcareous tubes characteristic of the latter group. The radioles arise from two semi-circular lobes, which may or may not be joined. In life, the radioles, when extended, resemble a fan, hence the common term of 'fan-worm'. Perhaps more expressively, the term 'feather-duster' also has been used to describe these anterior appendages (Hartman 1951).

The family Sabellidae comprises two sub-families; the Fabriciinae and the Sabellinae (see Chapters 3.2. and 3.5). The Fabriciinae most commonly occur in the intertidal zone or in shallow water and, in general, the body is only a few millimetres in length and there are only few pairs of radioles. Within the Sabellinae, there is a wide range of body size and numbers of radioles, from small taxa bearing a superficial resemblance to the Fabriciinae to relatively large animals of ten or more centimetres in length, bearing many pairs of radioles. Figure 1.2.1 shows the basic features common to the Sabellidae as a family. The main characters are described in more detail below, with a brief overview of the variations found therein.

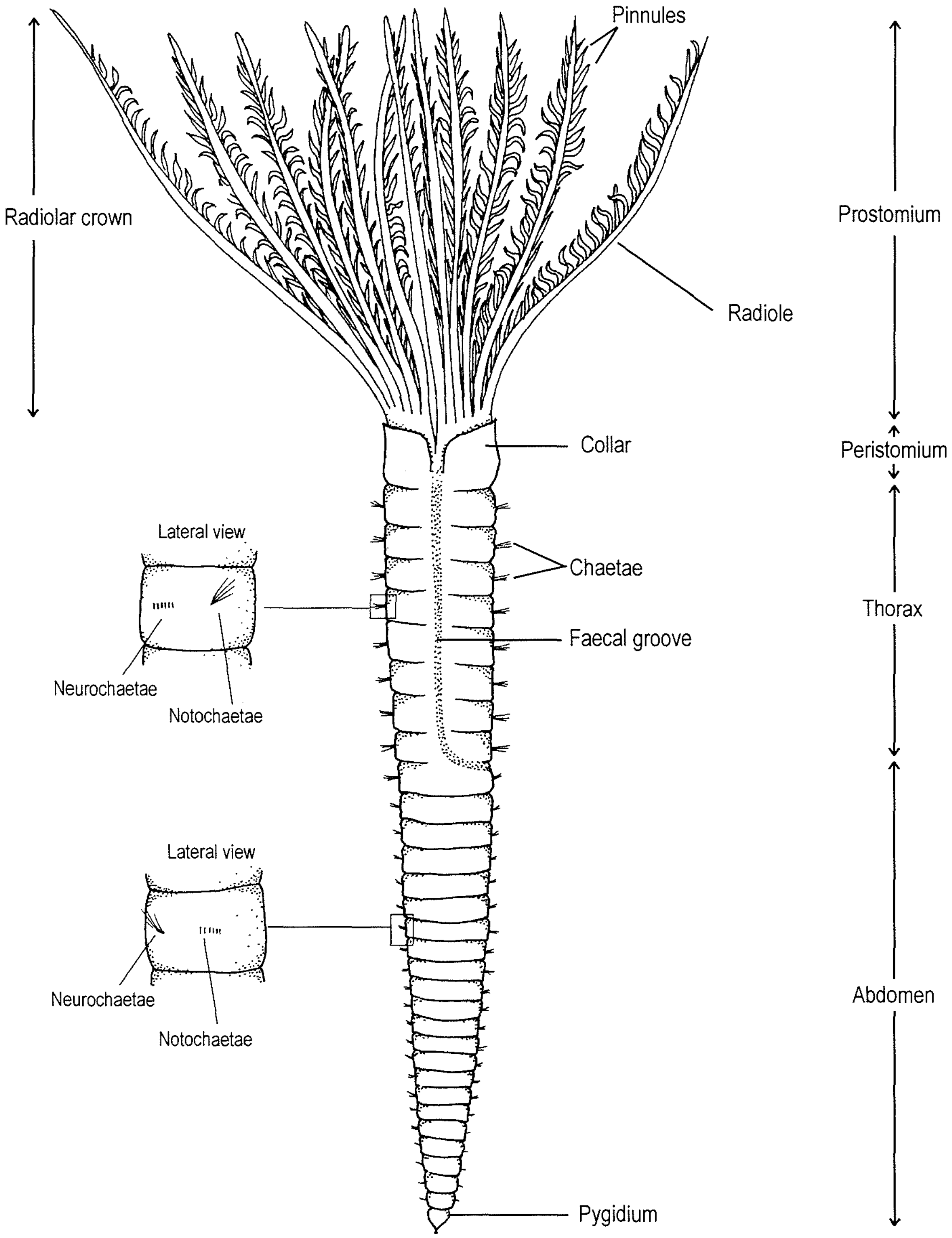

Figure 1.2.1. Generalised body plan of a hypothetical sabellid polychaete, in dorsal view. Note that in this example, the collar segment (peristomium) is completely separate from the first thoracic chaetiger. In some sabellids, the two segments are partially or completely fused, such that the first tuft of chaetae appears to arise from the base of the collar.

The radiolar crown in sabellid polychaetes is derived from the prostomium, whereas the collar is of peristomial origin (see also Section 1.2.3). The thorax usually, but not always, comprises eight segments which are equipped with lateral tufts of bristles, known as chaetae. As in many other polychaetes, there are two discrete tufts of chaetae on each segment, the dorsal-most being the notochaetae and the ventral-most the neurochaetae.

In some sabellids, the first chaetigerous segment, hereafter referred to as chaetiger 1, is distinct from the peristomial segment, from which the collar, where present, is derived. In this case, there is a distinct inter-segmental groove between the peristomium and chaetiger 1 (see Figures 1.2.1. and 1.2.6a). In other cases, chaetiger 1 apparently is fused with the peristomium and is not preceded by an inter-segmental groove (see Figure 1.2.7a). Most common in soft-bottom sabellins is an intermediate stage, where the inter-segmental furrow between the peristomium and chaetiger 1 is present dorsally, but is incomplete ventrally (see Figure 1.2.8b). This state is referred to as partial fusion of chaetiger 1 with the peristomium.

In sabellids, the number of thoracic segments generally is constant throughout the life of the individuals, although some ontogenetic variations have been described in the literature. In the Fabriciinae, the number of abdominal segments also appears to be constant. In most of the Sabellinae, the number of abdominal segments increases as the animal grows, by the addition of segments immediately anterior to the pygidium. However, in a few sabellin taxa, notably *Euchone* Malmgren, *Amphicorina* Quatrefages and some taxa currently assigned to *Jasmineira* Langerhans, the number of abdominal segments remains constant; the animal appears to grow simply by increasing the length and width of the extant segments.

The abdomen may comprise as few as three segments, such as in the Fabriciinae, or more than 50 segments as in some Sabellinae. All abdominal segments also bear noto- and neurochaetae, except the final segment, the pygidium.

1.2.2 Radiolar crown

The radiolar crown in the Sabellidae is derived from the prostomium. The crown arises from a pair of semicircular branchial lobes, which are fused dorsally in the Sabellinae, but not in the Fabriciinae. Each lobe may bear from three pairs of radioles, as is common in the Fabriciinae and a few sabellin taxa, to over twenty pairs, as in many sabellins of a large body size.

Each radiole bears several to many pinnules (see Figures 1.2.1 and 1.2.3). The pinnules may be arranged in pairs along the length of the radiole, as is the case in most of the Sabellinae, or these may alternate along its length as is the case in the Fabriciinae and some Sabellinae. Pinnules may be approximately the same length all along the radiole, or be of varying lengths. Most typical for the latter condition is for the mid-radiolar pinnules to be longest, such that when the crown is ‘collapsed’, most radiolar pinnules appear to terminate at the same height distally. These two forms of the radiolar crown are here termed ‘feather-like’ and ‘snowflake-like’ (Figure 1.2.2, see also Chapter 2.4 for a further discussion on radiolar forms). Although generalisations should be avoided, it is reasonable to adopt the ‘rule of thumb’ that all fabriciins and a few sabellin taxa have a ‘snowflake-like’ radiolar crown, whereas most sabellins display the ‘feather-like’ arrangement.

In the Sabellinae, each radiole has an internal cartilaginous skeleton, comprising at least two rows of cells, while the pinnules have a single row of skeletal cells. In the Fabriciinae, some taxa lack these structures while in others, the radioles have a single row of skeletal cells. At the base of the radioles, the cells are broader, and are fused together to form a skeletal base for the radioles.

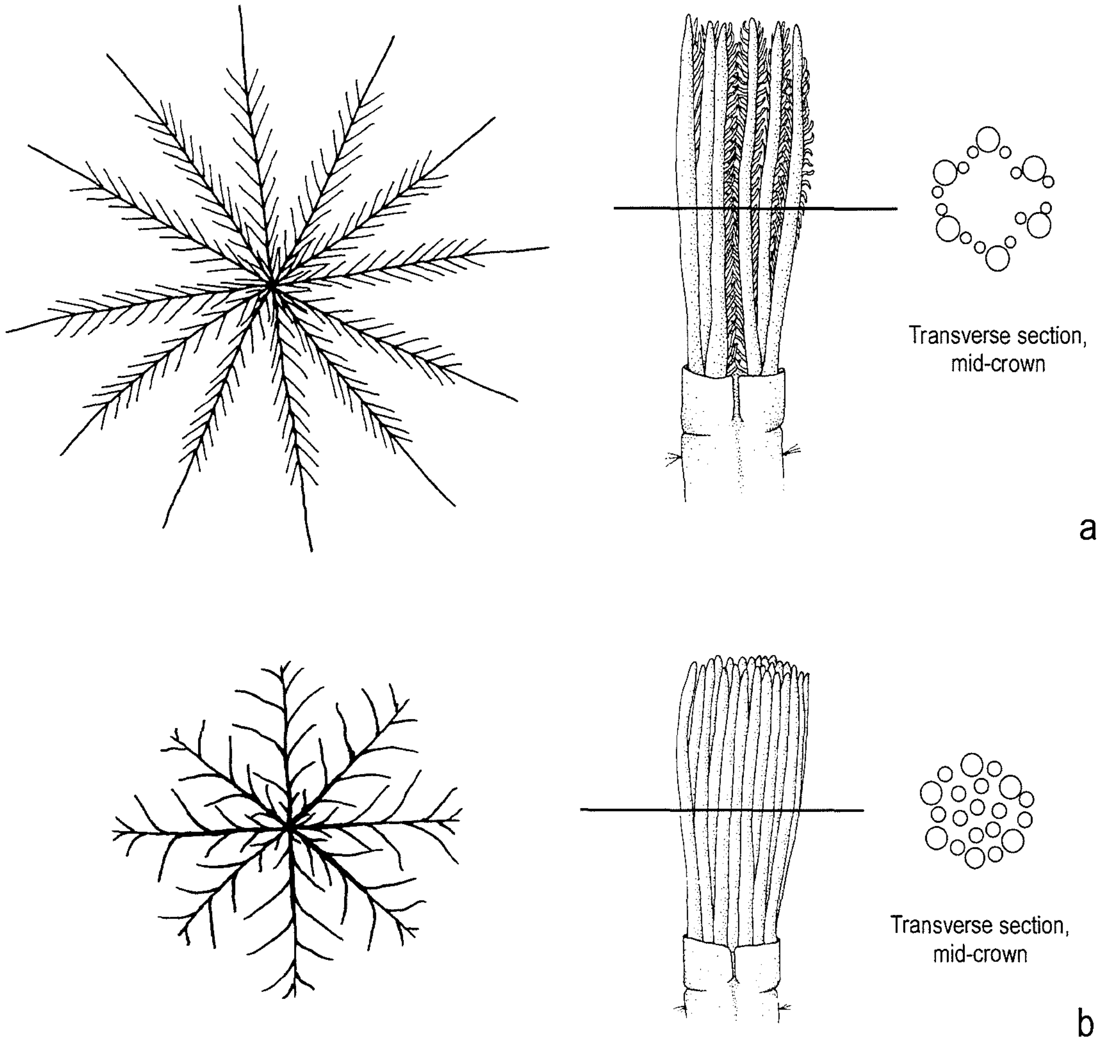

Figure 1.2.2 Schematic illustration of a) 'feather-like' and b) 'snowflake-like' radiolar crowns, in expanded (left) and collapsed (middle) attitudes, respectively. The approximate appearance of the two crown types in transverse section is shown to the right of the figure.

Ventrally in the radiolar crown, some sabellids have one or several pairs of appendages that lack pinnules (Figure 1.2.3). Throughout the literature, these have been referred to as ventral radiolar appendages, nude or bare filaments, ventral filamentous appendages, to name but a few. In the interests of brevity and clarity, the term 'ventral cirri', modified from the term 'buccal cirri' coined by Krøyer (1856) is used here to refer to these structures. The ventral cirri generally are equipped with a single row of skeletal cells. They appear to be involved in particle handling and have been observed to be used in tube building (see Chapter 4.4.2).

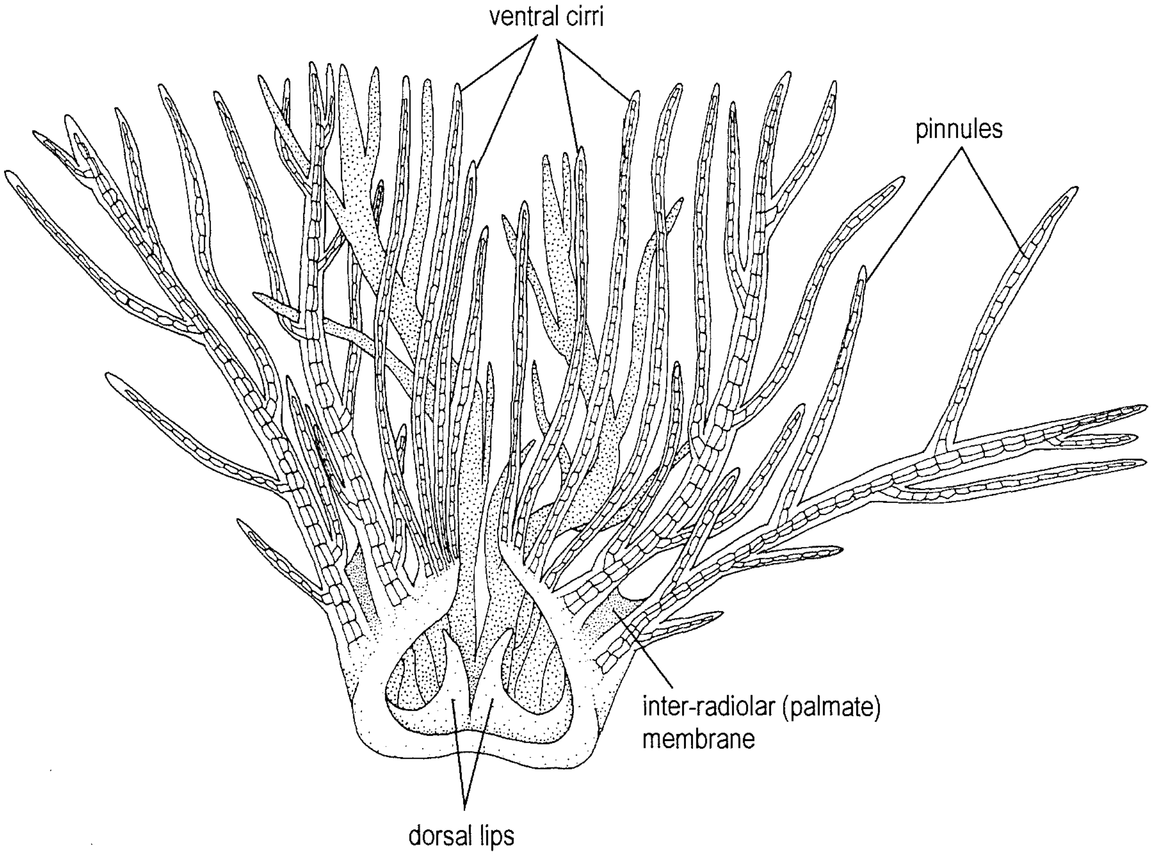

Figure 1.2.3. Radiolar crown (detached) of Euchone x *in ventral view (see Chapter 2.4), showing radioles with alternating pinnules and ventral cirri. Note the mid-dorsal fusion of the branchial lobes.*

Inside the radiolar crown are several lip-like structures, which also are thought to be used in particle handling (Nicol 1931; Lewis 1968). In sabellids which have ventral cirri, the dorsal, and sometimes also the ventral, lips generally are elongate and pointed. In sabellids which lack ventral cirri, one or both of the pairs of lips tend to be rounder and fleshier in form. Figure 1.2.4 illustrates three of the many forms of lip structure within the Sabellidae. The examples given are all members of the Sabellinae.

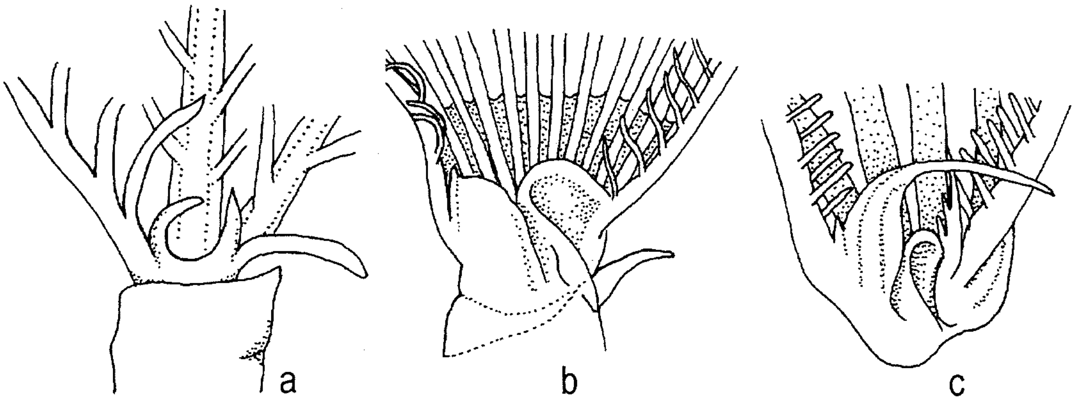

Figure 1.2.4. Schematic illustration of three different lip structures within the radiolar crown in a) Amphicorina paramobilis *(Rouse), modified after Rouse (1994), b)* Potamilla neglecta *(Sars), after Knight-Jones (1983) and c)* Demonax langerhansi *Knight-Jones, after Knight-Jones (1983).*

In *Amphicorina paramobilis* (Rouse), which possesses ventral cirri, both the dorsal and ventral lips are elongate and pointed. *Potamilla* (Sars) lacks ventral cirri, and the dorsal and ventral lips are low, rounded and relatively thick. In *Demonax langerhansi* Knight-Jones, which also is without ventral cirri, the ventral lips are rounded and cupped, as in the previous example, but the dorsal lips are of a different shape. Knight-Jones (1983) indicated the "tapered dorsal lip on the left". However, in a later review of lip structures, Fitzhugh (1989) considered only the swelling on the ventral side to be the dorsal lip proper; the elongate structure was referred to as the "dorsal radiolar appendage". The small filament on the upper dorsal surface of the dorsal lip was referred to as the "dorsal pinnular appendage".

A certain ambiguity still surrounds the terminology of the dorsal and ventral lip structures, particularly in the smaller sabellids in which those structures until recently have not been given detailed attention in the literature. Because the radioles and pinnules contain skeletal cells, correct usage of the terminology would demand that a dorsal radiolar appendage should be equipped with internal skeletal elements. If these are lacking, an elongate continuation of a dorsal lip may very well merely be a long dorsal lip. However, Rouse & Gambi (1997) used the term "dorsal radiolar appendage" to refer to a structure which lacked an internal skeleton, which, in a strict sense, may have been an incorrect usage of the terminology (Rouse, *pers. com.*). In any case, it is clear that the morphology of dorsal and ventral lips and their associated structures requires further attention. For the present purposes, it is sufficient to note that the lips may be elongate or cup-shaped and that a variety of accessory structures may or may not be present, with or without skeletal elements.

1.2.3 Collar

In many sabellids, the base of the radiolar crown is enclosed within a thin, often membrane-like collar. It is important for further taxonomic and systematic study to understand the origin of this structure. Although in some cases the form of the collar appears similar between certain fabriciin and sabellin taxa, the feature is not homologous. In other words, sabellin and fabriciin collars are derived from different parts of the body and therefore do not share the same evolutionary history. The fundamental difference in collar origin between the Fabriciinae and the Sabellinae is illustrated schematically in Figure 1.2.5.

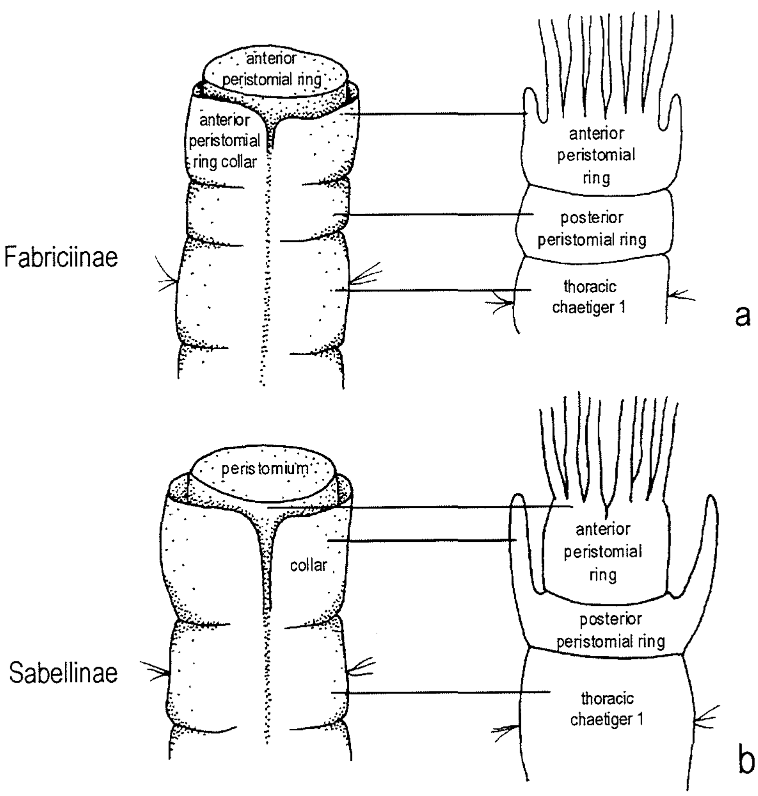

Figure 1.2.5.

Schematic illustration of the different peristomial origins of the sabellid collar. Note that on the left hand side of the figure, the peristomium is depicted as if the radioles were severed below their bases.

In the Fabriciinae, the peristomium in general is clearly divided into two rings, termed the anterior peristomial ring (APR) and posterior peristomial ring (PPR), respectively. The collar, or more correctly termed anterior peristomial ring collar, when present, arises from the anterior ring of the peristomium, such that the PPR is usually visible. Conversely, in the Sabellinae, the collar is modified from the posterior part of the peristomium and extends distally, thereby partially or wholly covering the anterior part of the peristomium, the APR. Because the ridge, or annulation, dividing the two rings of the peristomium is not generally visible, except in some cases as a slight constriction, the term here is omitted from descriptions of Sabellinae.

In the Fabriciinae, where the collar arises from the APR, the structure may be well developed all round (as in Figure 1.2.5, upper part), or be reduced to a ventral fleshy lobe, or may even be absent. Figure 1.2.6 illustrates three different collar states in the Fabriciinae.

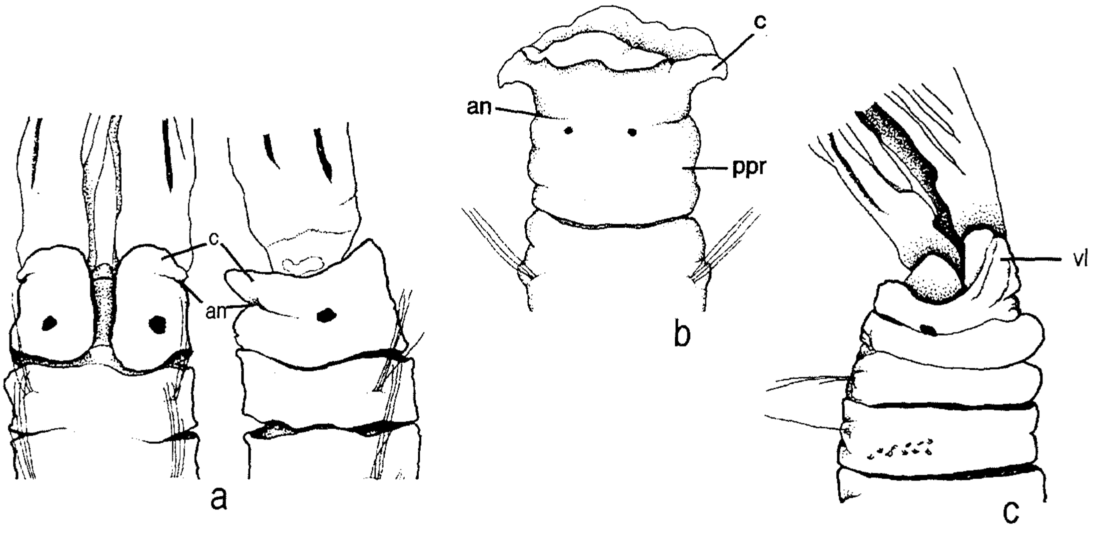

Figure 1.2.6. Various conditions of the fabriciin collar, modified from the anterior peristomial ring. a) Fabriciola mediaseta *Fitzhugh, well-developed all round, with dorsal gap, from Fitzhugh (1990a), b)* Pseudofabricia analis *Fitzhugh, dorsally intact, from Fitzhugh* et al. *(1994) and c)* Novafabricia triangularis *Fitzhugh, reduced to triangular ventral lobe, from Fitzhugh (1990b).*

There also is considerable variation in collar states within the Sabellinae (see Figure 1.2.7). In *Myxicola* Koch *in* Renier, the PPR collar is absent, but most sabellins have a collar that is well-developed all round. In *Chone* Krøyer and related taxa, the left and right parts of the collar often meet mid-dorsally (see Section 1.3.3 for further details). In large sabellins, such as *Sabella* L., there may be a very wide gap in the dorsal part of the collar, a condition curiously enough found also in the small-bodied *Amphicorina. Laonome* Malmgren is one of the few taxa where the collar appears to be intact dorsally, bearing only a low notch. Ventrally, the collar may be intact, as in *Chone duneri* Malmgren, incised, such as in most *Euchone*, or expanded to form overlapping lobes, such as in *Potamilla neglecta* (Sars).

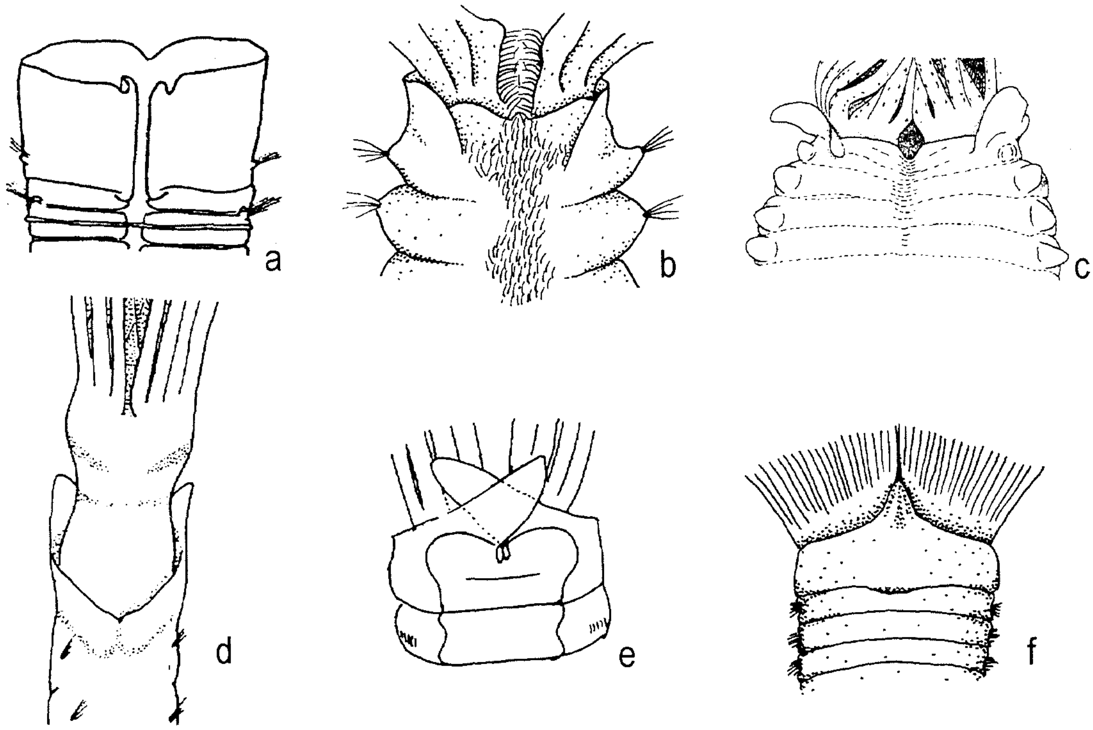

Figure 1.2.7. Some variations in the form of the sabellin collar, modified from the posterior part of the peristomium a) well developed dorsally and ventrally in Chone gracilis *Moore (from Banse 1972); b) with wide dorsal gap in* Amphicorina paramobilis *(Rouse) (stylised from SEM image in Rouse 1994, notochaetae added) and c)* Demonax micropthalmus *(Verrill) (from Perkins 1984); d) apparently intact dorsally in* Potamethus singularis *Hartman (from Knight-Jones* et al. *1991); e) expanded ventrally to form two overlapping lobes in* Potamilla neglecta *(Sars) (from Knight-Jones 1983) and f) absent in* Myxicola infundibulum *Renier (after Rioja 1923). Note that the triangular ventral lobe is of anterior peristomial origin.*

In certain sabellins, such as *Myxicola* Koch (Figure 1.2.7f) and many taxa within *Amphicorina, Jasmineira, Chone* and *Euchone*, the ventral part of the anterior peristomium (or APR) is modified to form a triangular lobe, often known as a ventral peristomial extension or ventral triangular lobe. This lobe may be divided into several smaller lobes distally, often giving the appearance of a bilobed structure at the ventral base of the radioles. In some instances, this may be referred to as "paired ventral extensions" or "crown supports". In any case, the feature is homologous with the anterior peristomial ring collar of the Fabriciinae (Figure 1.2.8).

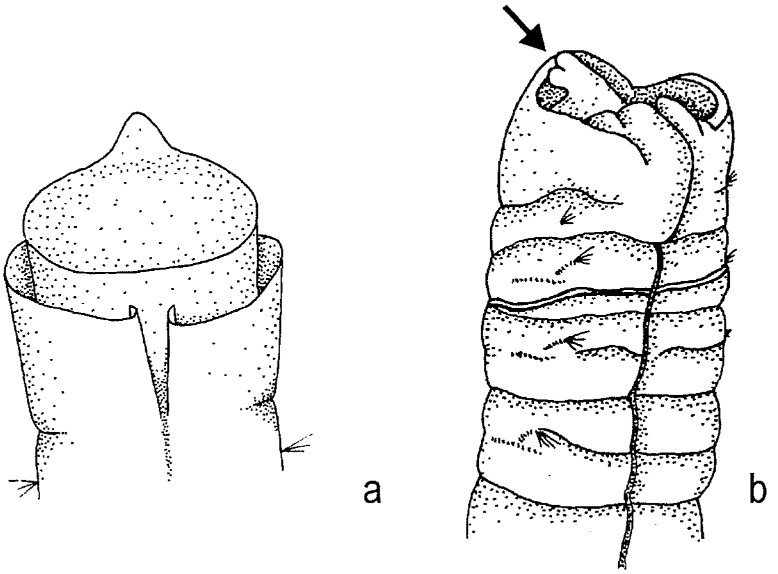

Figure 1.2.8. Modification of the anterior peristomial ring in some Sabellinae to form a ventral peristomial extension, homologous with the anterior peristomial ring collar in the Fabriciinae: a) schematic drawing showing the anterior and posterior parts of the peristomium (depicted as if radioles were severed below their bases and the anterior collar margin trimmed) and b) anterior of Chone *c.f.* paucibranchiata *(Krøyer) (study specimen from Pechora Sea, Akvaplan-niva collection) showing a bilobed ventral 'peristomial extension'.*

Further details on the homology of the ventral peristomial extensions in the Sabellinae and the posterior peristomial ring collar is given in Fitzhugh (1989, his Figure 17a).

1.2.4 Chaetal inversion

A peculiarity of the Sabellidae, although not unique to them, is the dorso-ventral inversion of the relative positions of the chaetae within the noto- and neurochaetae immediately posterior to (usually) the eighth chaetigerous thoracic segment (see Figure 1.2.1).

The evolutionary and adaptive significance of chaetal inversion has been the subject of much discussion. In spirorbid polychaetes for example, chaetal inversion would appear to be a feature well suited to life within a coiled calcareous tube (Knight-Jones & Fordy 1979), allowing efficient removal of faecal material. Spirorbids and serpulids, the latter being another sabellid-like group which inhabits a non-coiled calcareous tube, generally are considered in the older literature to be more highly evolved than the Sabellidae (e.g. Berrill 1977b; Uchida 1978). However, Knight-Jones (1981) proposed that the spirorbids are an ‘archaic’ taxa and further reasoned that sabellids have a coiled evolutionary history. Assuming that chaetal inversion is “adaptive for a coiled existence” (Knight-Jones 1981) opens the possibility for a range of hypotheses on the origin and possible function of chaetal inversion in the Sabellidae. However, the present thesis uses parsimony to reveal phylogenetic relationships between taxa and, as such, intuitive exploration in the absence of phylogenetic hypotheses is avoided. A recent phylogenetic study of the Polychaeta as a whole shows the Sabellidae and Serpulidae (including spirorbids) as sister taxa (Rouse & Fauchald 1997), such that the precise relationship between the taxa remains unresolved at this point. In the absence of a conclusive study on the relationships between taxa with chaetal inversion and their ancestors and descendants, further discussion on the origins of chaetal inversion is avoided.

1.2.5 Chaetae

Objectives

The initial aim of this section was to present an overview of chaetal types within the family Sabellidae in general. However, there has been, and continues to be, a certain amount of controversy and ambiguity in the literature concerning chaetal structure, particularly that of the elongate bristles. This makes such an overview an extensive and rather ambitious task.

The confusion is in part due to the often subjective nature of light microscope observations, where the apparent shape of the chaetae is greatly influenced by the orientation of the preparation. In the newer literature, increasing attention is given to chaetal morphology and electron microscopy is widely used to clarify details. However, it is not always easy to compare these descriptions with others that use only light microscopy. In some instances, re-examination of previously described specimens may result in a completely different interpretation of the chaetal types present. Many taxon descriptions, particularly in the older literature, present only a single view of a single chaeta, such that the extent of variation between chaetae cannot be assessed. In addition, it is a recognised phenomenon that the shape of the chaetae in some taxa may vary to a greater or lesser degree between anterior and posterior segments within both the thorax and abdomen. Despite this, many descriptions, even recent ones, do not specify from which segment the illustrated chaeta is taken.

Thus, presenting a superficial overview of chaetal types documented in the literature inevitably will either perpetuate existing ambiguity or omit areas requiring further attention. Therefore, the approach taken here is to highlight the difficulties encountered and to describe in brief the main types of sabellid chaetae of relevance to the taxa considered in more detail in the subsequent chapters.

A review of the main types of noto- and neurochaetae within the Sabellidae as a whole is given in Fitzhugh (1989). The information is not repeated here. Instead, the main general chaetal characteristics of the Sabellidae are noted below. An overview of the different types of chaetae found in *Chone*, *Euchone* and *Jasmineira* is given in Chapter 1.3.4. Further details on sabellid chaetae may be found in a variety of publications, including Knight-Jones & Perkins (1998), Giangrande (1992), Fitzhugh (1989), Kryvi (1989), Perkins (1984) and Knight-Jones (1981).

The terminology debate

Compounding the problems mentioned above are the discrepancies in chaetal terminology used between different publications. At present, there is no set of terminology that is accepted by all sabellid workers and, as a result, there are considerable discrepancies in the terminology used between authors in the literature. In particular, the terminology relating to thoracic notochaetae, and to some extent abdominal neurochaetae, is in urgent need of standardisation. The problem is recognised, and recent steps have been taken to standardise sabellid anatomical terminology via an electronic mail discussion group for workers on the Sabellida (in a broad sense, including taxa such as serpulids, spirorbids, sabellongids and sabellarians). However, resolution of the ambiguity is a complex task and is outwith the scope of the present work.

Fitzhugh (1989) addressed the problem of variation along a morphological continuum for uncini, by dividing the structures into a series of recognisable zones, and describing each of these individually, rather than using discrete terms. However, he did not extend this approach to the elongate chaetae. Instead, he assigned a specific term to each of the main types of elongate chaetae found in the Sabellidae. However, Fitzhugh (1989: p.38) did acknowledge that some taxa possess chaetae which may "represent a continuum of several chaetal[1] types" rather than being discretely recognisable forms in themselves. Further than this, the difficulties in characterising chaetae that show subtle inter-variations in form are not generally recognised. This is largely because objective comparisons between sabellid taxa for the most part have been carried out at higher taxonomic levels such as genus or family. The operator is forced to make certain generalisations about the chaetal types

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[1] as 'setal'

found within the taxon and, as a result, the more subtle inter-specific variations are obscured.

Describing chaetae in terms of their constituent components may offer a solution to the problem of ambiguous terminology. However, this is clumsy and entails wordy descriptions of chaetae, whereas before a single term might have sufficed. For taxonomic publications this is of lesser importance, because the text is (or should be) accompanied by informative illustrations which serve as the reference points. However, a number of problems arise when chaetal types are coded objectively for cladistic analysis, involving issues of character independence and homology, which are discussed in more detail in Chapter 3.

At the present time, there is no clearly defined right or wrong approach to characterising and describing sabellid chaetae. One of the tasks of the present thesis is to devise an adequate means of characterisation of the chaetal types found in a few selected taxa. Extrapolation of this work and integration into a larger scheme encompassing the Sabellidae as a whole remains for future research. The approach taken here is to describe the basic structure and composition of chaetae in general, and to divide the structures into a series of recognisable descriptive regions or characters, using appropriate examples. Where there is ambiguity as to terminology, this is indicated in the text. For the uncini, the terminology and partitioning into descriptive regions follows Fitzhugh (1989). For the elongate chaetae, the general terminology follows that commonly used for polychaete chaetae, augmented by certain specific terms used by Knight-Jones & Perkins (1998). The partitioning into descriptive regions is presented here as a possible solution to the ambiguities described above, and it is expected to be subject to further discussion and eventual amendment in the subsequent literature. To ease comparative discussions, a preferred term is selected for the main chaetal types and subsequently is used in an informal sense. The use of these terms is continued in the ensuing cladistic analyses and a justification for this approach is given in Chapter 3.5.5.

General form and function

Polychaete chaetae may be referred to as being composed of "secretions from the parapodia forming the armature of these structures" (Fauchald 1977[2]). In the Sabellidae, as in many other polychaetes, the chaetae may take the form of long elongate bristles or stout hooks known as uncini. The uncini and elongate chaetae occupy discrete positions in the parapodia. As a result of chaetal inversion (see Figure 1.2.1 and Section 1.2.4), the relative position of the elongate chaetae and the uncini are reversed in the abdomen relative to the thorax. Thus, the thoracic notochaetae and abdominal neurochaetae comprise elongate chaetae, whereas the thoracic neurochaetae and abdominal notochaetae take the form of uncini. It should be noted that in some taxa there are other specialised chaetae interspersed with the uncini, known as companion chaetae. Because the main taxa with which the present thesis is concerned do not possess companion chaetae, these are not discussed further here.

The elongate bristles in the thorax are thought to be used in rotation of the worm within its tube, which is a necessary activity in most sabellids to spread secreted mucus evenly whilst forming the tube (Knight-Jones 1981). In some taxa, tube strengthening or repair also involves application of mucus and sediment particles around the tube opening (Nicol 1931, see also Chapter 4.4.1). In certain taxa with a reduced abdomen, the thoracic chaetae are largely responsible for horizontal locomotion (Clark 1964; Knight-Jones 1981). However, such worms, when placed on a soft sediment substratum, bury using their pygidium to probe the surface, such that it is the abdominal chaetae that pull the worm into a vertical position within the sediment (Lewis 1968). The elongate bristles often have slender, flexible tips, which would appear to give maximal purchase against the tube wall (Knight-Jones 1981).

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[2] as 'setae'

The uncini and other types of hooks in the Sabellidae are reputed to function as anchors, gripping the tube wall in such a way as to prevent the worm being pulled out by a predator and to counteract gravity such as to maintain a suitable position within the tube. This concept was presented as the 'anchor-function' hypothesis by Woodin & Merz (1987), where a correlation was found between tube type and uncinal orientation. It is tempting to develop such observations into intuitive hypotheses of selection and adaptation in polychaetes which possess uncini. However, Fitzhugh (1991b) warned against drawing broad conclusions based on morphological features, in isolation from a broader understanding of the phylogeny of the organisms in question.

In transverse section, the elongate sabellid chaetae, in common with those of most annelids, comprise a central core of fused chitinous rods surrounded by a region of irregular lacunar spaces (Perkins 1984). Exterior to this is an outer shell, or casing, which appears to be composed of loosely fused rods. Superficially, as seen in SEM, the ends of these rods may resemble an external armour of scales or plates, whereas in light microscopy, the rods appear as striations (see Figure 1.2.9).

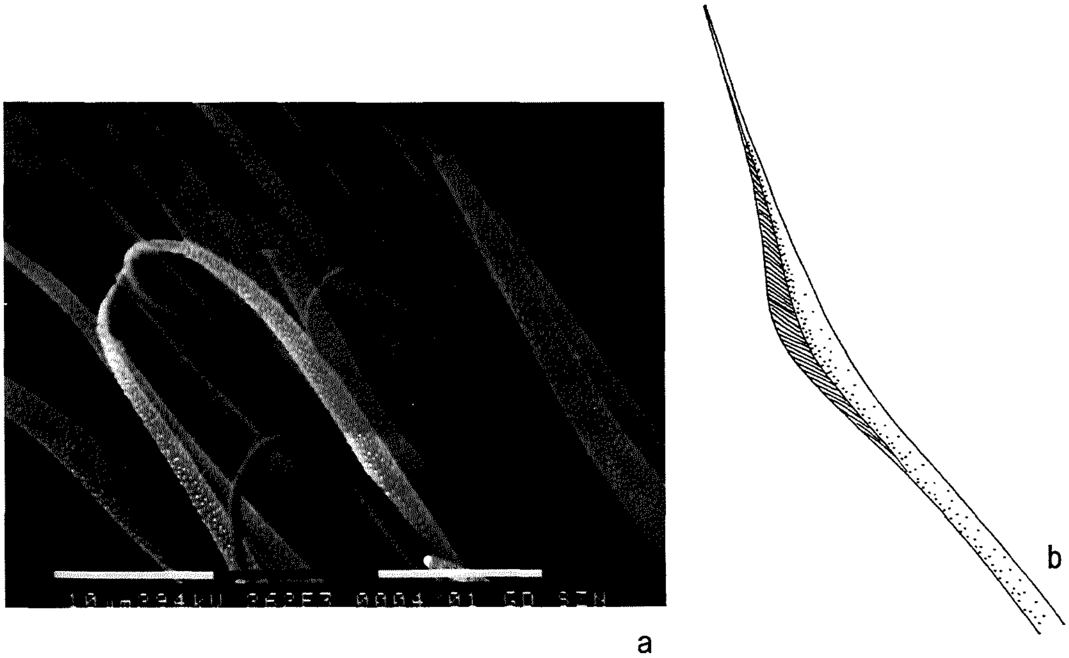

Figure 1.2.9 Elongate thoracic notochaetae a) distal portion seen in scanning electron microscopy and b) as seen in light microscopy. Image in a) from study specimen of Chone y *(see Chapter 2.5), Norwegian Sea (personal collection), drawing in b) from study specimen of* Jasmineira caudata *Langerhans from the North Sea (Akvaplan-niva collection).*

The sabellid chaetae specialised to form uncini also are composed of chitinous rods, which are evident as striations following the curvature of the uncini. However, the outer shell generally is smoother.

"Capillary" and "hooded" chaetae

The sub-distally swollen outer casing of certain types of the elongate sabellid chaetae has led to their being referred to as 'hooded' (e.g. Perkins 1984; Fitzhugh 1989), either narrowly or broadly. This terminology has been maintained throughout the last decade. However, Knight-Jones & Perkins (1998) avoid the use of 'hooded', because this term is considered more appropriate for the quite different hood of, for example, spionid chaetae (Knight-Jones *pers. com.*), where there is a toothed hook encased in a semi-transparent membrane referred to as the hood. Further diversity in chaetal hoods also is seen in many other polychaete groups, such as maldanids, capitellids and lumbrinerids. A detailed comparative structural investigation of hooded chaetae would be extremely useful in resolving such debates on terminology. However, for the present purposes, to avoid confusion and because the present work relies on the description of external chaetal morphology only, the term 'hood' is avoided here also. In the literature, the elongate chaetae typically found in sabellid notopodia are often referred to as long or short capillary chaetae, or simply 'capillaries'. This somewhat ambiguous term appears throughout many areas of invertebrate morphology and as a consequence also is avoided in the present work.

Elongate chaetae (thoracic notochaetae and abdominal neurochaetae)

The elongate thoracic notochaetae in the Sabellidae may be divided into four descriptive regions: the distal taper, the 'knee' area (*sensu* Knight-Jones & Perkins 1998), the proximal taper and the emergent part of the shaft (see Figure 1.2.10).

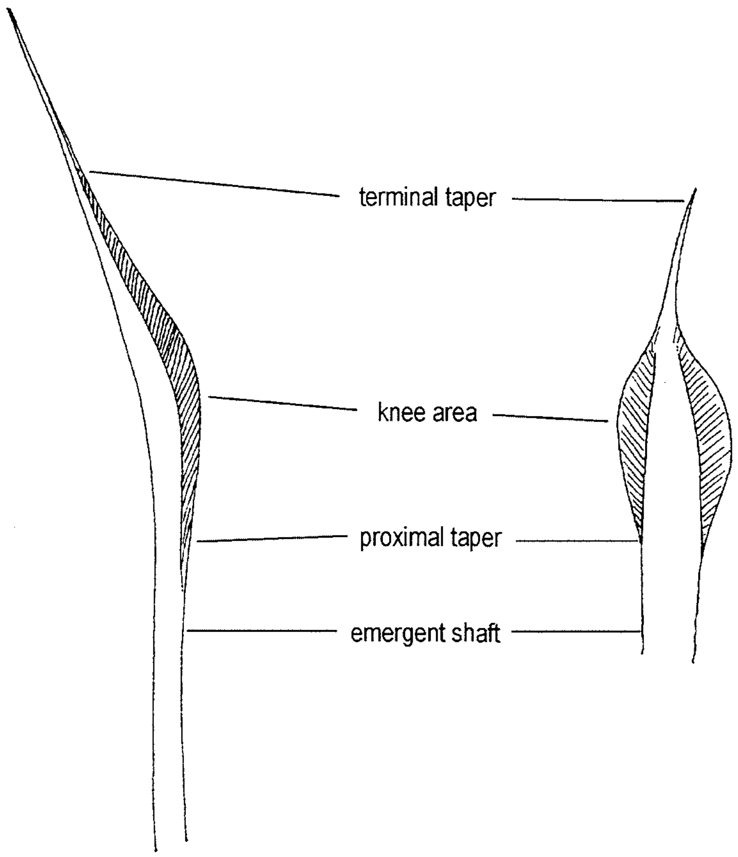

Figure 1.2.10. The main descriptive regions of sabellid elongate chaetae.

The distal taper may be long or short, smooth and gradual or abrupt, and geniculate (i.e. bent) or not. The ‘knee’ area may or may not be enlarged or ‘swollen’ to a greater or lesser extent and this swelling may be restricted to the ‘knee’ side of the chaeta or present also on its reverse side. The chaeta may or may not be geniculate at the base of the proximal taper and the emergent shaft may be short or long. In addition, attention is paid to the plane of flattening (where present) in relation to the direction of the geniculate bend of the chaeta.

There exists a variety of forms of elongate chaetae within the Sabellidae, the main types of which are illustrated in Figures 1.2.11 and 1.2.12. The terminology used by Fitzhugh (1989) is indicated in the figure captions. Until the terminology debate is resolved, these types of chaetae mainly will be referred to hereafter in terms of their component parts. Further details on the chaetal types found in *Chone, Euchone* and *Jasmineira* are given in Chapter 1.3.4.

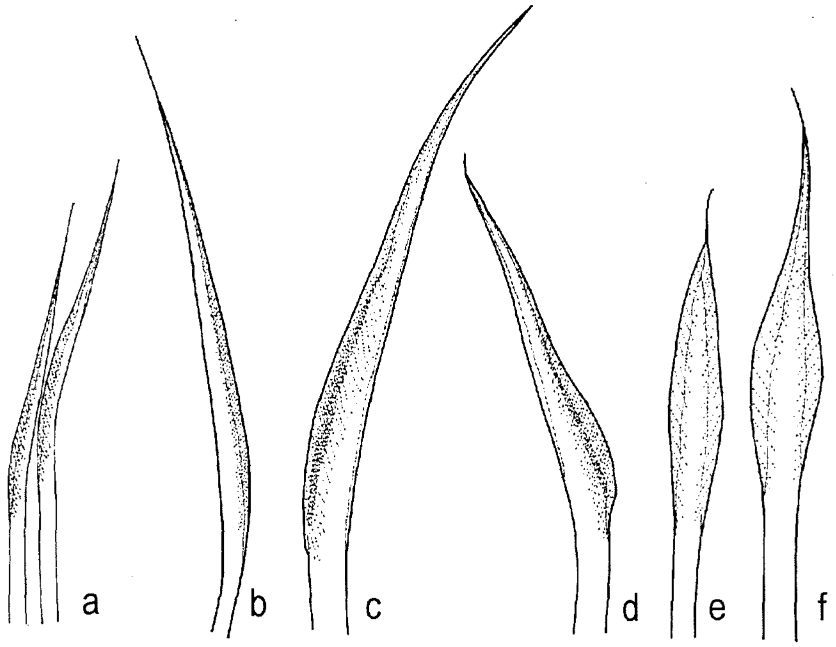

Figure 1.2.11. Some elongate chaetal types found in the Sabellidae, from Fitzhugh (1989). Terminologies used by the latter author are as follows: a) and b) "elongate narrowly hooded"; c) long "spine-like"; d) short "spine-like"; e) short "broadly hooded" and f) long "broadly hooded" chaetae.

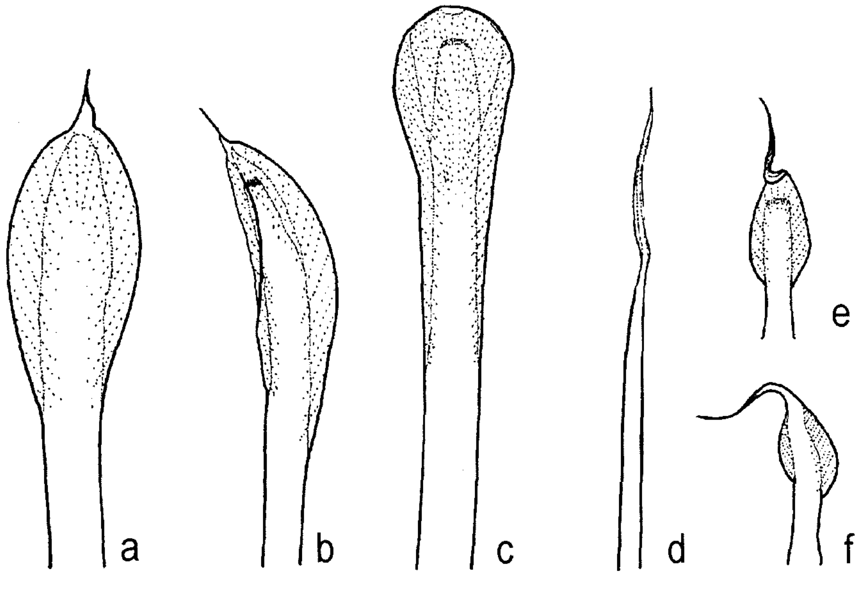

Figure 1.2.12. Some specialised forms of sabellid elongate chaetae, from Fitzhugh (1989): a) spatulate[3]; b) same, lateral view c) frontal view, note lack of pointed tip, or mucron; d) bayonet; e) "pseudospatulate" and f) same, oblique view.

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[3] as 'paleate' in Fitzhugh (1989)

The elongate chaetae are arranged either in short parallel rows, or in a spiral. In many sabellids there are two or more types of thoracic notochaetae contained within the same notopodial tuft. In this case, the different chaetal types most often occupy discrete positions within the notopodia.

In general, there is less variation within the abdominal neurochaetae, which usually are elongate geniculate chaetae. Although bearing a superficial resemblance to the elongate chaetae often present in the thorax, those in the abdomen tend to be considerably narrower. In some sabellids, the abdominal chaetae decrease in length towards the pygidium, whereas in others, the chaetae are long in posterior segments.

Uncini (thoracic neurochaetae and abdominal notochaetae)

Fitzhugh (1989) recognised sabellid uncini to comprise four main descriptive characters, using terminology consistent with that used in previous work (e.g. Knight-Jones 1981), these being the teeth, neck, breast and handle. The distal-most part of sabellid uncini comprises a series of teeth arranged in rasp-like rows. Usually, there is a single large main tooth, which subsequently will be referred to as the main fang. Above this lies the rasp-like arrangement of smaller teeth. In some taxa there are one or several medium sized teeth above the main fang and below the rows of smaller teeth. This condition often is referred to as the presence of teeth of unequal size above the main fang.

Proximal to the dentate region of the sabellid uncinus is the neck, which may vary in shape and form between taxa. Proximal to the neck there may be a rounded region of the uncinus, known as the breast. When present, the breast extends in the same direction as the main fang, to a greater or lesser degree, according to the taxon in question. In some taxa, the breast continues proximally (in the opposite direction to the main fang) to form the handle, which also shows considerable variation in size.

Figure 1.2.13 illustrates a range of uncini found in the thorax of various sabellid polychaetes, showing these features, where present.

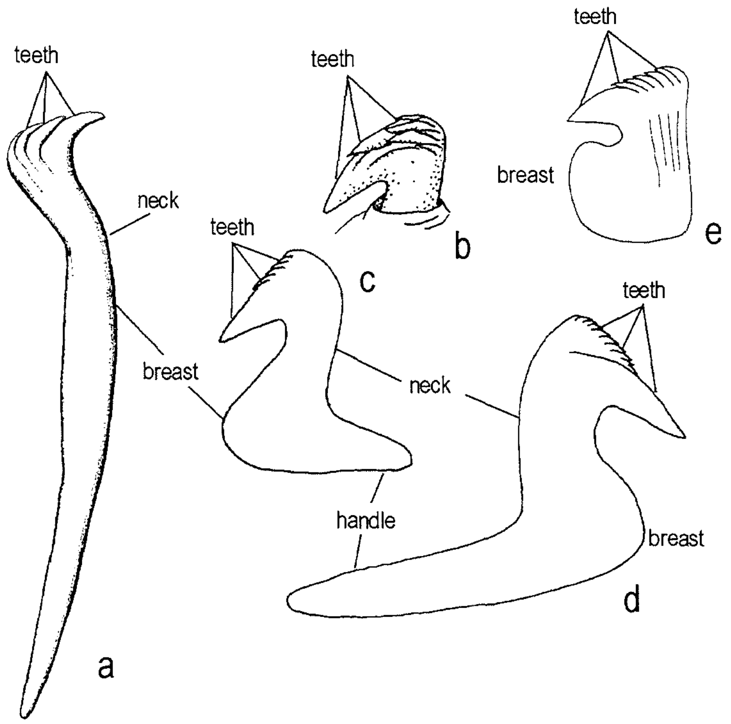

Figure 1.2.13.Examples of thoracic neurochaetae (uncini): a) Amphicorina alata[4] *(Ehlers), from Hartman (1953), with reduction of breast and absent handle, b)* Amphicorina paramobilis *(Rouse) drawn from SEM in Rouse (1994), with unequal sized teeth above main fang, c)* Sabella spallanzanii *(Gmelin), after Knight-Jones & Perkins (1998), d)* Megalomma bioculata *Ehlers, after Perkins (1984), with long handle and e)* Laonome kröyeri *Malmgren (from Banse 1963), lacking handle.*

The abdominal uncini (notochaetae) also take the form of multi-dentate uncini, although often quite different in form from those present in the thorax. In the Fabriciinae, the abdominal uncini take the form of rasp-like plates, often referred to as 'pectinate' uncini, where the teeth are approximately equal in size. In the Sabellinae, there usually is one main tooth, or fang, and a series of smaller teeth arranged in rows. Figure 1.2.14 shows several different forms of abdominal uncini in the Sabellidae.

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[4] some uncertainty as to the correct systematic status of that taxon; originally described within *Fabricia*

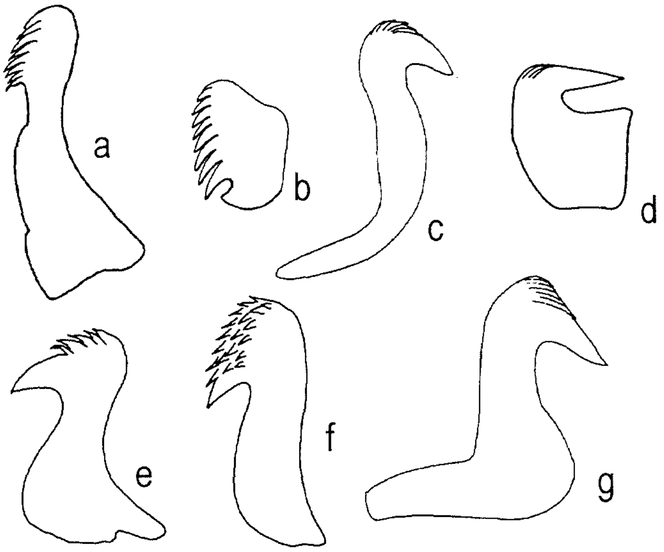

Figure 1.2.14. Examples of abdominal notochaetae (uncini); a) Fabricia stellaris stellaris *(Müller), from Fitzhugh (1990b), b)* Amphicorina *cf.* michaelsen *Banse, from Hartmann-Schröder & Hartmann (1981), c)* Jasmineira pacifica *Annenkova, from Banse (1979), d)* Chone infundibuliformis *Krøyer, from Banse (1972), e)* Jasmineira *cf.* oculata *Langerhans, study specimen from Norwegian Sea, f) same, oblique view and g)* Demonax micropthalmus *(Verrill), from Perkins (1984).*

In addition to the variation in appearance of uncini according to angle of view (see Figure 1.2.14e and f), the exact shape also may vary with position within the group of uncini, or torus. Therefore, slight deviations in the shape of uncini in preparations from those depicted in the literature may be expected.

Chaetae and systematics

Prior to the publication of Fitzhugh (1989), the main distinguishing criterion between the sub-families Fabriciinae (sometimes also referred to as the Fabricinae) and the Sabellinae was the form of the thoracic uncini. Sabellids possessing the stout, multi-dentate hooks, with a reduced breast and long, narrow, gently-curving handles, often referred to as 'acicular' in the literature (see Figure 1.2.13a and b), were assigned to the Fabriciinae. The Sabellinae comprised taxa with the so-called 'avicular', or 's' or 'z-shaped' uncini, which also have a multi-dentate proximal part, but a rounded breast and wider handles (depicted in Figure 1.2.13c and d).

The most recent revision of the Sabellidae is discussed in Chapter 2.3. Fitzhugh (1989) restricted the diagnosis of the Fabriciinae, and included several taxa with ‘acicular’ uncini within the Sabellidae. Thus, the form of the thoracic uncini no longer is of systematic value at the sub-family level. However, the ‘rasp-like plates’ or ‘pectinate’ abdominal uncini that are present in most, if not all, of the taxa within the revised Fabriciinae are not found in the Sabellinae. Thus, it is the abdominal, rather than the thoracic, uncini which now are of greatest systematic value at the sub-family level.

1.2.6 Eyespots and ocelli

Many sabellids are equipped with one or more pairs of ocelli, or eyes, ranging in form from complex lensed structures to simple patches of photoreceptive cells. These structures often fade in alcohol, making them difficult to observe in preserved material.

In adult sabellids, photoreceptive organs generally are located at the anterior or the posterior end of the worm (usually on the pygidium) or both. Interestingly, pygidial eyespots most often are present in small taxa which are known to be discretely motile, such as the Fabriciinae and some Sabellinae such as *Amphicorina* (see Figure 1.2.17a, b and Section 1.2.9). Because these organisms move pygidium-first, dragging their tubes behind them, the utility of eyespots located on the pygidium is unquestionable.

Anterior eyespots are commonly present on the anterior peristomial ring collar in the Fabriciinae (see Figure 1.2.6a, b), often in addition to pygidial eyes. In some large sabellins, which do not appear to be motile, various types of photoreceptive ocelli are located on the radioles, either as a single sub-distal compound eye on each radiole, or arranged in a longitudinal series on the outer part of the radioles. Some examples of radiolar eyes are depicted in Figure 1.2.15.

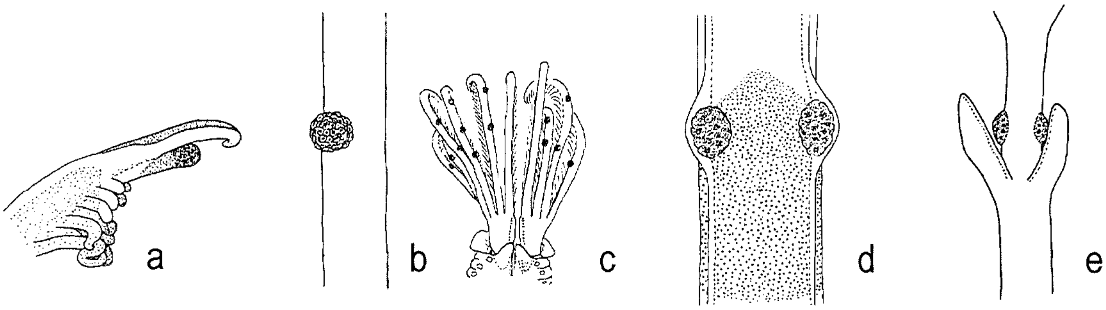

Figure 1.2.15. Radiolar eyes in the Sabellidae: a) subdistal compound eyes in Stylomma palmatum *(Quatrefages), b) and c) unpaired eyes in* Pseudopotamilla reniformis *(Bruguière), d) paired eyes within radiolar ridges in* Bispira mariae *Lo Bianco and e) paired, with associated stylodes in* Branchiomma *sp. Illustrations a) from Knight-Jones & Perkins (1998); b)-e) from Knight-Jones* et al. *(1991).*

1.2.7 Otocysts and spermathecae

Most sabellids are equipped with a pair of otocysts which provide orientational information and usually are located dorso-laterally in the peristomial segment (Figure 1.2.16). The otolith is lined with innervated fine hairs, which are stimulated by the gravitational action of the otolith. Polychaete otocysts are poorly studied, so it is not clear whether the otolith is self-secreted, or whether it comprises a purpose-gathered particle.

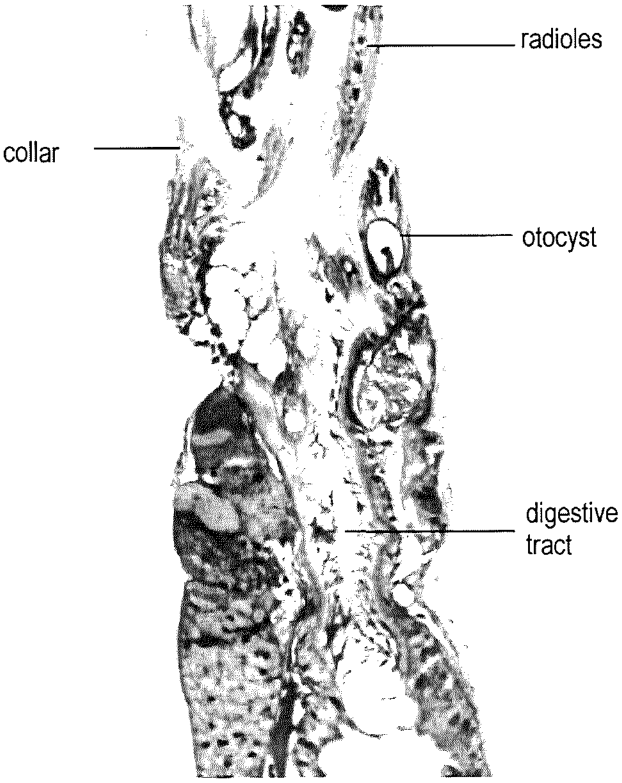

Figure 1.2.16.

Transverse lateral section of the anterior of Euchone x *(see Chapter 2.3), showing the otocyst. Histological preparation of study specimen from Norwegian Sea, Akvaplan-niva collection.*

Some sabellids have sperm storage organs, termed spermathecae, which are generally located in the anterior of the worm. There is considerable variation between taxa in the position and ultrastructure of spermathecae so far studied in the literature, a review of which is not appropriate here. In many taxa within the Fabriciinae, spermathecae have been observed in the radiolar crown (reviewed in Rouse 1996). Within *Amphicorina*, there is a diversity in the location of the spermathecae. *Amphicorina mobilis* (Rouse) and *A. bicoloris* (Rouse) have spermathecae associated with the radiolar crown and the peristomial collar, respectively, whereas in *A. brevicollaris* (Rouse), the spermathecae are part of the dorsal lips (Rouse 1992b).

Prior to the above studies of Rouse, little, if any, attention had been given to anatomical study of spermathecae in the Sabellidae. At present, a considerable amount of comparative information exists for the Fabriciinae, but knowledge is more limited for the Sabellinae. It is clear that further knowledge is required to address the question of why there is such variation in the spermathecal structure and its location amongst organisms that have a similar brooding strategy. This issue is discussed in more detail in Rouse (1996).

1.2.8 Glandular patches and 'shields'

Like many other polychaete groups, the epithelium in the Sabellidae is equipped with a variety of glandular cells. These may be evenly distributed around the circumference of each segment, or occur in clusters or rings. In some taxa, the main glandular areas are located in patches on the ventral surface of the worm, where they appear as elevated squarish areas of the epithelium, inspiring the term 'glandular shields'. These differentiated glandular patches may occupy the entire ventral surface of each segment, or be interrupted by a mid-segmental constriction. In some cases, such as in *Euchone papillosa* (Sars) and *Jasmineira candela* (Grube) (see Chapter 2.5), the glandular patches are prominent and roundish, and in the abdomen are bisected by the faecal groove to form one or two pairs of raised 'buttons' on those segments. In fact, these 'wart-like' glandular shields inspired the etymology of *Sabella tuberculosa* (Krøyer), which now is synonymous with *Euchone papillosa* (see Table 2.3.1).

Some sabellid workers, such as Banse (1970, 1972) relied heavily on the Hofsommer (1913) method of methyl green surface staining to reveal the distribution of glandular cells. This type of staining often reveals discrete glandular areas that are not raised relative to the rest of the epithelium. Therefore, is prudent to refer to glandular shields as being differentiated or not, rather than being present or absent, as is most common in the literature.

1.2.9 Pygidium and anus

The pygidium is the posterior-most part of the worm, and usually, although not always, takes the form of a fleshy, triangular lobe. In some taxa, such as *Chone filicaudata* Southern and *Jasmineira caudata* Langerhans, there may be a small terminal filament. In other taxa, such as *Sabella pavonina* Savigny, the pygidium may take the form of a pair of rounded anal papillae, or a scoop-like structure as in *Pseudofabriciola analis* Fitzhugh. Figure 1.2.17 shows some examples of pygidial form.

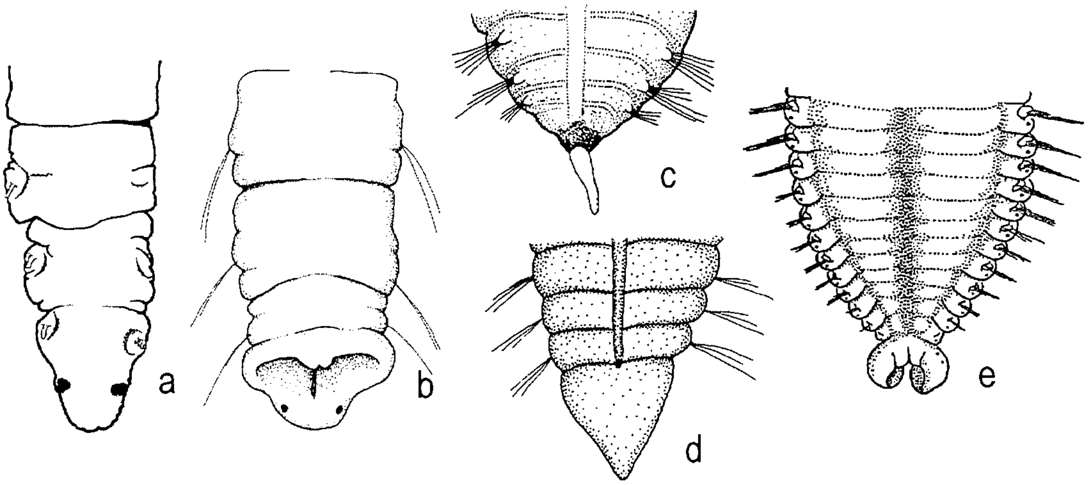

Figure 1.2.17. Examples of sabellid pygidia: a) Novafabricia tenuiseta *Fitzhugh, with eyespots, from Fitzhugh (1990c); b)* Pseudofabriciola analis *Fitzhugh, scoop-like, from Fitzhugh* et al. *(1994); c)* Chone filicaudata *Southern, with terminal filament, from Southern (1914); d) in* Chone *sp., without appendages, study specimen from Norwegian Sea, personal collection and e) in* Sabella pavonina *Savigny with anal papillae, from Nicol (1931).*

In the Sabellidae, the anus is ventral and, at least in the Sabellinae, usually is immediately anterior to the pygidium. However, many descriptions do not specifically address the anus, such that the feature is surrounded in some ambiguity. Preservation of material causes the anal opening to constrict, making it difficult to see in preserved specimens.

Fitzhugh *et al.* (1994) drew attention to the "anal depression" in *Pseudofabriciola analis* and commented that it is reminiscent of the anal depression in *Euchone*. However, it should be noted that the two structures, although bearing a superficial resemblance, are not directly equivalent. Whereas the depression in *P. analis* is formed by a modification of the pygidium, the depression in *Euchone* occurs immediately anterior to the pygidium (see Chapter 1.3.5), with the pygidium itself being unmodified.

1.2.10 Faecal groove

The faecal groove in sabellids can be very marked, almost resembling an elongate incision, or it may be a less obvious groove. In all cases, the feature is lined with cilia and serves to transport faecal pellets from the posterior ventral anus to the anterior of the worm, where they finally are expelled into the water column.

The faecal groove starts at the anus, and extends in a straight, mid-ventral line to the last abdominal segment. At this point, the groove twists at an angle of 90 degrees and continues laterally until it occupies a mid-dorsal position. At this point, another 90 degree twist occurs, and the faecal groove then extends mid-dorsally towards the anterior of the worm, terminating within the dorsal folds of the collar, where present.

1.2.11 Tube

In general, the tubes made by sabellid polychaetes are composed of sediment particles bound together in a mucus matrix. Within this, there may be much variation in the tube structure between the different groups of organisms. Even within taxa, the type of tube made may differ somewhat between areas, according to the type of ‘building material’ available to the individuals. In general, the tubes of sabellids inhabiting coarser substrata are thicker and harder than those which live partially or fully submerged within soft sediments. Unless otherwise stated, the following examples are taken from personal experience with material collected from soft-bottom sediments (see Chapter 1.5 for definition) in the northern north Sea, Norwegian sea and the Arctic seas.

Some taxa, such as *Euchone papillosa* and *Laonome kröyeri* Malmgren appear to be very selective in the size of particles used for tube building (*pers. ob.*). Generally, the tubes comprise firmly-bound fine silt-clay particles, of a very uniform particle size. Conversely, the tubes of certain *Jasmineira* (see Chapter 2.5) are easily recognisable by their rather loose construction and their irregular ‘lumpy’ appearance, due to the incorporation of a variety of particle sizes. In the latter case, it is not uncommon to find orbital foraminiferans and small shell fragments incorporated into the tube. Interestingly, in *Euchone x* (see Chapter 2.4), where the tube is constructed of silt-clay particles of uniform sizes (reminiscent of *E. papillosa* and *L. kröyeri*), it also is occasionally adorned with orbital foraminiferans at the anterior end. This is rarely seen in *L. kröyeri* tubes from the same sampling areas.

Myxicola infundibulum (Renier), which has a radiolar crown webbed for almost the entire length of the radioles, and rings of abdominal uncini which almost encircle the abdominal segments, constructs an unusual tube which is completely vertically submerged within the sediment. The tube is largely composed of mucus, with some adhering sediment particles, such that when removed from the sediment, the tube is ‘floppy’ and gelatinous in texture.

The tube of *Chone paucibranchiata* (Krøyer) also is rather unusual, being hard and almost parchment-like, composed of stiffened mucus, sometimes with a thin layer of sediment particles on the outside. The tubes of this taxon often are covered in a rusty-brown substance, rather like the dorsum of certain scale-worms within *Pholoe* Johnston. It is possible that this phenomenon is due to oxidation of ferrous substances in the sediment. The only known exception to the general rule of sediment-mucus tubes in the Sabellidae is *Calcisabella* Perkins, which constructs a cylindrical calcareous tube reminiscent of the Serpulidae (Perkins 1991).

Thus, as in other aspects relating to the Sabellidae, there is a good deal of variation in tube structure. Once familiar with the fauna in a particular area, the tubes of certain sabellids are readily distinguishable from those of other polychaetes. However, the discerning eye will spot slight variations in tube construction of the (presumed) same taxon between different sampling areas, usually due to slightly differing sediment compositions.

1.3 Morphological characteristics of *Chone*, *Euchone* and *Jasmineira*

1.3.1 Phylogeny and resemblances

Chone Krøyer, *Euchone* Malmgren and *Jasmineira* Langerhans form part of a group of closely-related taxa (Fitzhugh 1989). Together with *Desdemona* Banse, *Amphicorina* Quatrefages and *Panousea* Rullier & Amoureux, the taxa form an intermediate group between the Fabriciinae and the more derived, or highly evolved, sabellins such as *Sabella* L. The three taxa *Chone, Euchone* and *Jasmineira* were selected for further taxonomic study in the present thesis, due mainly to their abundance in soft sediments in deep waters off the Norwegian coast and, as such, a wealth of study material was available. The taxa also are among the least understood of the Sabellidae and amongst which there has been a good deal of confusion, both in the literature and consequently also in identification of reference and study material.

Chone and *Euchone* share a very similar external morphology, with the exception of minor variations in chaetal shape. In addition, in *Euchone*, the posterior abdominal segments prior to the pygidium are modified ventrally to form a depression, which usually is spoon-shaped (see Chapter 1.3.5). Although there is a considerable degree of morphological variation within *Jasmineira*, many taxa classified within this taxon bear a striking external resemblance to *Chone*. However, examination of the shape of the abdominal uncini usually removes such ambiguities.

1.3.2 Crown

Most, if not all, *Chone* taxa have 'feather-like' radiolar crowns. Within *Euchone*, there is a group of small taxa which have 'snowflake-like' crowns, whereas the remainder of the larger taxa show the 'feather-like' radiolar arrangement (see Chapter 3.5.). A similar situation is evident within taxa currently contained within *Jasmineira* (see Chapter 2.5). However, it is worth noting that the 'type species' of all three taxa have the 'feather-like' crown typical of the majority of Sabellinae.

1.3.3 Collar

Typically, taxa within *Chone, Euchone* and *Jasmineira* have a well-developed collar (derived from the posterior peristomial ring), as depicted in Figure 1.2.5a. In the subsequent discussions, this form of collar is referred to as '*Chone*-like'. The '*Chone*-like' collar (PPR) is attached dorsally to the peristomium (APR), and curled inwards, giving the appearance of a dorsal split (see Figure 1.3.1a). In the literature, the feature often is referred to as a 'dorsal incision'. However, this should not be confused with the 'ventral incision' or 'ventral notch' which is simply a notch or slit in the collar. To avoid confusion, the term 'dorsal gap' is here used to denote the mid-dorsal space (if any) between the left and right parts of the collar.

Interestingly, in taxa such as *Amphicorina*, the dorsal collar margins do not curl back and attach onto the peristomium (the anterior peristomial ring), leaving a wide dorsal gap (see Figures 1.2.7b and 1.3.1b). In larger sabellins such as *Sabella* and *Demonax* Kinberg, the dorsal collar margins also are unattached, and the dorsal gap often is very wide (see Figure 1.2.7c).

In life, the collar often projects above the level of the tube, and can be expanded, or 'flared'. Usually, specimens preserved in their tubes have flattened collars. The collar in flattened and expanded states is depicted in Figure 1.3.2. In many taxonomic descriptions of sabellids with well-developed collars, attention is given to the lateral notch. However, it is often the case that when the collar is flattened against the body, the excess becomes folded laterally. This fold can give the appearance of being a lateral notch (Figure 1.3.2b). It is recommended that caution be exercised in the description and interpretation of 'lateral notches'. In the present work, the feature is ignored as a descriptive character.

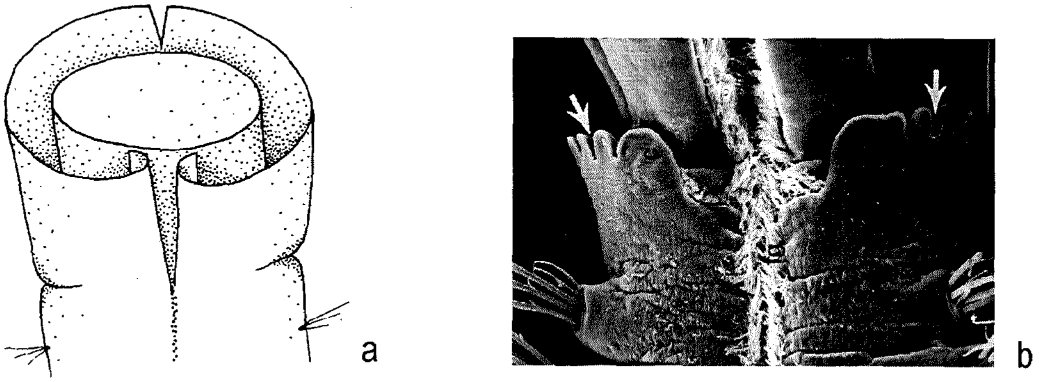

Figure 1.3.1. The dorsal gap; a) schematic illustration of a generalised Chone*-like collar, dorsal view from above, depicted as if the radioles were severed below their bases. Note the dorsal attachment of the collar margins to the peristomium and the ventral incision; b) scanning electron micrograph showing the collar in* Amphicorina annae *(Rouse) with free dorsal margins and a wide dorsal gap. Note also that in this taxon, the anterior collar margins are scalloped. Image from Rouse (1994).*

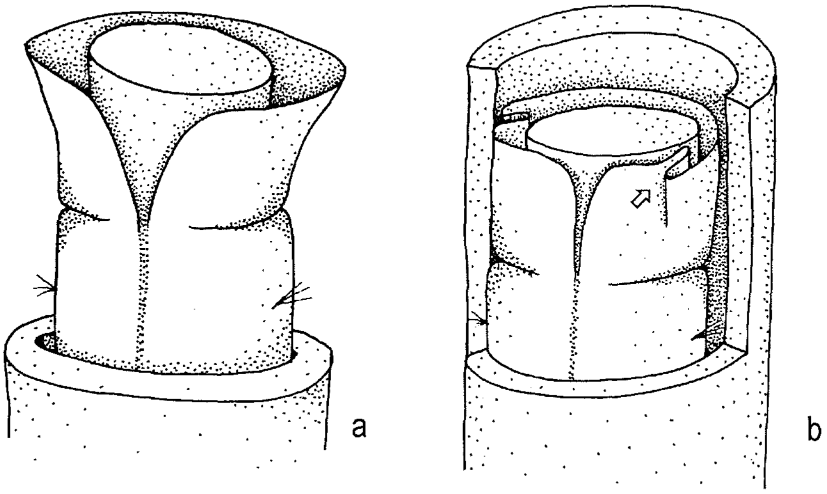

Figure 1.3.2. Dorso-lateral view of a generalised sabellid collar, in a) expanded and b) flattened states. The arrow in b) indicates the lateral fold caused by compression of the collar upon retraction of the worm into its tube. Note that the peristomium is depicted as if severed below the level of the radiolar bases.

1.3.4 Chaetae

In *Chone*, *Euchone* and *Jasmineira*, two or three different types of notochaetae are present within each notopodial tuft, each occupying a discrete position. Figure 1.3.3 shows the notopodium of the second thoracic chaetiger in *Jasmineira caudata* Langerhans and *Jasmineira oculata* Langerhans. The general arrangement applies to most *Chone*–like taxa, with some minor variations.

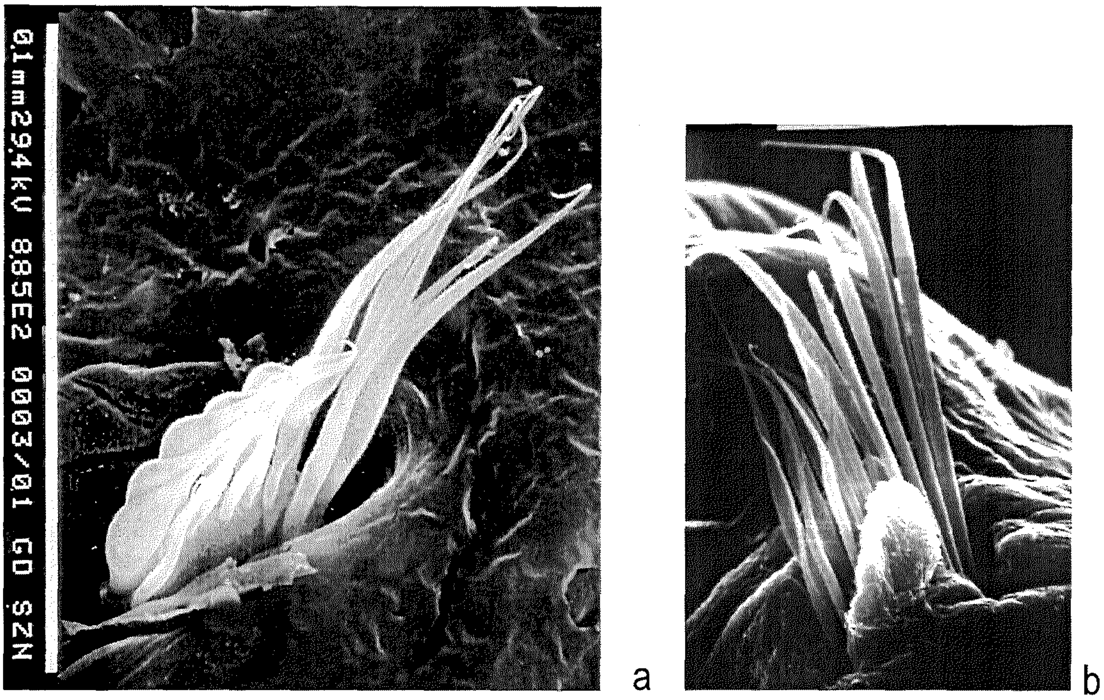

Figure 1.3.3. Relative positions of the different types of thoracic notochaetae - SEM images of the second thoracic notopodia in a) Jasmineira caudata *Langerhans and b)* Jasmineira oculata *Langerhans. The superior notochaetae are those in the upper right hand corner. Amongst the inferior rows of chaetae, the anterior row of bayonet chaetae is foremost, with the posterior row comprising spatulate-like chaetae in a) and short, broadly swollen chaetae in b). Both images of study material from the North Sea, Akvaplan-niva collection. Note the fleshy pre-chaetal lobe in b).*

The superior elongate geniculate chaetae occupy a dorsal position within the notopodium. There are two types of inferior chaetae, arranged in parallel rows, at an oblique angle to the superior notochaetae. Those of the anterior row take the form often referred to as bayonet chaetae in the literature. The posterior inferior notochaetae present in the three taxa in question may be broad, superficially resembling spatulate chaetae, as in Figure 1.3.3a, or one of the more slender forms such as in Figure 1.3.3b. Interestingly, most (but certainly not all) *Chone* have spatulate chaetae, whereas all known descriptions of *Euchone* document the presence of narrower chaetal forms, often referred to as "pseudo-spatulate" chaetae. Detailed examination of these chaetae has revealed that these generally are not "pseudo-spatulate" at all (as in Figure 1.2.11e and f), but tend more towards the type depicted in Figure 1.2.11d, and referred to by Fitzhugh (1989) as short "broadly hooded". These have a short emergent shaft, are slightly geniculate at the proximal taper, broadly swollen at the 'knee' region and have a distal taper of intermediate length. It should be noted that the plane of flattening is flush with the angle of the geniculate bend, rather than being perpendicular to it as in the true spatulate form.

The uncinal form depicted in 1.2.14d is typical for both *Chone* and *Euchone*. However, as in many other aspects of sabellid morphology, there is considerable variation both between the constituent taxa as well as within any given individual. It is not uncommon for the abdominal uncini to differ markedly in shape between anterior and posterior segments. Considering the development of the individual, this is perhaps not surprising. In individuals that grow by the addition of segments immediately posterior to the pygidium, the uncini in the anterior segments are ontogenetically older than those in the posterior segments. In certain *Euchone* taxa, Banse (1970) noted the presence of the quadrangular-shaped uncini that are typical for *Amphicorina* within the same torus as the more typical hook, and pointed out that the former occurred in the dorsal, ontogenetically first-formed, parts of the torus. Making the assumption that *Amphicorina* (as *Oriopsis* Caullery & Mesnil) is a more "primitive" taxon to *Euchone*, Banse (*op. cit.*) suggested that this supports the "ontogeny recapitulates phylogeny" hypothesis, first proposed by Hæckel. Further, in *Euchone* the uncini in the segments forming the anal depression (see below) often are markedly different from those in the pre-depression segments, having higher crowns of teeth above the rostra.

1.3.5 Anal depression

Characteristic of *Euchone* is the modification of the posterior segments immediately anterior to the pygidium to form a marked depression (Figure 1.3.4).

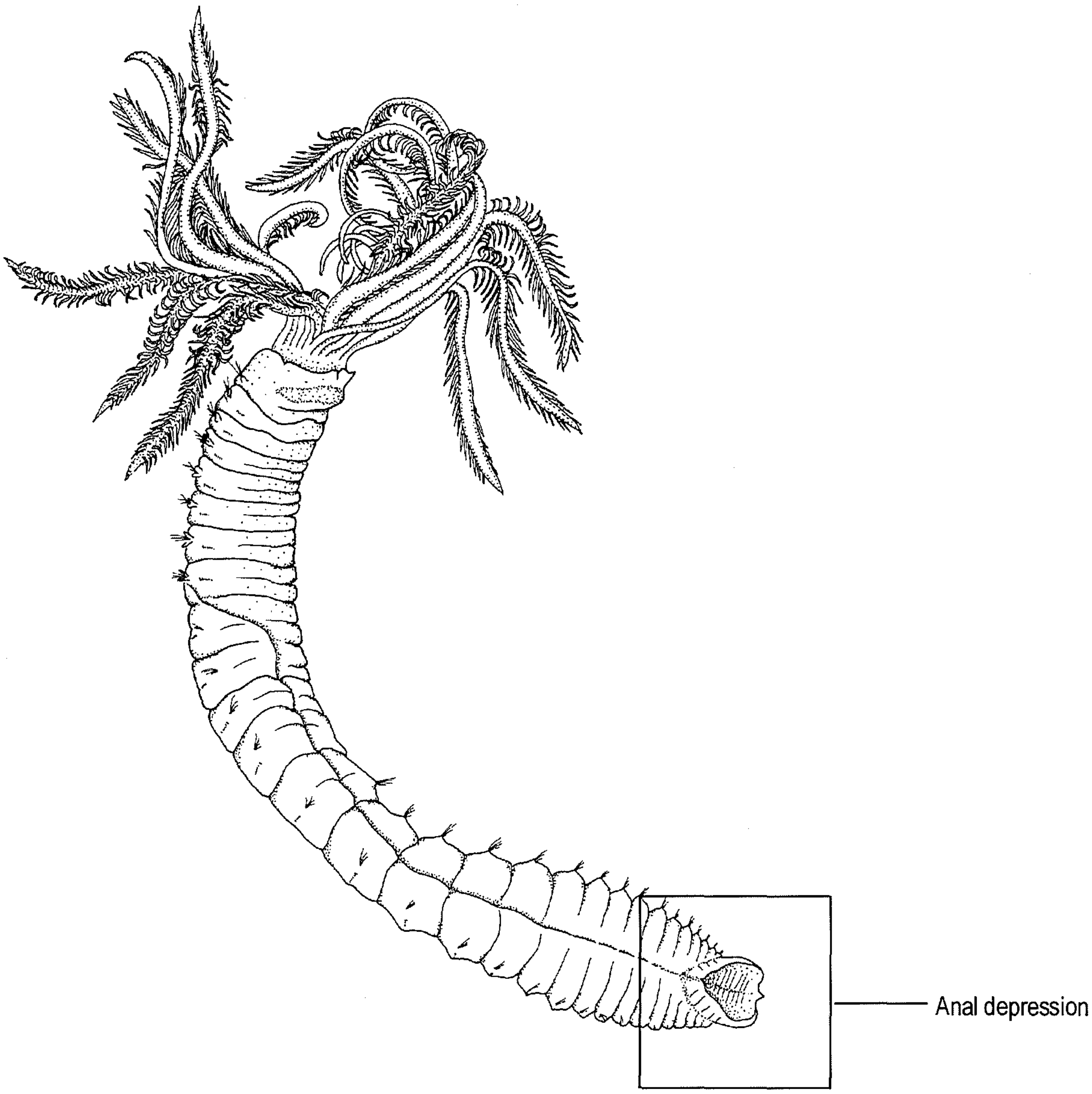

Figure 1.3.4. The anal depression in Euchone. *Study specimen of* Euchone *cf.* elegans *Verrill from the Barents Sea, Akvaplan-niva collection.*

In some taxa, the depression resembles a deep scoop and is bordered by lateral wings, which are formed by modification of the epithelium surrounding the depression. The anal depression can be so pronounced in some taxa that it sometimes is referred to as the 'anal funnel'. In some taxa, the depression comprises many segments, whereas in others, it comprises only three segments (see Figure 1.3.5b).

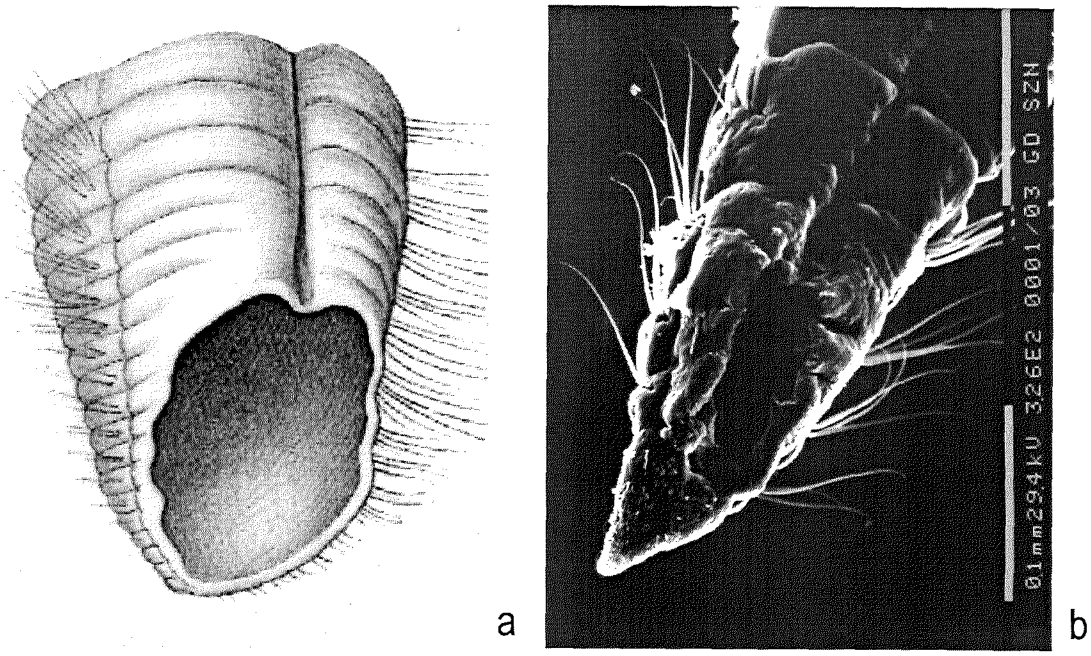

Figure 1.3.5. Two examples of the anal depression in Euchone*: a) comprising more than ten segments in* Euchone pallida *Ehlers, from Ehlers (1908) and d) comprising three segments only in* Euchone x, *from Chapter 2.4.*

Curiously, an intermediate type of anal depression is evident in *Euchone limnicola* Reish, in which the lateral wings are absent, remaining only as a ridge bordering an area of ventral flattening. (see Figure 1.3.6).

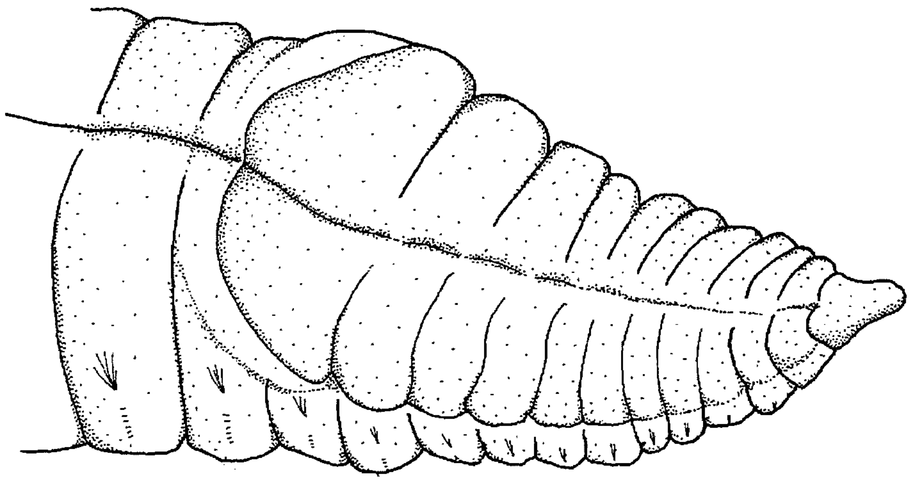

Figure 1.3.6. Atypical anal depression in Euchone limnicola *Reish, lacking lateral wings. Specimen from Australia, kindly donated by Matt McArthur.*

A further discussion of variations in the anal depression is given in Chapter 2.3.4.

1.4 Behaviour and the importance of scale

1.4.1 Feeding

In the general literature, sabellid polychaetes generally are referred to as being suspension feeders (Nicol 1930; Fauchald & Jumars 1979) . However, the partitioning of benthic animals into trophic guilds, or functional groups based on feeding modes is far from a simple task (Fauchald 1992). Spionid polychaetes that generally are described as deposit feeders (Day 1967) have been shown to switch to suspension feeding with increased water flow, coiling their long feeding palps into helices and capturing near-bottom suspended particles (Taghon *et al.* 1980).

Similarly, although all sabellids certainly can and do feed from suspended matter, it is clear that some sabellids also include surface deposit feeding in their behavioural repertoire. Small sabellids, such as the fabriciin *Fabricia* Blainville, have been observed undertaking both suspension and deposit feeding, depending on current flow (Lewis 1968) and, by analogy, it is plausible that other members of the sub-family Fabriciinae might behave in a similar manner. The sabellin *Euchone x*, which also is of a small body size and possesses a 'snowflake-like' radiolar crown, has been observed to utilise both deposit and suspension feeding strategies (see Chapter 4).

Selection of feeding strategy in benthic organisms not constrained to one particular feeding mode appears largely to be governed by physical factors, mainly the advection rate of suitable particles into the feeding area of the animals and the rate of sediment deposition or erosion (Strelzov & Gurevich 1978), which in turn influences microbial food availability (Miller *et al.* 1984). In addition, animal densities and competition also may play a major role in the feeding behaviour of polychaetes. For example, in certain spionid polychaetes, depressed growth and emigration were seen when animals were kept at in high densities while deposit-feeding, but not when the animals engaged in suspension feeding (Taghon 1992). A preference for particular particle sizes, which may in turn limit the distribution of taxa to certain sediment types or habitats, may be a function of the adhesive strength of the mucus on the feeding appendages (Jumars *et al.* 1982), although more active processes also may be involved.

It is important to retain a sense of scale when considering the feeding strategies of marine organisms (see Schmidt-Nielsen 1984). This is particularly important when considering sabellid polychaetes, members of which exhibit a wide range of adult body sizes (see Rouse & Fitzhugh 1994). In general, members of the Fabriciinae and some Sabellinae are between five and ten millimetres in total length (i.e. including the crown), whereas larger animals, such as those within *Sabella* L. or *Potamilla* Malmgren may be many centimetres in length (Nicol 1930; Knight-Jones & Perkins 1998). Even within a taxon such as *Euchone* Malmgren, there may be inter-taxon size differences of an order of magnitude. For example, the Antarctic taxon *Euchone pallida* Ehlers may attain a body length of seven centimetres or more (*pers. ob.*), whereas *Euchone x* is less than 1 cm in length (see Chapter 2.4).

It is shown that even very small-scale heterogeneities in bottom sediments significantly affect the behaviour of the inhabitant fauna (Watling 1989). Studies of *Fabricia* (Lewis 1968) and *Euchone x* (see Chapter 4) show that these often inhabit soft flocculent sediments, in which the tube is vertically buried, such that only a few millimetres project from the sediment surface. Feeding at the tube opening, the worm is active within the boundary layer at the sediment-water interface. On such a small scale, the high porosity of the flocculent upper sediment layers means that there is no clear distinction between the sediment and the overlying water. Within the boundary layer, depending on the rate of current flow, there usually is a great deal of re-suspension of newly-settled particles and, in conditions of near-zero flow, it is likely that the worms themselves may create an active re-suspension current. Thus, on a small scale, and in soft sediments, the distinction between suspension and deposit feeding may be purely hypothetical.

On the other hand, taxa such as *Euchone papillosa* (Sars), although also inhabiting soft sediments, are far larger in body size, up to five centimetres or more, and their tubes project up to 7 or 8 cm into the water column (*pers. ob.*). It is conceivable that these animals, on emerging from their tubes, encounter a water body well above the boundary layer of the sediment-water interface. Therefore, re-suspended material might be of lesser importance as a dietary component than to smaller sabellids.

Many large sabellids (over 5 cm in length) settle and build their tubes on hard substrata such as rocky outcrops (erosion areas) or mooring chains. For these animals, the only means of protection is the tube itself, which generally is thick-walled, solid and relatively inflexible (*pers. ob.*). Thus, not being able to bend the tube, food supply would appear physically to be limited to suspended particulate matter. A main reliance on suspension feeding certainly appears to be the case in both *Sabellastarte* (Fitzsimons 1965), *Sabella* (Nicol 1930) and *Eudistylia* (Merz 1984). The small-bodied *Chone paucibranchiata* (Krøyer), which generally is less than 5-10 mm in length, also is found in stiff, almost horny tubes, which are vertically orientated in soft sediment and relatively inflexible. Thus, it is unlikely that these organisms are capable of bending their tubes to any significant degree and suspension feeding appears to be the only viable option also in this case. However, due to the small size of the latter taxa, the exploitation of near-bottom re-suspended particles cannot be excluded.

Some generalisations in hypotheses of sabellid feeding strategies might be excused. For example, a large-bodied sabellid inhabiting a stiff tube attached to a hard substratum and projecting several centimetres into the water column is likely to rely on suspension feeding. Conversely, a small-bodied sabellid inhabiting soft sediments, with most of the tube submerged within it might adopt a flexible strategy, combining suspension and deposit feeding, according to the prevailing conditions. However, on a small scale, the distinction between hard substrata and soft sediments is by no means clear. A bare rock surface usually is pitted with various indentations, small crevices and irregular edges. Unless the current is very strong, some particulate matter usually settles into these depressions. This opens a small-scale niche of soft sediment within a habitat which, on a larger scale, might be classified as being hard-bottom. Discussions of large and small-scale sediment heterogeneity and its effect on the structure and function of benthic faunal assemblages are given in Zenkevich 1927, 1963; Kusnetsov 1970, Watling 1989).

These considerations of scale also apply to conditions in the water column, which often are used as background information in faunal studies. Information on, for example, particulate matter or oxygen content of 'bottom water' usually is obtained from water samples collected either by diver or by remotely operated water bottles. A diver may obtain water from a few centimetres above the sediment-water interface, whereas a remotely-operated sampler may be unable to collect water from less than a metre above the sediment. Conditions in the water column a metre, or even several centimetres, above the sea floor may be quite unlike those experienced by a worm of a few millimetres in length, feeding and respiring in the boundary layer at the sediment-water interface. This is exemplified by a study of benthic fauna in the estuaries of the large Russian rivers, the Ob and Yenisey, along a transect from the river estuary and upwards. At a considerable distance up-river, the faunal assemblages contained typically brackish-water taxa, whilst 'CTD' recordings of 'bottom-water' detected only fresh water (Cochrane *et al.* 1997).

In conclusion, it is advisable to consider all the environmental information available before drawing conclusions as to feeding and general behavioural strategies. Further, it is essential to place these within the context of the scale of the environment as perceived by the individual and in which it exists.

1.4.2 Reproduction

The existence of a wide variety of reproductive strategies amongst benthic invertebrates is widely recognised and reviewed in works including Thorson (1950) and Barnes *et al.* (1993). Wilson (1991) identified a total of 17 different sexual reproductive strategies within the Annelida. Many workers further have discussed the co-ocurrence of free-spawning behaviour, small, externally fertilised eggs which undergo planktotrophic development (e.g. Olive 1985; Brusca & Brusca 1990 and Raff 1996). Traditionally, broadcast spawning was seen as the 'primitive' reproductive mode, whereas other fertilization methods, yolk-dependent lecithotrophic or direct development were seen as the more 'highly-evolved' condition (e.g. Jägerstein 1972; Franzén 1977; Nielsen 1985; Barnes *et al.* 1993 and van den Biggelaar *et al.* 1997). In this context, amongst the amongst the annelid taxa studied in Wilson (1991), only just over a quarter were classed as being true broadcast spawners.

Following the notion of brood protection being a highly evolved behaviour, Westheide (1984) noted that in certain interstitial polychaetes only very few eggs were produced inside a single female, and that these tended to be large and yolky. Brood protection behaviour would ensure maximum survival of the small number of larvae produced. It was concluded that interstitial polychaetes "migrated into the habitat", the evolution of which required the "development of specific genital organs as well as patterns of behaviour that guarantee fertilisation of all eggs" (Westheide *op. cit.*), but supporting evidence was not presented. In any case, it should be borne in mind that complete reproductive success in marine organisms cannot be "guaranteed".

The difference in sperm structure between organisms with different reproductive strategies has long been recognised. Almost a century ago, Retzius (1904) proposed the term 'primitive sperm' to describe those found in 'lower' metazoans. These have a rounded head comprising an anterior acrosome and a nucleus, a short mid-piece and a free axoneme containing the 9 + 2 microtubular arrangement. Franzén (1956) noted that this type of sperm was present only in metazoans which display true broadcast spawning, with external fertilisation occurring within the water column and feeding larvae that develop in the plankton. Further, it became clear that metazoans displaying some form of copulation or parental behaviour possess a different type of sperm, with a more elongate nucleus than the 'primitive' form (Franzén 1956, 1977). This type of sperm became known as 'modified' or 'derived' sperm.

The relationships between reproductive strategies and sperm ultrastructure have been the subject of considerable further investigation. Rouse & Jamieson (1987) found round-headed spermatozoa in various broadcast-spawning polychaetes and elongate sperm in those displaying brood protection behaviour. However, because they were not convinced of the phylogenetic aspects of the different sperm types, a new terminology was proposed. Ect-aquasperm replaces the previous term of 'primitive' sperm, and refers to the round-headed form that is released directly into the water column for fertilisation. Ent-aquasperm refers to spermatozoa that swim in water, but which do not fertilise in the water column as such, and are in some way gathered or stored by the female. Introsperm refers to the spermatozoa that occurs in taxa which rely on internal fertilisation.

The relatively recent phylogenetic revision of the family Sabellidae (Fitzhugh 1989) has provided an opportunity for objective assessment of the notion of 'primitive' and 'derived' spermatozoa in this family. That study showed the small-bodied Fabriciinae to be plesiomorphic to, or less derived than, larger sabellin taxa such as *Sabella*. This is interesting in light of the fact that *Sabella penicillus* L.[5] has been shown to possess ect-aquasperm (Græbner & Kryvi 1973a, b), the type of spermatozoa previously believed to be 'primitive'. Likewise, an elongate ent-aquasperm, previously thought to be 'derived', is documented in *Fabricia stellaris stellaris* (Müller) (as *F. sabella* Ehrenberg) (Franzén 1975). The spermatozoa of several investigated sabellin taxa within *Amphicorina* Quatrefages (as *Oriopsis* Caullery & Mesnil) showed considerable morphological inter-taxon variation, but they could be classed as ent-aquasperm (Rouse 1992a). These observations contradict the previous notion of 'primitive' and 'derived' spermatozoa, since it appears to be the more derived sabellins which have the 'primitive' sperm and vice-versa. A phylogenetic study of a range of sabellid taxa was carried out, using both external morphology and reproductive characteristics (including sperm ultrastructure) as analytical characters (Rouse & Fitzhugh 1994). That study showed brooding of direct-developing larvae to be the plesiomorphic, or ancestral, condition in the Sabellidae, with external fertilisation and swimming larvae occurring in the more highly evolved taxa. Thus, in the Sabellidae, the hypothesis that taxa displaying brood protection behaviour have evolved from broadcast-spawning ancestors is not supported (McHugh & Rouse 1998). Rouse (1995) drew attention to the utility of sperm ultrastructure in systematics, and suggested using the character at various hierarchical levels.

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[5] May refer to *Sabella pavonina* Savigny or *S. spallanzanii* (Gmelin) (see Knight-Jones & Perkins 1998)

As noted in Chapter 1.4.1, there exists a large range of adult body sizes range within the Sabellidae. Interestingly, there also appears to be a relationship between body size and reproductive strategies in the Sabellidae, with the smaller taxa tending to be those which display brood protection whereas broadcast spawners tend to be large-bodied (Rouse & Fitzhugh 1994). The latter strategy appears to involve expelling a large number of small eggs for a high egg volume, whilst brooding sabellids invest a small number of large eggs for a small total egg volume. However, although some generalisations may be made concerning reproductive strategy, body size and phylogeny of sabellid polychaetes, it is important to realise that traits and characteristics may co-vary and there are likely to be exceptions in nature to any explanatory hypotheses developed. As a general conclusion, it should be noted that, as with feeding behaviour, scale also is an important factor in the reproductive strategies amongst the Sabellidae.

1.5 Glossary of terms

The following glossary encompasses the most important terms and phrases used throughout the thesis. Morphological, systematic and ecological terms are included together and are listed alphabetically. Morphological terms are explained in the specific context of the Sabellidae, but also may be applicable to other related taxa.

Abdomen	– segments posterior to the point of chaetal inversion; usually refers to chaetigerous segment 9 and onwards
anal depression	– posterior segments in *Euchone* modified to form a spoon-shaped depression.
anal funnel	– see anal depression
anterior peristomial ring	– anterior part of peristomium, joining to radiolar bases (in Fabriciinae; may be modified as collar; either well-developed or rudimentary)
apomorphy	– a derived or descendant character or character state
bare filaments	– see ventral cirri

branchial crown	– see radiolar crown
branchial lobes	– see radiolar lobes
breast	– (of uncini) the part proximal to the main fang; may be rounded or reduced
chaetae	– chitinous bilateral projections, usually present on all segments except the prostomium (modified as radioles) and peristomium (often collar-bearing) and pygidium (may be slender hair- or bristle-like, or in the form of stout, multidentate hooks)
chaetal inversion	– the phenomenon of 'twisting' of the worm, usually immediately posterior to the eighth body segment, such that in the subsequent segments dorsal becomes ventral
character	– feature or attribute (morphological, ethological etc.)
character polarisation	– the determination of which of two or more homologous characters represent the ancestral, or plesiomorphic, state
collar	– thin, almost membranous structure of peristomial origin; often enveloping the radiolar bases, usually with mid-dorsal gap
derived	– relatively highly evolved (amongst the taxa being considered)
dorsal gap	– gap between left and right dorsal attachment points or free ends of the collar
dorsal incision	– see dorsal gap
ect-aquasperm	– round-headed sperm found in broadcast spawning polychaetes
ent-aquasperm	– sperm found in polychaetes which display some form of mating and/or brood protection behaviour
faecal groove	– ciliated groove for transport of faecal material from the anus to the tube opening; (in sabellids) extends mid-ventrally from the anus to the posterior margin of the thorax, then shifting to a mid-dorsal position and

	extending anteriorly to the peristomium (see also chaetal inversion); often terminates within the dorsal folds of the collar
filamentous appendages	– see ventral cirri
geniculate	– (of chaetae) with a sub-terminal bend
handle	– terminal part of uncinus; may be absent, short or elongate
hard-bottom	– areas of the sea floor not covered by sediment particles (depending on scale), usually refers to rocky or boulder bottoms; also known as erosion areas
homology (homologous)	– characters shared between a group of taxa that are derived from a common ancestor; see also synapomorphy
homoplasy (homoplastic)	– similar characters arising several times in the phylogeny
ingroup	– the group of taxa under investigation
inter-radiolar web	– thin membranous web connecting the radioles from their bases and upwards; present in some sabellids; ranges in extent from very low, almost imperceptible to up to ¾ of the length of the radioles, or more; also known as the palmate web or membrane
introsperm	– sperm that is transferred directly from the male to the female, without entering seawater
lateral notch	– (of sabellin collar) lateral indentation in the collar margin (often confused with simple folding of collar when animal is preserved in the tube)
lateral wings	– parts of posterior segments surrounding the anal depression; modified into a marked ridge bordering the feature
lips	– structures within the radiolar crown used in particle handling; may be elongate or rounded
main fang	– (of uncinus) large, sub-distal 'beak-shaped' tooth

manubrium	– (of fabriciin uncini)
modified sperm	– see ent-aquasperm
monophyly/ monophyletic group	– a group of taxa derived from an included common ancestor which does not exclude any of its descendants
neurochaetae	– ventral-most tuft of chaetae; in thorax as uncini, in abdomen usually as elongate, geniculate chaetae (see chaetal inversion)
notochaetae	– dorsal-most tuft of chaetae; in thorax usually as elongate, geniculate chaetae; in abdomen as uncini (see chaetal inversion)
ocelli	– photoreceptive organs
otocyst	– organ supplying orientational information; usually spherical; lined with innervated fine hairs and containing an otolith.
otolith	– particle within the otocyst; acts by gravity
outgroup	– a taxon, or group of taxa, closely related to the taxon group under investigation, used as a 'reference' taxon to determine character polarity; often the sister-taxon
interstitial	– refers to the pore space between sediment particles (water-filled in aquatic environments)
palmate web/ membrane	– see inter-radiolar web
paraphyly/ paraphyletic group	– an artificial grouping of taxa of which not all are derived from a common ancestor, or from which some of its descendants are excluded
peristomium	– non-chaetigerous segment between radiolar crown (derived from prostomium) and 1st thoracic segment (bearing chaetae); see also anterior and posterior peristomial ring
pinnules	– bilateral filaments, paired or alternating along the length of the radiole; involved in particle capture.

plesiomorphic	– the ancestral state; an apomorphy of a more inclusive taxon than that being considered
polarity	– the direction of phylogeny of a particular character or character state
polyphyly/ polyphyletic group	– a group of taxa whose ancestor is included in another taxon
posterior peristomial ring	– posterior part of peristomium; in Fabriciinae present as visible ring; in Sabellinae usually modified as collar
primitive sperm	– see ect-aquasperm
prostomium	– anterior-most part of worm; specialised to form the radiolar crown
pygidium	– fleshy lobe, often triangular, forming the posterior-most abdominal segment; may have a short terminal filament or other modification
radiolar crown	– refers to all the appendages derived from the prostomium; encompasses all radioles and their pinnules, ventral cirri, lips and the radiolar bases.
radiolar lobes	– pair of semicircular lobes, dorsally fused in the Sabellinae, from which the radioles arise; attached to the anterior part of the peristomium
radiolar skeleton	– internal framework within the radioles and their bases (sometimes also the pinnules), comprising single, double or multiple rows of cartilaginous cells; absent in some Fabriciinae
radioles	– elongate structures arising from the radiolar lobes; used in feeding and also may have a respiratory function
setae	– see chaetae
sister-group	– two taxa that are most closely related to each other than they are to any other taxon
sister-taxon	– one of the two taxa within the sister-group

soft-bottom	– (according to Norwegian Standard NS 9423) areas of the sea floor where it is possible to obtain quantitative samples by grab or box corer; usually refers to sand or mud sediments, but may contain an admixture of gravel or boulders; also known as accumulation areas
spermathecae	– external receptacles in females where gathered sperm are stored prior to fertilisation
symplesiomorphy	– a character or character state which is common to all the members of a clade; not necessarily unique to the clade in question; can be a synapomorphy of a more inclusive clade than that under investigation
synapomorphy	– a derived character or character state (apomorphy) which unites all the members of a particular clade
teeth	– (of uncini) series of small pointed structures usually arranged in several rows above the main fang; may be of similar or unequal sizes
thorax	– anterior segments, usually eight, between the peristomium and the point of chaetal inversion
transformation series	– a group of homologous characters, or character states, ranging from the ancestral state through various evolved states
uncini	– stout chitinous, multidentate hooks present in the thoracic notopodia and abdominal neuropodia (see chaetal inversion); often differing in form between thoracic and abdominal segments
ventral cirri	– elongate filament-like structures arising from the ventral-most parts of the radiolar bases; resembling radioles but lacking pinnules; involved in particle handling
ventral incision	– (of sabellin collar) notch or slit in the ventral margin of the collar

TAXONOMIC PART

"All things bright and beautiful,
All creatures great and small,
All things wise and wonderful,
The Lord God made them all."

Cecil Francis Alexander (1818-1895)

2 Taxonomic part

2.1 Acknowledgements

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2.2 Introduction

2.2.1 The role of taxonomy

In Chapter 1 sabellid polychaetes were seen to represent a group of morphologically, physiologically and behaviourally complex organisms. As is the case in many scientific disciplines, the more detailed the observations become, the more complex and diverse the organisms appear to be. Many of the characters found in the study taxa are difficult to assign to discrete categories and may indeed represent transitional stages. Most taxonomic and systematic works, including the present one, are forced to limit the level of observational detail to a chosen level that is adequate to fulfil the study aims.

In the present study, it is accepted that for each complex and potentially ambiguous issue resolved, several more areas requiring further research will be exposed. Ideally, of course, all these would be given due attention. However, to do so would deny other workers the information as it is obtained. Therefore, the strategy taken here is to present the findings that were possible within the framework of the present study and merely to highlight areas that are yet unresolved. The latter is equally important, because to deny the existence of uncertainty is to create a barrier to further achievement.

Many workers have discussed the role of taxonomy. Simpson (1969) stated that taxonomy is "the theoretical study of classification, including its bases, principles, procedures and roots". Snaydon (1973) described taxonomy as being "concerned with the classification, description and naming of variation amongst organisms". In an ecological context, Heywood (1973) simply considered taxonomy to "provide a data-processing and retrieval service for biology".

Mayr (1969) adopted a broader viewpoint and discussed the multiple role of taxonomy in biological sciences. In addition to and describing the diversity of life, taxonomy was considered to be fundamental to phylogeny reconstruction and also to reveal evolutionary phenomena. Further, taxonomy is an essential component in the study of biogeography and economically or medically important organisms. Mayr (*op. cit.*) also considered the "classification"[1] provided by taxonomic work to be invaluable for branches of biology including evolutionary biochemistry, immunology, ecology, genetics, ethology and historical geology.

Whilst agreeing with the above, the present work considers the overall function of taxonomy to be an effective means of communication about organisms. Therefore, ideally, taxonomic study must be flexible enough to fulfil the needs of different audiences, at different levels of communicative detail. The present work targets three main user groups: taxonomists who are interested in the research of their peers; systematists who use the information to reveal groups of organisms and benthic

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[1] the present work prefers the term 'systemising' (see Pleijel 1999).

taxonomist, contain enough information to allow unambiguous assessment of comparative morphology and be clear enough that the non-specialist can use the information for taxon determination.

In general, therefore, taxonomic works should:

- include all taxonomic information available at the present time;
- indicate areas of uncertainty, where accurate presentation of information is limited due to character ambiguity or specimen availability;
- give information that is comparable with previous records of related taxa;
- ensure that the description contains sufficient information to allow systematic character coding, particularly if an appropriate character matrix exists;
- use illustrative visual diagrams that highlight details and which can be photocopied without loss of information;
- highlight key differences between the study organisms and related taxa;
- use tabular keys to reduce problems of subjectivity associated with dichotomous keys, particularly when encountering incomplete or damaged specimens;
- include ecological and reproductive information, where available.

It is important that the taxonomist keeps abreast of developments in any of the fields of the target audience. If any of the aims of the target audiences change, it is important that the information conveyed by the taxonomist is augmented as appropriate. For example, if the systematics of a group of organisms is revised, and the description of the higher taxon is emended, subsequent descriptions of taxa within that group must address all the features highlighted by the systematic revision. Similarly, the ecologist is helped greatly if the taxonomist includes details such as the size of any eggs present in relation to body size, their location within the body cavity, the presence of larvae in the tube, as well as the more traditional descriptions of tube construction and sedimentology of the source locality.

2.2.2 Scope and aims

The taxonomic part of this thesis aims to examine the diagnosis of *Euchone* and to present an overview of the taxa included therein. Further, it is aimed to present descriptions or re-descriptions of a limited number of taxa. One taxon new to science, *Euchone x*, is described that is amongst the dominant sabellids found in soft-bottom sediments in the North Sea and the Norwegian Sea. A re-description is given of *Jasmineira candela* Grube, together with a description of specimens frequently mis-identified as that taxon. These specimens are believed to belong to *Jasmineira oculata* Langerhans, which was synonymised with *J. candela* by Fauvel (1927) and consequently not given further attention in the literature. *Chone y* is described from the northern North Sea and Norwegian Sea, with a discussion of *Chone longocirrata* Sars, *Chone collaris* Langerhans and *Chone duneri* Malmgren. Finally, a brief overview is given of some further soft-bottom sabellins from the North Sea, Norwegian Sea and Arctic waters that are in need of taxonomic study.

2.2.3 Terms and abbreviations

The following terms and abbreviations apply to illustrations in Chapter 2.

AD	- anal depression
C	- collar
Ci	- cilia
DL	- dorsal lips
FG	- faecal groove
GG	- glandular girdle
IRM	- inter-radiolar (palmate) membrane
LW	- lateral wings
P	- pygidium
PE	- peristomial extensions
Pi	- pinnule
R	- radiole
RC	- radiolar crown
SE	- skeletal elements
VC	- ventral cirri
VL	- ventral lips

2.3 *Euchone* Malmgren - historical and taxonomic perspectives

2.3.1 A chronological overview of taxa within *Euchone*

In addition to the various original descriptions, useful information was obtained from Banse (1970, 1972), Hartman (1965a), Malmgren (1866), the TRITON Index to Organism Names (BIOSIS UK at *http://www.york.biosis.org/triton/nameind.htm*) and the Ward & Fauchald (1997) Polychaete Bibliography.

Table 2.3.1 lists in chronological order taxa currently systemised within *Euchone* Malmgren, or later assigned to or removed from that higher taxon. Some taxa are of uncertain status due to missing or damaged type, or reference specimens. Also, some taxa have not been given much, if any, attention in the more recent literature, or have not been recorded since their description. Ascertaining the status of such taxa is beyond the scope of the present study, but the table does serve as a useful historical guide and starting point for the present and future taxonomic studies.

As an example of taxa of uncertain status, Banse (1970) commented that *Euchone rosea* Langerhans, according to the description (Langerhans' material lost), is not distinguishable from *Euchone olegi* Zaks, as characterised by Buzhinskaya (1967). However, re-examination of two specimens of this material identified as *E. olegi* showed these to conform to *Euchone limnicola* Reish (*pers. ob.*). The type specimen of *E. olegi* was reputed to be in Moscow, but appears to be lost (Sikorski, *pers. com.*). Until type material becomes available for examination, the identity of *E. olegi* remains uncertain. Further research also should re-examine the status of 'sub-species', such as *Euchone rubrocincta normani* McIntosh, the type locality of which is close to that of the 'main' taxon, *Euchone rubrocincta* (Sars). The synonymy of *Euchone tuberculosa* (Krøyer) with *Euchone papillosa* (Sars) should be assessed as well as the status of *Euchone papillosa* var. *rigida*, Tauber, which here is suspected to refer to *E. tuberculosa*. Also, *Euchone southerni incisa* Banse, from the Falkland Islands, should be compared with other taxa from similar latitudes, as well as with *Euchone southerni* Banse, which originally was described from Ireland

Table 2.3.1. List of taxa currently or previously recognised within Euchone *Malmgren, with author, date and type locality, in chronological order. Original affiliations to genera are maintained. Locations of type material are given as far as has been ascertained; '?' indicates incomplete or unavailable information.*

Author	Date	Taxon name	Type locality	Type material	Remarks
Sars	1851	*Sabella papillosa*	Finnmark, Northern Norway	?	removed to *Euchone* by Malmgren (1866); also recorded as *Chone papillosa* (Sars 1861); that work published as Sars (1862) often cited as (1862, for 1861).
Krøyer	1856	*Chone flabelligera*	Tromsø, Northern Norway	?	later synonymised with *Euchone papillosa* (Malmgren 1866)
Krøyer	1856	*Sabella analis*	Greenland	?	removed to *Euchone* by Malmgren (1866)
Krøyer	1856	*Sabella rigida*	Greenland	4 syntypes ZMC	synonymised with *Euchone tuberculosa* by Malmgren (1866); cited in Malmgren (1866) as ?*Sabella rigida*
Krøyer	1856	*Euchone tenuissima*	Norway	believed lost	as *Sabella tenuissima*, later *Chone tenuissima*; indicated in Tauber (1879) as being junior synonym of *Euchone papillosa*
Krøyer	1856	*Sabella tuberculosa*	Greenland	approx. 5 syntypes ZMC	removed to *Euchone* by Malmgren (1866), believed synonymous with *Euchone papillosa* var. *rigida* (Tauber 1879) and with *E. papillosa (*Hartman 1959); formalised by Banse (1972); in need of re-assessment
Sars	1862	*Chone rubrocincta*	Northern Europe (syntypes include Norway & Ireland)	3 syntypes ZMO	removed to *Euchone* (Malmgren 1866)
Ehlers	1871	*Euchone rubella*	Spitsbergen	?	synonymised with *E. analis,* authority uncertain
Verrill	1873	*Euchone elegans*	Maine, USA	5 syntypes USNM 7513	

Tauber[*]	1879	*Euchone papillosa* var. *rigida*	Øresund, Denmark	?	original reference reads (under section on *E. papillosa*): var. *rigida* Kr. lib. cit. P. 18. Here interpreted as referring to *Sabella rigida* in Krøyer (1856), later synonymised with *E. tuberculosa*, as (in Tauber's opinion) distinct from *E. papillosa sensu* Sars; requires further investigation.
Langerhans	1884	*Euchone rosea*	Madeira	believed lost	
Moore & Bush	1904	*Euchone alicaudata*	Japan	holotype USNM 5496	
Ehlers	1908	*Euchone pallida*	East of Kerguelen Islands, Antarctica	?	
McIntosh	1916	*Euchone lawrenci*	Eastern Canada	?	
McIntosh	1916	*Euchone rubrocincta normani*	England	?	apparently synonymised with *Euchone rubrocincta* by Banse (1970)
Moore	1923	*Euchone magna*	California, USA	holotype USNM 17281	removed to *Chone* by Hartman (1969)
Zaks	1933	*Euchone olegi*	Sea of Japan	believed lost	missing from Moscow Museum (Sikorski, *pers. com.*)
Ushakov	1950	*Euchone derjugini*	Kamkchatka, Northeast Russia	location unknown	not in St. Petersburg (Bushinskaya, *pers. com.*) or Moscow (Sikorski, *pers. com.*)
Ushakov	1950	*Euchone longifissurata*	Okhotsk Sea, Northeast Russia	location unknown	not in St. Petersburg (Bushinskaya, *pers. com.*) or Moscow (Sikorski, *pers. com.*)
Banse	1957	*Euchone trilobata*	Falkland Islands	AHF	as *Desdemona*, removed to *Euchone* by Banse (1970)
Reish	1960	*Euchone limnicola*	California, USA	holotypes AHF. paratypes AHF, USNM, BMNH	variant spelling of *E. limicola* in Hartman (1966)

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[*] here interpreted as new combination, rather than new 'sub-species' (see 'remarks').

Day	1961	*Euchone capensis*	South Africa	paratypes UCT	
Hartman	1965b	*Euchone incolor*	Continental shelf off New England, Atlantic Ocean	AHF	Banse (1970) gives extensive details of holdings
Reish	1965	*Euchone trisegmentata*	Bristol Bay area, Bering Sea	holotype USNM 30456	synonymised with *E. incolor* by Banse (1970)
Hartman	1966	*Euchone arenae*	San Pedro region, California, USA	AHF	
Reish	1968a	*Euchone barnardi*	Bahia de Los Angeles, Gulf of California, Mexico	USNM 38403	synonymised with *E. incolor* by Banse (1970); note Figures 19 and 20 in Reish (1968a) should be reversed
Reish	1968a	*Euchone cortezi*	Bahia de Los Angeles, Gulf of California, Mexico		synonymised with *E. arenae* by Banse (1970)
Reish	1968b	*Euchone eniwetokensis*	Marshall Islands	holotype, 1 paratype USNM	removed to *Chone* by Banse (1972)
Banse	1970	*Euchone hancocki*	Lasuen Seamount, off Southern California	AHF	Banse (1970) gives extensive details of holdings
Banse	1970	*Euchone southerni*	Ballynakill Harbour, Northwest Ireland	holotype, paratype(s) NMI 77.1908	
Banse	1970	*Euchone southerni incisa*	Falkland Islands	holotype UCT FAL 370K, paratype FAL 370KK	recorded as *Euchone rosea* by Kirkegaard (1959) *partim* and Day (1967) *partim*
Banse	1972	*Euchone velifera*	California, USA	holotype AHF Poly 0256, 2 paratypes AHF Poly 0453	
Fauchald	1972	*Euchonella magna*	Southern gulf of California, Mexico	holotype AHF	should be removed to *Euchone* (Fitzhugh 1989)

Hartman	1978	*Euchone heteroseta*	South Georgia Island, Antarctica	holotype AHF	
Hartman	1978	*Euchone scotiarum*	Weddell sea, Antarctica	holotype USNM 47091	
Hutchings & Murray	1984	*Euchone variabilis*	Botany Bay, New South Wales	paratypes AHF Poly 1431, 2 at BMNH ZB 1983.1762.63, 4 at USNM 81479	
Ruff & Brown	1989	*Euchone bansei*	Cape Cod, Massachusetts to Cape Lookout, North Carolina	holotype USNM 115738, paratypes at USNM 115738-745, BMNH ZB 1987.620.634	
Hartmann-Schröder & Rosenfeldt	1989	*Euchone undulocincta*	Joinville, Antarctica	holotype ZMH P-19642, 5 paratypes ZMH P- 19643	
Cochrane	n.n.	*Euchone x* (name withheld, see Chapter 2.4, this thesis)	Northern North Sea/ Norwegian Sea	Pending lodging: TMU, BMNH, ZMC	previously confused with *Euchone incolor*

Key to abbreviations: AHF – Allan Hancock Foundation, Los Angeles; BMNH – Natural History Museum, London, UK (code refers to previous title of British Museum of Natural History); TMU –Tromsø Museum, Zoology, University of Tromsø, Norway; UCT - University of Cape Town, South Africa; USNM - National Museum of Natural History, Smithsonian Institution, Washington DC, USA., ZMC – Zoological Museum, Copenhagen, Denmark; ZMH – Zoological Museum, Hamburg, Germany; ZMO – Zoological Museum, University of Oslo, Norway.

2.3.2 Taxa within *Euchone* Malmgren

Table 2.3.2 lists the taxon names currently recognised within *Euchone* Malmgren and synonyms, where taxon names either have been included within or removed from *Euchone* subsequent to description of the taxa.

Table 2.3.2. List of taxon names currently recognised within Euchone *Malmgren* and synonyms.

Taxon names within *Euchone*	Synonyms
Euchone alicaudata Moore & Bush	*Euchone trisegmentata* Reish (see *Euchone incolor*)
Euchone analis (Krøyer)	*Chone tenuissima* (Krøyer) (see *Euchone papillosa*)
Euchone arenae Hartman	*Euchone rubella* Ehlers (see *Euchone analis*)
Euchone bansei Ruff & Brown	*Chone flabelligera* (see *Euchone papillosa*)
Euchone capensis Day	*Euchone eniwetokensis* Reish (see *Chone eniwetokenis*)
Euchone x (see Chapter 2.4, this thesis)	*Euchonella magna* (Fauchald) (see *Euchone magna)*
Euchone derjugini Ushakov	*Euchone barnardi* Reish (see *Euchone incolor*)
Euchone elegans Verrill	*Euchone rigida** (Krøyer) (see *Euchone papillosa*)
Euchone hancocki Banse	*Euchone magna* Moore (see *Chone magna*)
Euchone heteroseta Hartman	*Euchone tuberculosa* (Krøyer) (see *Euchone papillosa*)
Euchone incolor Hartman	*Euchone cortezi* Reish (see *Euchone arenae*)
Euchone lawrenci McIntosh	*Euchone papillosa* var. *rigida** (*sensu* Tauber)
Euchone limnicola Reish	*Chone rubrocincta* (Sars) (see *Euchone rubrocincta*)
Euchone longifissurata Ushakov	*Euchone tenuissima* (Krøyer) (see *Euchone papillosa*)
Euchone magna (Fauchald)	
Euchone olegi Zaks	
Euchone pallida Ehlers	
Euchone papillosa (Sars)	
Euchone rosea Langerhans	
Euchone rubrocincta (Sars)	
Euchone rubrocincta normani McIntosh	
Euchone scotiarum Hartman	
Euchone southerni Banse	
Euchone southerni incisa Banse	
Euchone trilobata Banse	
Euchone undulocincta Hartmann-Schröder & Rosenfeldt	
Euchone variabilis Hutchings & Murray	
Euchone velifera Banse	

* pending reassessment of the synonymy of *E. tuberculosa* with *E. papillosa*.

As far as has been ascertained, a total of 28 species are (or should be) recognised within *Euchone*, including two sub-species. Included are *Euchone x*, which is pending formal recognition (species name withheld), and *Euchone magna* (Fauchald), which is in need of redescription and formal re-designation.

2.3.3 Diagnosis of *Euchone* Malmgren

Euchone Malmgren, 1866, emended Banse (1970), Fitzhugh (1989).

Euchone Malmgren (1866): 405.- Langerhans (1881): 111.- Saint-Joseph (1894): 250.- Bush (1905): 190.- Hofsommer (1913): 327.- McIntosh (1923): 281.- Fauvel (1927): 339.- Berkeley & Berkeley (1952): 121.- Ushakov (1955): 418.- Day (1967): 744.- Banse (1970): 389.- Banse (1972): 481.- Hartmann-Schröder (1971): 520-521.- Fitzhugh (1989): 68.- Hartmann-Schröder (1996): 551.- Kirkegaard (1996): 378.

Sabellidae with abdominal segments less than 33. Semicircular branchial lobes sometimes united by inter-radiolar (palmate) membrane. Collar conspicuous, sometimes bilobed. Postsetal girdle of glands on second chaetiger. Ventral shields sometimes present. Anal depression with lateral wings formed by variable number of caudal segments. Three types of thoracic notochaetae: upper, or upper-anterior chaetae limbate; lower, anterior chaetae narrowly limbate (bayonet-type); and lower, posterior chaetae usually sub/pseudo-spatulate. Thoracic neuropodial uncini avicular. Abdominal notopodial uncini with rounded or square bases; abdominal neurochaetae limbate.

Remarks:

Euchone is classified within the Sabellinae (see Chapter 3.2 and 3.4 for further details). There still is some uncertainty as to the relationships between *Euchone* and related genera (including *Chone* Krøyer which it most resembles) as well as *Amphicorina* Quatrefages (previously *Oriopsis* Caullery & Mesnil), *Jasmineira* Langerhans and *Desdemona* Banse. Both *Chone* and *Euchone* share similar chaetal characteristics and a well-developed membranous collar, homologous to the posterior peristomial ring of the Fabriciinae and sometimes referred to in the recent literature as the posterior peristomial ring collar. It also generally is the case that members of both genera have a well developed inter-radiolar (palmate) membrane, although this is reduced or possibly absent in some of the smaller species with few radioles (Banse 1970).

2.3.4 Remarks on the anal depression

At present, *Euchone* is distinguished from *Chone* solely by the presence of the anal depression (see also comments in Fitzhugh 1989). Despite this apparently simple diagnosis, there has been, and continues to be, some confusion in the literature, as well as in specimens examined here, between *Chone*, *Euchone* and, to some extent, *Amphicorina.* A full review of variations in anal depression morphology within *Euchone* is beyond the scope of the present study, but some general observations are relevant.

An almost transitional state of the anal depression is evident in *Euchone limnicola* Reish, in which lateral wings are absent. Although not depicted in the original description, this is illustrated in Hartman (1966). In both type and non-type specimens examined, the 'depression' is bordered anteriorly by a dermal flap, parallel to the segmental boundary of the first 'depression' chaetiger (*pers. ob.*) of holotype and study material from the Sea of Japan, Australia, New Zealand and the UK). The species appears to be becoming globally established in harbour areas, and apparently has been spreading rapidly in recent years (Garwood, McArthur, Read & Wilson, *pers. com.*). *Euchone limnicola* presents a systematic challenge because the presence of lateral wings bordering the anal depression currently is diagnostic of *Euchone.* Two options therefore exist: 1) re-designation of the species, or 2) modification of the generic diagnosis from "…anal depression with lateral wings…" to "...with well-developed or rudimentary lateral wings…". Further systematic investigations of *Euchone*, incorporating cladistic analyses, will address this and other related issues (see Chapter 3.5).

From the illustration of the small Antarctic species *Euchone scotiarum* Hartman, depicted by Hartmann-Schröder & Rosenfeldt (1989), it is not clear whether the anal depression in that species constitutes a simple groove in the posterior three segments, or whether lateral wings are present. The posterior end of the animal is not depicted in the original description. The anal depression in *Euchone incolor* Hartman appears poorly developed or apparently absent in some smaller specimens (Banse 1970), although lateral wings are clearly depicted in the original description (Hartman 1965b) and evident in some paratype material (*pers. ob.*). The description of *Euchone trisegmentata* Reish (referred by Banse, 1970 to *Euchone incolor*) also depicted the depression with clear lateral wings. However it should be remarked that when specimens are fixed within their tubes the lateral wing margins may become flattened inward, almost meeting mid-ventrally, which can make the depression extremely difficult to see under light microscopy. Thus, the depression in certain small species of *Euchone* may appear less conspicuous than generally is the case for larger species.

There also appears to be a degree of ambiguity between a posteriorly enlarged faecal groove or dorso-ventral compression in certain species of *Chone*, and a poorly developed anal depression in some *Euchone*. This is illustrated in the literature, whereby *Chone eniwetokensis* Reish originally was assigned to *Euchone*, and was described as having six chaetigers comprising the anal depression. However, the species later was assigned to *Chone* because of the apparent lack of an anal depression (Banse 1970). It was, however, noted by Banse (1970) that the posterior segments were dorso-ventrally compressed, perhaps giving the illusion of a depression. Re-examination of type material should clarify this ambiguity.

Interestingly, a number of other species outwith *Euchone* also display marked dorso-ventral flattening or constriction of the posterior segments, to the extent that they resemble a rudimentary anal depression, although entirely lacking lateral wings.

Amphicorina longipyge (Hartmann-Schröder & Rosenfeldt), described from Antarctic waters under *Oriopsis*, is depicted with a marked mid-ventral constriction in the posterior three to four abdominal segments (see Figure 2.3.1). The authors refer to the phenomenon as being an extension of the anus, but it is clear that the matter warrants further attention. Similarly, a specimen from Australian waters identified as *Amphicorina cf. michaelseni* (Banse) (as *Oriopsis*) by Hartmann-Schröder & Hartmann (1989) is depicted with a similar posterior constriction.

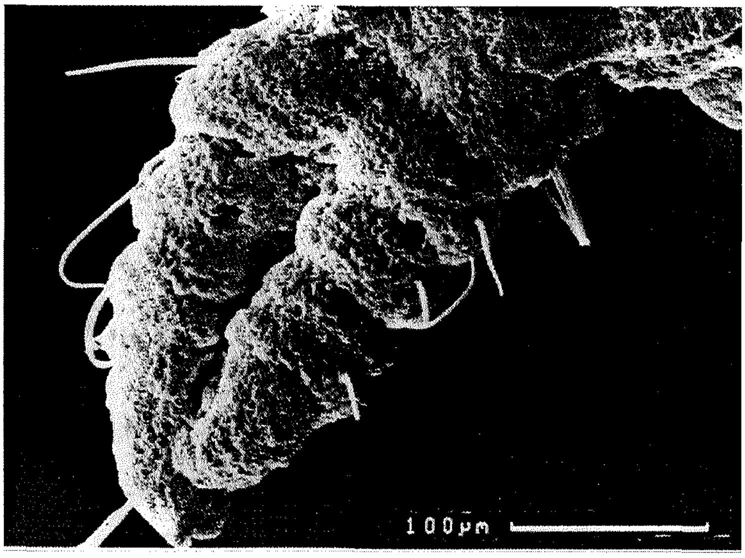

Figure 2.3.1. SEM image from the description of Amphicorina longipyge (Hartmann-Schröder & Rosenfeldt) showing mid-ventral constriction of posterior segments. From Hartmann-Schröder & Rosenfeldt (1989)

These transitional and rudimentary states should be borne in mind when considering the anal depression as a feature diagnostic of *Euchone*. Few, if any, segments are added to the depression after it has developed and the numbers of segments it comprises seems to be relatively constant within species, making it a useful feature in species diagnoses. However, in light of the foregoing, it should be treated with care at a higher taxonomic level. Until an extensive revision of these taxa has been carried out, the current diagnosis of *Euchone* will be continued in the present work. Thus, all *Chone*-like species with an anal depression comprising a variable number of segments and with lateral wings will be referred to as *Euchone*. The diagnosis is here extended to encompass taxa in which the lateral wings are reduced to a ridge, such as in *Euchone limnicola*. Species with posterior dorso-ventral flattening, mid-ventral constriction of the posterior segments or those showing a posterior enlargement of the faecal groove will not be considered within the taxon in the present chapter. The issue is clarified in Chapter 3.5.

Banse (1970, 1972) indicated the taxonomic utility of using the number of pre-depression and depression segments as a species diagnostic character in *Euchone*. While generally it is accepted that abdominal segments are added immediately anterior to the pygidium during growth of *Chone* individuals, the number of abdominal segments in *Euchone* appears constant throughout development. This is supported by examination of a large quantity of material, comprising several *Euchone* species of a wide size range (*pers. ob.*). In *Chone*, the abdomen increases in length by the addition of numerous, narrow segments immediately anterior to the pygidium, whereas in *Euchone* the extant segments seem simply to increase in size.

2.3.5 Some comments on uncini as diagnostic characters

Many diagnoses of sabellid taxa rely heavily on the form of the uncini. For example, a diagnostic characteristic of *Amphicorina* is the presence of unequally-sized teeth above the main fang (see Figure 1.2.13b), although the feature also appears in some fabriciin taxa. This form of the thoracic uncini, together with differences in collar morphology, is a useful character for distinguishing *Amphicorina* from *Desdemona*, which it closely resembles. The thoracic uncini in *Desdemona* do not have unequal sized teeth above the main fang, the posterior peristomial ring collar is absent and the anterior peristomial ring lobe is wide ventrally, not narrow, as in *Amphicorina* (see Fitzhugh 1989). In this context, the validity of the designation of *Desdemona antarctica* Hartmann-Schröder & Rosenfeldt, which clearly is depicted with *Amphicorina*-type thoracic uncini (Figure 2.3.2) and a well-developed collar, warrants further investigation.

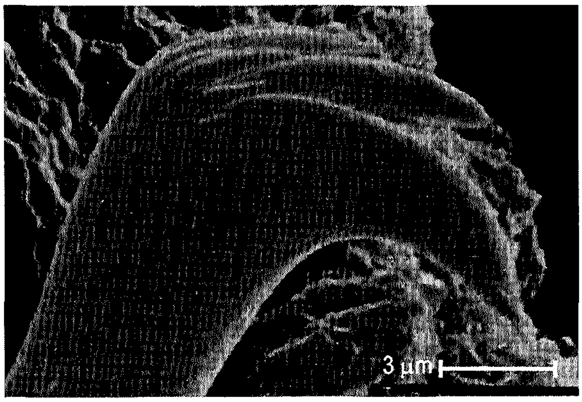

Figure 2.3.2.
Thoracic uncinus as depicted in the description of Desdemona antarctica *Hartmann-Schröder & Rosenfeldt, showing the presence of unequal teeth above the main fang. From Hartmann-Schröder & Rosenfeldt (1989).*

Similarly, in Chapter 2.6, a species of *Chone* new to science is described, which also possesses *Amphicorina*-like thoracic uncini.

Similarly, in Chapter 2.6, a *Chone* taxon new to science is described, which also possesses *Amphicorina*-like thoracic uncini.

The form of sabellid abdominal uncini also is of diagnostic utility. The typical shape of *Chone* and most *Euchone* abdominal uncini is the squarish form, where the breast is modified into a pointed structure beneath the main fang (see Figure 1.2.14d). Whereas this is the most common form for taxa within *Chone*, there is a great deal of variation within *Euchone*. In some taxa, such as the 'type species' *Euchone analis* (Krøyer), the uncini resemble those of *Chone*. In other taxa, notably *Euchone elegans* Verrill, the base is rounder and there is a posterior elongation (Figure 2.3.3) reminiscent of the handle seen in the uncini of larger sabellin taxa such as *Sabella* L. (compare with Figure 1.2.14g).

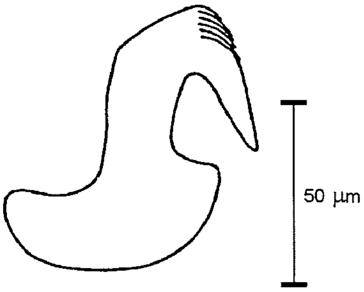

Figure 2.3.3.
Uncinus from the 7th abdominal segment in Euchone rubrocincta *(Sars), from Banse (1972). Note the posterior handle and rounded base, resembling the form seen in larger sabellins, such as* Sabella *Savigny and* Demonax *Kinberg.*

Banse (1970) noted that amongst the 'small' *Euchone*, in retrospect mainly those taxa with a 'snowflake-like' radiolar crown (see Chapter 1.2.2), the form of the abdominal uncini may vary even within a single parapod of a single specimen. Whereas the ontogenetically first-formed dorsal-most uncini resemble the quadrangular form typical of *Amphicorina*, those occupying a more ventral position within the parapod often are of the more typical *Chone* form (Banse 1970). Thus, as in other aspects of sabellid morphology, care should be taken to avoid over-generalisation of these diagnostic features.

Such anomalies and marked variations in form may be informative in taxonomic and systematic terms and, as such, should be given due attention. When depicting uncini, it should be stated from which segment, and if possible also from which part of the

2.4 *Euchone x*[1] from the northern North Sea and Norwegian Sea

2.4.1 Special thanks

I thank Randi Olsen, Helga Marie and Reidar Myklebust for laboratory facilities and much appreciated assistance with histology and photography. Saga Petroleum AS and Statoil are acknowledged for use of specimens collected for environmental monitoring. Type and study material from the Allan Hancock Foundation was kindly loaned by Leslie Harris, Los Angeles County Museum of Natural History. I thank Roy Lyså for scanning some of the figures and for initiation in computer graphics.

2.4.2 Summary

Euchone x is described from the northern North Sea/Norwegian Sea. *Euchone x* most resembles *Euchone incolor* Hartman and *Euchone hancocki* Banse, but is distinguished by the presence of three pairs of radioli, eight abdominal segments and a pre-chaetal glandular girdle on the third abdominal segment. In addition, the peristomium of *Euchone x* greatly protrudes from the collar, which is markedly higher ventrally than dorsally. Both these states are far more pronounced than is usual amongst the members of *Euchone*. The taxon is one of several *Euchone* with most radiolar pinnules terminating at the same height distally ('snowflake-like'), as in the Fabriciinae and some Sabellinae such as *Amphicorina* Quatrefages. Three segments form the anal depression, which often is poorly developed; when evident, it is bordered by prominent lateral wings. In common with many *Euchone* taxa, the number of abdominal segments remains constant throughout the life of the individual, in contrast to most, if not all, taxa within *Chone*, whereby segments are added immediately anterior to the pygidium as the animal grows. Population densities of *Euchone x* may be high in favourable conditions, suggesting a degree of opportunism. The need for a detailed review of variations in morphology within *Euchone* is discussed and some areas for further research are outlined.

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[1] New taxon name withheld until formal publication in a form recognised by the International Code of Zoological Nomenclature, Article 8.

2.4.3 Introduction

Samples of macrobenthic faunal assemblages collected around various petroleum installations in the Norwegian sector, in the transitional area between the North Sea and the Norwegian Sea in 1989 and subsequent years were found to contain extremely large numbers of very small sabellids, up to 6 000 individuals per m^2, which presented an identification challenge. In 1989, these were simply identified as Sabellidae indet. (Mannvik *et al.* 1990). In 1991, the identification task fell upon myself and the specimens sampled seemed even smaller than in the previous survey. Being unable to detect an anal depression in the specimens, I resorted to examination of the abdominal uncini, the radiolar crown and the structure of the peristomium.

The abdominal uncini most resembled the quadrangular form typical of *Amphicorina* Quatrefages, at the time referred to as *Oriopsis* Caullery & Mesnil. The radiolar crown was of the 'snowflake-like' form (see Chapter 1.2.2) typical for *Amphicorina* and members of the Fabriciinae. However, Banse (1970) pointed out that some of the 'small' *Euchone* Malmgren also possess this radiolar arrangement. The specimens possessed a bilobed structure protruding ventrally from the collar, which also is reminiscent of *Amphicorina* (although in hindsight I realised that this is common in other small individuals within *Euchone* and *Chone* Krøyer). Based on these observations, I mis-identified the specimens as *Oriopsis* sp. (Mannvik *et al.* 1992).

In processing samples from a subsequent survey, I became aware of the presence of an anal depression in approximately one out of fifty individuals, generally those that were preserved out of their tubes. It soon became clear that the specimens should be determined as *Euchone*. Mainly using the work by Banse (1970), again I mis-identified the specimens as *Euchone incolor* Hartman (Pearson *et al.* 1994), although I was aware that the number of abdominal segments and the form of the anterior end were not entirely consistent with the taxon description. Findings of these individuals generally were recorded as *Euchone* sp. (Pearson *et al.* 1993, 1995, 1996; Holte *et al.* 1992, 1993a, 1994; Mannvik *et al.* 1992, 1995a, b, 1996, 1998a, b) awaiting the discovery of their correct identity. Thus the present research arose.

Holte *et al.* 1992, 1993a, 1994; Mannvik *et al.* 1992, 1995a, b, 1996, 1998a, b) awaiting the discovery of their correct identity. Thus the present research arose.

2.4.4 Materials and methods

Specimens were obtained using a 0.1 m^2 van Veen grab, deployed from various offshore supply vessels, chartered from Møkster Shipping on an annual basis between 1989 and 1996. The majority of the specimens were collected from the Snorre, Troll Vest and Åsgard oil fields (Figure 2.4.1).

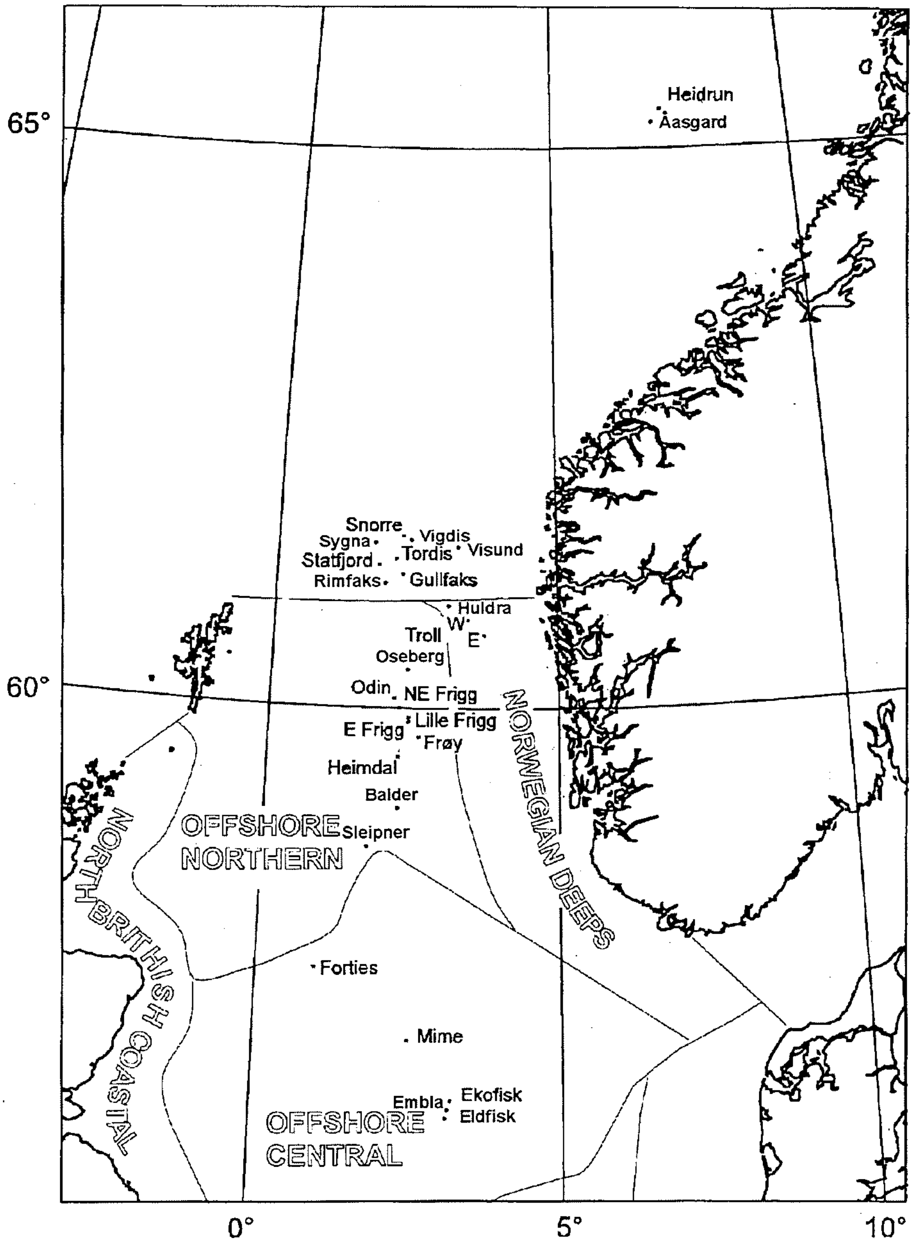

Figure 2.4.1. Overview of general sampling area (modified from Pearson et al. 1996).

Specimens retained on 1 mm round-mesh sieves immersed in running seawater were fixed in 10-15 % borax-buffered formalin in seawater. The samples were sorted within a few weeks of fixation and further preserved in 70-75 % ethanol. An Olympus SZH zoom dissecting microscope equipped with drawing attachment and x2 objective was used for low-power work. High power observations were made using an Olympus BH2 light microscope, with a x100 oil immersion objective. Specimens used for histological work were fixed in formalin as above (for practical reasons), then transferred through a rehydration series, post-fixed in 1% osmium tetroxide, and then transferred through a dehydration series. The specimens were placed in 95% ethanol, followed by two changes of clean, absolute alcohol. Dehydrated specimens were infiltrated and embedded in Epon araldite, and 1 µm sections cut with glass knives using a Reichert-Jung FC4D Ultracut microtome. Sections were stained with 0.3% toluidine blue in 0.1M phosphate buffer and mounted in 'Histokit' mounting medium. Specimens for scanning electron microscopy were prepared according to Rouse (1994).

2.4.5 Results

Euchone x

The holotype and paratypes are pending deposition at the Natural History Museum, London, UK (BMNH) and further paratypes are pending lodging at Tromsø Museum, University of Tromsø, Norway (TMU) and the Zoological Museum, Copenhagen (ZMC).

Holotype and Paratypes: northern North Sea (Snorre Field, 61°30'N, 2 °10'E).
Type locality: northern North Sea, slope of Norwegian continental shelf.
Material examined[2]: From the slope between the North Sea Plateau and the Norwegian Trench: Snorre Field (Saga Petroleum a/s, 61°30'N, 2°10'E), over 300

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[2] For formal publication, the exact sampling positions for specimens examined and those designated as reference material will be given.

specimens, Troll Vest oil field (Saga Petroleum a/s, 60°45'N, 3°25'E), in excess of 400 specimens. Norwegian Sea: Åsgard Field (Statoil, 65°05'N, 07°00'E), approximately 200 specimens. Positions given as approximate field centre, due to presence of multiple wells. Specimens were collected from an extensive network of sampling stations around these positions.

For comparison, paratypes WHOI C1 (six specimens) of *Euchone incolor* Hartman, 1965 were examined, as well as paratypes 2298-53 (seven specimens) of *Euchone hancocki* Banse, 1970, both lots from the Allan Hancock Foundation, Natural History Museum, Los Angeles.

Note. Where appropriate, the present terminology largely follows that of Knight-Jones & Perkins (1998), Fitzhugh (1989) and Banse (1970, 1972). The term 'lobes', referring to the two halves of the crown, is maintained, in keeping with the diagnosis of *Euchone* (Malmgren 1866). The use of 'ventral cirri' is adapted from the terminology of Krøyer (1856), and refers to the apinnate filaments at the ventral margin of each half of the crown.

Description[3]. Body long, slender (see Figure 2.4.2). Cylindrical thorax and anterior abdomen, becoming rectangular in transverse section posteriorly. Eight thoracic and eight abdominal segments, the posterior three forming the anal depression. Middle segments elongated, with indistinct inter-segmental boundaries, with length:width ratio of approximately 2:1, reaching up to 5:1 in reproductive females. Pronounced inter-segmental constrictions in posterior four abdominal segments. Three pairs of radioles, with 7-12 pinnules alternating along their length, terminating in a short, finely tapering pinnule-like filament (Figure 2.4.5). Radiolar mid-rib not markedly thicker than the pinnules. Mid-radiolar pinnules longest, with most pinnules terminating at the same level distally. The most proximal pinnules are short. Inter-radiolar membrane extremely low, almost invisible, lateral flanges absent. Collar

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[3] The taxon name *Euchone x* currently is not defined by any synapomorphy, or feature that distinguishes it from its closest relatives. Instead, the taxon possesses a unique combination of the various features (see Chapter 3.5).

very low, oblique, higher ventrally than dorsally, exposing the anterior peristomium on all sides. Ventral anterior peristomial extensions prominent, bilobed. Marked glandular ridge behind chaetae of second chaetiger, evident on all specimens. Pre-chaetal glandular ridge on the third abdominal chaetiger, not always apparent. Ventral shields not differentiated. Methyl green staining, using the Hofsommer (1913) method, as well as histological preparations, shows thoracic inter-segmental rings of glandular tissue, as well as some scattered mucus cells on the epithelium. The collar also carries glandular patches.

Figures 2.4.3. and 2.4.4 illustrate the chaetal types. Anterior superior thoracic notochaetae limbate; long, tapering, geniculate at the base of the final taper and slightly swollen at the knee, three per fascicle. Posterior superior notochaetae also limbate; shorter, geniculate at the base of the final taper and swollen at the knee (sometimes referred to in the literature as subspatulate or pseudospatulate), three per fascicle. Inferior thoracic notochaetae short, tapering capillaries (also referred to as 'bayonet' type), three per fascicle. Thoracic uncini acicular, long handled, with one main fang and, usually, five rows of secondary teeth, five per fascicle. Abdominal neurochaetae long, needle-like, tapering, without marked swellings. Abdominal uncini quadrangular, with approximately square bases and a reduced manubrium, five to seven per fascicle. Some variation in uncinal shape within the torus and between segments down the body. One main fang and five to six rows of secondary teeth in anterior abdominal segments. Posterior abdominal uncini somewhat larger than in anterior abdominal segments, and with more rounded bases. Anal depression often very small, or with lateral margins flattened inwards, not always clear in light microscopy. Pygidium conical.

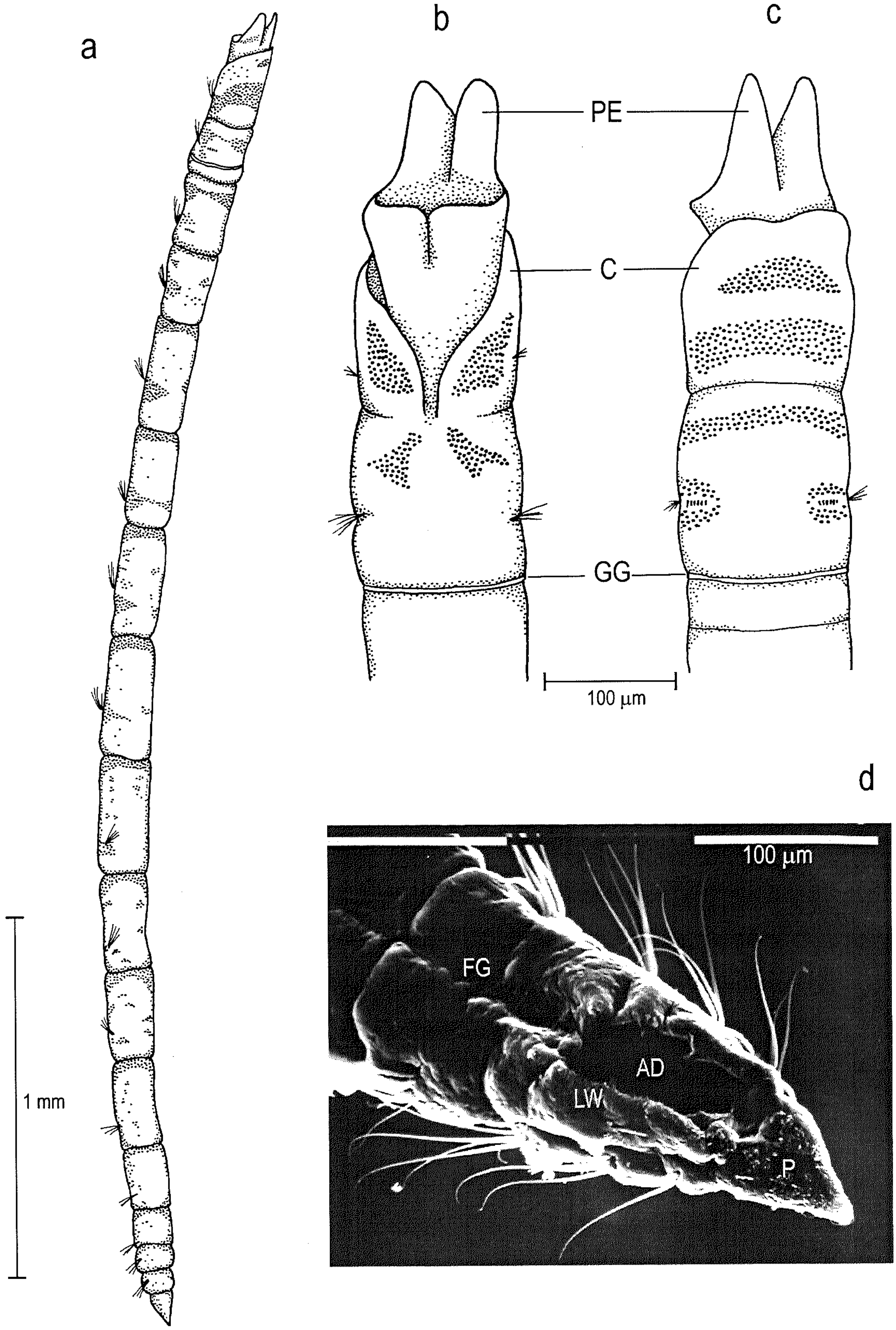


Figure 2.4.2. Euchone x. *External morphology, showing methyl green staining pattern a) whole animal, crown removed, dorso-lateral view, b) dorsal view of anterior, c) ventral view of anterior, c) ventral view of anterior. See Chapter 2.2.3 for key to abbreviations.*

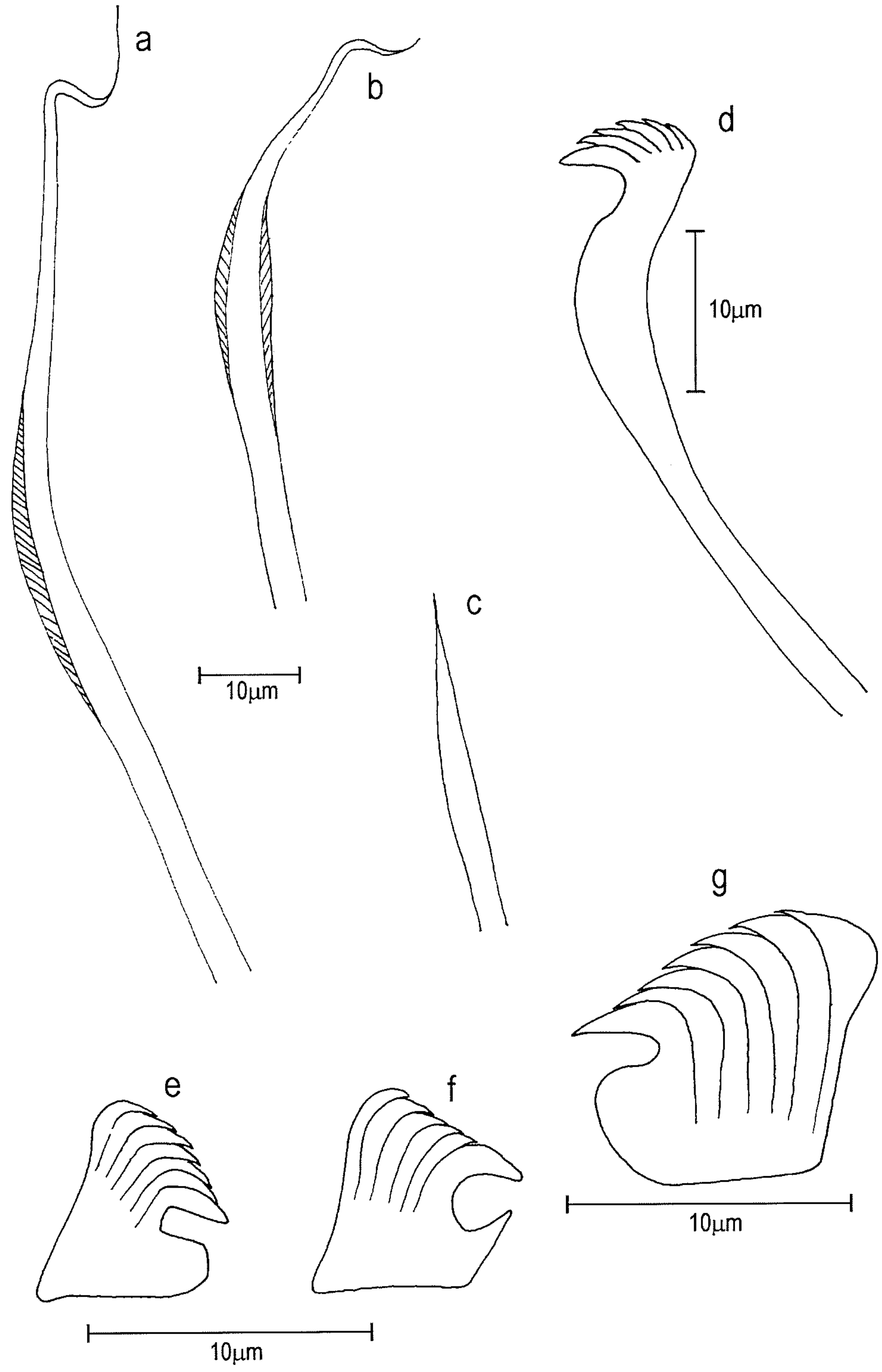


Figure 2.4.3. Euchone x. *Thoracic notochaetae occupying a) anterior superior, b) posterior superior and c) posterior inferior positions in the notopod. d) thoracic neurochaeta (uncinus) from chaetiger 6, from the most dorsal part of the torus. Abdominal notochaetae from e) abdominal segment 1, from most dorsal part of the torus, f) abdominal segment 2, mid-torus and e) depression segment 3, mid-torus.*

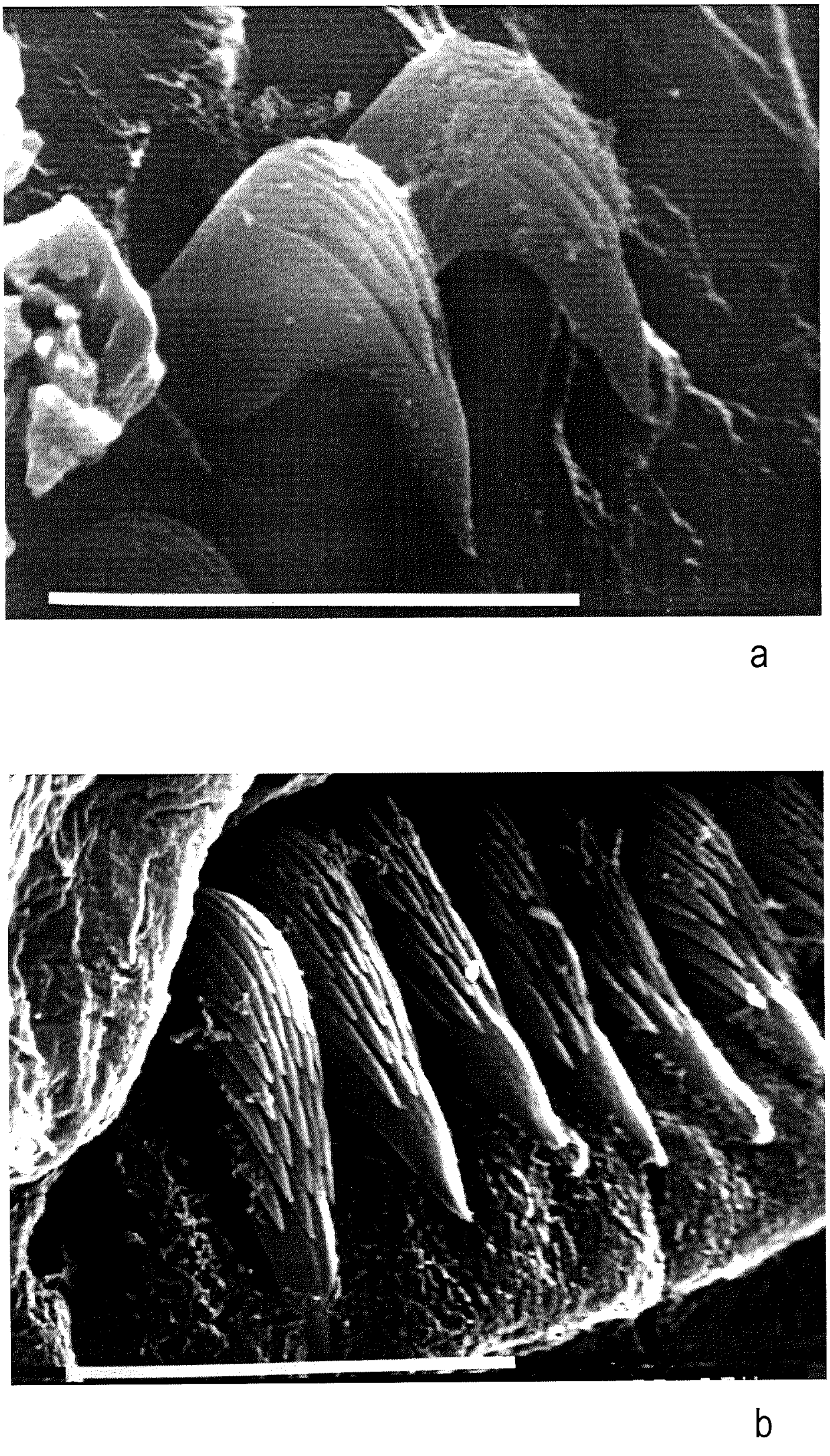


Figure 2.4.4. Euchone x. *Scanning electron micrograph of uncini from a) thoracic chaetiger 2 and b) abdominal chaetiger 2. Both scale bars 10μm.*

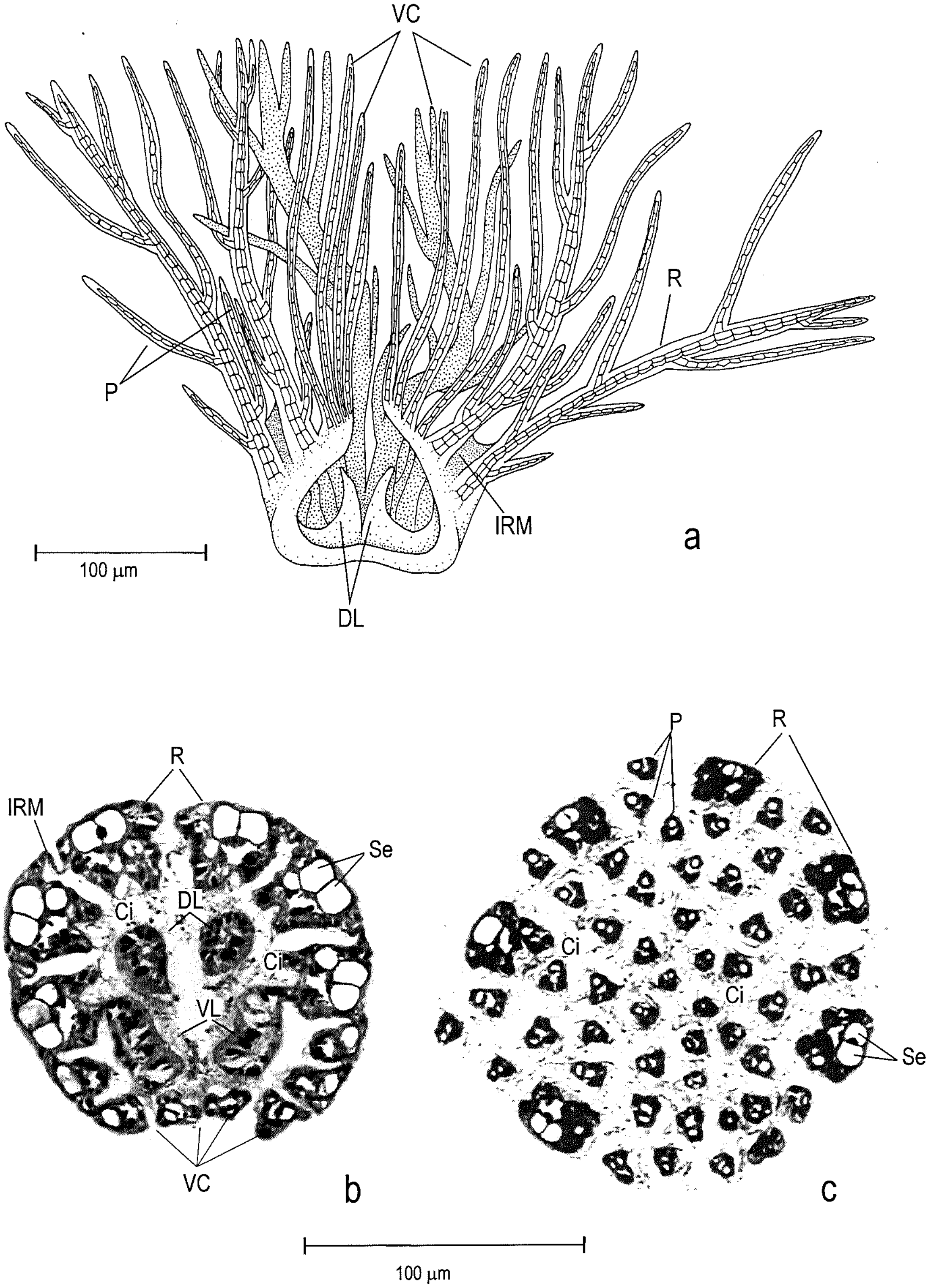


Figure 2.4.5. Euchone x. *a) radiolar crown (detached), with dorsal radioles indicated by stippling. b) transverse histological section of the base of the crown, showing dorsal and ventral lips. c) transverse histological section near the tip of the crown, showing numerous pinnules (compare with Figure 1.2.2). b) and c) photographed using phase-contrast light microscopy. See Chapter 2.2.3 for key to abbreviations.*

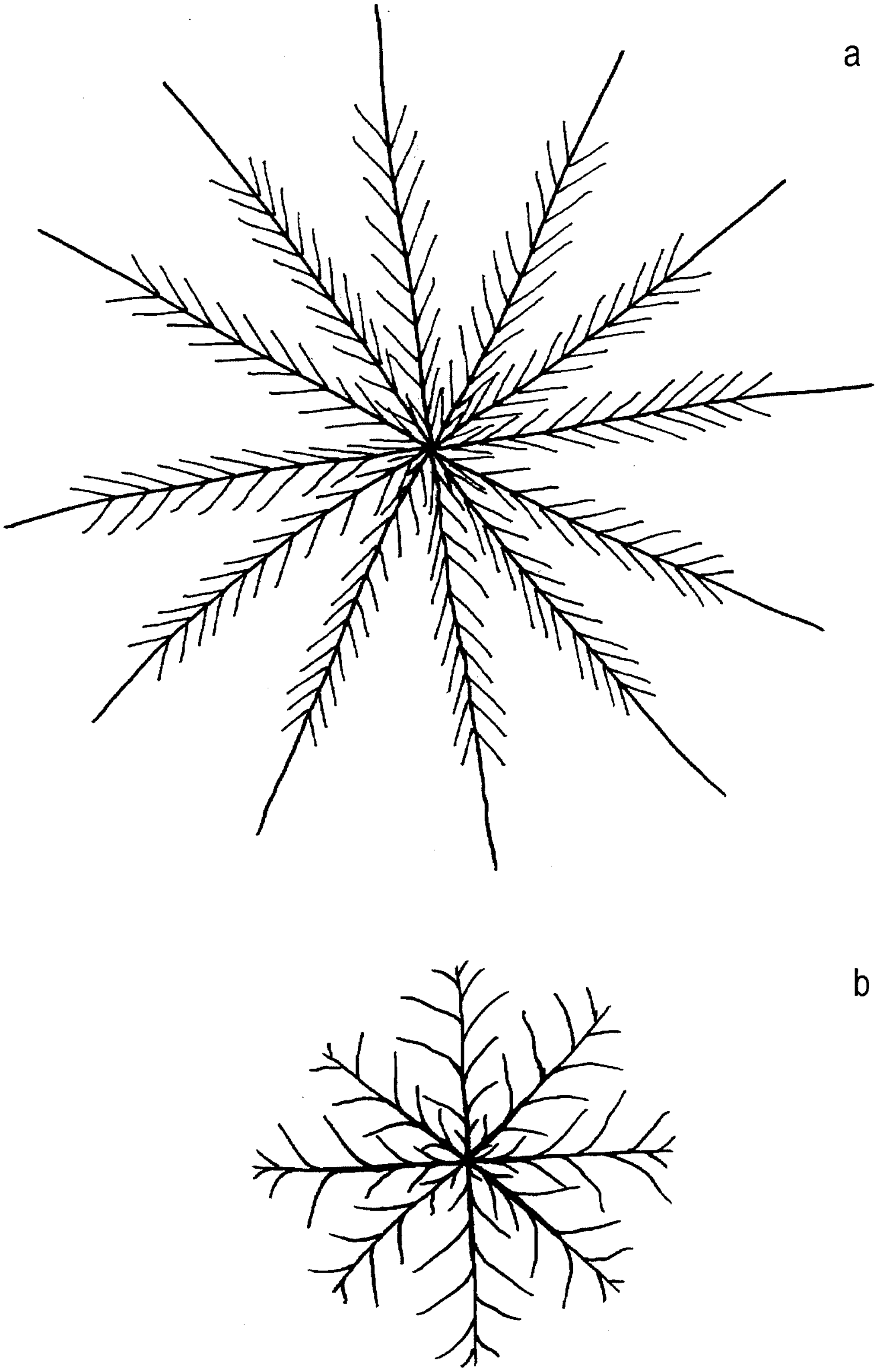


Figure 2.4.6. Schematic illustration of the two main types of sabellid radioles. a) 'feather-like' and b) 'snowflake-like'.

Measurements. Specimens from type locality measuring 3-5 mm in length, including crown and 0.1-0.15 mm in width. Crown approximately 0.4-0.8 mm in length.

Colour. Live animals opaque, with yellow-green gut, depending on contents, clearly visible through the body wall. Preserved animals in alcohol white to pale yellowish.

Tube. Tube of fine mud particles, firmly bound with mucus and closely fitting the occupant. Occasionally adorned with small calcareous orbital Foraminifera, or dark grains. Tube up to six times longer than the occupant, terminating in a mucus trail devoid of adherent sediment particles.

Reproduction. Gonochoric. Females found in May with oocytes in the coelomic cavity extending from thoracic chaetiger five through to abdominal chaetiger four. Oocytes in coelom approximately 40-50 μm in diameter. Reproductive segments each generally contain approximately 7-10 oocytes.

Distribution. Present records from the northern North Sea and the Norwegian Sea, from 59°72'N to 65°52'N and 2°01'E to 7°00'E. Recorded bathymetric distribution, 100-344 m.

Substratum. Found in silty sediments, often with an admixture of fine sand. Patchily distributed, but often in high densities, up to 5 000 individuals per m^2 (Mannvik *et al.* 1996, Pearson *et al.* 1996).

Comments: Based on comparative examination of type material, *Euchone x* bears most resemblance to *Euchone hancocki* and *Euchone incolor*. Table 2.4.1 lists the main distinguishing external features of the three taxa.

Table 2.4.1. Tabular summary of the main distinguishing external features of Euchone x *and the two most closely related Atlantic taxa,* Euchone incolor *Hartman and* Euchone hancocki *Banse.*

Taxon	No. of abdominal segments	Peristomium	Collar	Abdominal girdle	No. of pairs of radioles
E. x	8	greatly exposed all round	much higher ventrally	pre-chaetal on third abdominal segment	3
E. incolor	9	dorsally slightly exposed	slightly higher ventrally	pre-chaetal on third abdominal segment	3
E. hancocki	8	not exposed	roughly even	post-chaetal on first abdominal segment	4

The examined specimens both of *Euchone hancocki* and *Euchone incolor* generally were stouter than *E. x*, with a far lower segmental length:width ratio. There was no sign of elongation in middle segments in the former specimens, although this may be a seasonal phenomenon associated with reproduction. *E. hancocki* has pronounced inter-segmental constrictions along the whole body, which are lacking in *E. x*. Banse (1972) showed that staining with methyl green in *E. hancocki* resulted in most of the body being fairly densely stained, except the glandular girdles, the segmental borders, mid-segmental 'rings' and the faecal groove. The staining was strongest in the entire thoracic pre-chaetal area, and on the second and third chaetigers ventrally. In *E. incolor*, patches of stained cells occurred mainly ventrally and laterally, but their extent and positions varied between sampling locations (Banse 1972). The staining pattern in *E. x* (see Figure 2.4.2) shows bilateral clusters of staining cells dorsally on the first two thoracic chaetigers, as well as anterior and posterior to almost all segmental boundaries. Ventrally, a small crescent-shaped patch of stained cells appeared near the anterior collar margin, as well as around the uncinal tori of anterior chaetigers. In the specimens examined, the anal depression was more clearly visible in *E. hancocki* and *E. incolor* than was generally the case in *E. x*, but the possibility that this may be a function of maturity and preservation of the specimens in question cannot be ignored.

2.4.6 Discussion

It has been suggested that a minimal or reduced crown in the Sabellidae reflects a "discretely motile existence, with a secondary reliance on surface deposit feeding in addition to a moderate filtering capacity" (Fauchald & Jumars 1979). A further discussion on sabellid feeding strategies and mobility is given in Chapter 3. A radiolar crown with only three pairs of radioles occurs in the Fabriciinae *sensu stricto*, as well as among some of the smaller sabellins, such as *Amphicorina*. Because the radiolar crown of *Euchone x* comprises only three pairs of radioles and is relatively short in relation to body length, this supports the hypothesis that the animals are capable of both surface deposit feeding as well as suspension feeding (Chapter 4).

Euchone x is one of the few *Euchone* taxa that have only three pairs of radioles, with pinnules alternating along their length (see Chapter 3.5). The longest pinnules arise from mid-radiole, such that most of the pinnules terminate at approximately the same height distally, as also is the case amongst the Fabriciinae and other sabellins such as *Amphicorina.* This arrangement may allow a maximal filtering capacity, given the small number of radioles. It should be noted, however, that several *Chone* taxa, such as *Chone paucibranchiata* (Krøyer) and *Chone murmanica* Lukash, possess only few pairs of radioles. However, the pinnules in those taxa are paired, rather than alternating along the length of the radioles, and are of a similar length throughout, with the tips extending beyond the pinnules in the typical sabellin arrangement. An intermediate radiolar form exists in *Desdemona* Banse, in which most of the alternating pinnules terminate at the same height distally, although the tips of each radiole are elongated. Interestingly, an unnamed interstitial sabellid with three pairs of radioles and with pinnules terminating at approximately the same height distally, was described as having paired, rather than alternating pinnules (Berrill 1977a).

The radiolar crown of *Euchone x* here is termed 'snowflake-like', in contrast to the more typical 'feather-like' sabellin arrangement (Figure 2.4.6). The latter is reminiscent of the term 'feather-duster polychaetous annelids' coined by Hartman (1951), but here it is considered specifically in the context of radioles with pinnules of approximately equal length from proximal to distal. This differs from the 'snowflake-like' radiolar crown, which is characterised by the longest pinnules being mid-radiole (see also Chapter 1.2.2). It is proposed that this difference in radiolar form merits further attention in sabellid taxonomy. Because differences in crown structure are likely to reflect differences in feeding strategies, this character is considered to be of ecological as well as taxonomic and systematic importance.

The form of the dorsal and ventral lips within the crown also is expected to provide valuable taxonomic and systematic information (Fitzhugh & Rouse *pers. com.*). In addition, it has been suggested that reproductive characters may be useful in revealing the phylogenetic relationships within the Sabellidae (Rouse & Fitzhugh 1994). Banse (1970, 1972) noted the variation in uncinal form between anterior and posterior abdominal segments in many *Euchone* taxa. This variation appears constant regardless of individual size (*pers. ob.*). Future work will further investigate this phenomenon, and it is likely that the feature will be of use in taxonomic descriptions.

Therefore, work currently is in progress to further our understanding of the taxonomy and systematics of *Euchone* and the inter-relationships with *Chone, Jasmineira*, *Amphicorina* and *Desdemona.* Taxonomic inconsistencies will be reviewed, and a more informative set of diagnostic characters will be developed. In particular, emphasis will be placed on the variation in chaetal characteristics between anterior and posterior abdominal segments, and a detailed examination of crown morphology, including pinnule arrangement and the form of the dorsal and ventral lips (Cochrane *in prep.*). Particular attention will be given to taxa with three segments comprising the anal depression and three pairs of 'snowflake-like' radioles. The first stage of this extensive and long-term task is presented in Chapter 3.5.

The discovery of very high densities of *Euchone x* in certain environments perhaps suggests a certain degree of opportunism. A separate behavioural study of the taxon, together with an assessment of niche exploitation, is given in Chapter 4.

2.5 Redescription of *Jasmineira candela* Grube and reinstatement of *Jasmineira oculata* Langerhans

2.5.1 Special thanks

I sincerely thank Phyllis Knight-Jones for discussions on *Jasmineira* and for access to loaned material from the 1933 Uppsala expedition. Wyn Knight-Jones is gratefully acknowledged for translating the original description of *Jasmineira candela.* Both contributed comparative information on certain serpulids. I am grateful to Drs. G. Hartwich & B. Neuhaus, Museum für Naturkunde, Berlin, for loaning the holotype of *Jasmineira candela.* I thank also Fredrik Pleijel and Mme d'Hondt, Muséum National d'Histoire Naturelle, Paris, for lending specimens from the Prince Albert of Monaco expeditions. Akvaplan-niva a/s, Elf Petroleum Norge a/s and Saga Petroleum a/s are acknowledged for use of study specimens. I thank Dr. Peter Wirtz for a SCUBA-diving search for *Jasmineira oculata* in the Azores (unfortunately unsuccessful), and Drs. Nurez and Mari Carmen Brito Castro for lending material from the Canary Islands (unfortunately not containing *J. oculata*). Professor Arturo Ariño kindly sent copies of some less-accessible manuscripts.

2.5.2 Summary

A redescription is given of the holotype of *Jasmineira candela* Grube, 1863, which was re-examined and compared with specimens and records from other areas. Whereas records from Mediterranean waters conform well to the original description, specimens from the North Sea and Norwegian Sea consistently have fewer pairs of radioles, fewer chaetae per segment, a different arrangement of glandular patches, and generally are of a smaller body size. These specimens agree with the original description of *Jasmineira oculata* Langerhans, 1884, which later was assigned as a junior synonym of *Jasmineira candela.* The synonymy is discussed and the name *Jasmineira oculata* is reinstated. Because suitable material is not yet available from the type locality, a name-bearing neotype or neotype series cannot be established at the present time. The need for a revision of *Jasmineira* is outlined and some key areas for future research are proposed.

2.5.3 Introduction

Jasmineira Langerhans, 1880 was diagnosed on the basis of the presence of thoracic uncini with long manubria and the abdominal uncini taking the general sabellin form, which at the time referred to the z-shaped form with a rounded swelling of the breast. Langerhans noted the resemblance of *Jasmineira* to *Dialychone* Claparède, 1868, their main difference being that the abdominal uncini of the latter resemble the terebellid form rather than that of the Sabellinae (Langerhans 1880). At the time it was considered that, together with *Bispira* Krøyer, 1856, *Dasychone* M. Sars, *in* G.O. Sars 1872 and *Laonome* Malmgren, 1866, *Jasmineira* would form an intermediate group between the "*Sabella*" group of taxa (then including *Spirographis* Viviani 1805, *Branchiomma* Kölliker, 1858, *Potamilla* Malmgren, 1866 and *Sabella* L., 1767) and the "*Chone*" group (then including *Euchone* Malmgren, 1866, *Chone* Krøyer, 1856, *Dialychone* Claparède, 1870, *Oria* Quatrefages, 1865, *Fabricia* Blainville 1828, *Leptochone* Claparède, 1870 and *Myxicola* Koch, *in* Renier 1847). Extensive taxonomic and systematic revisions subsequently have taken place among these taxa and further historical information on sabellid systematics is given in Chapter 3.1.

At the time the taxon *Jasmineira* was erected, the most recent systematic works on sabellid polychaetes were those of Malmgren (1866, 1867) and Claparède (1868, 1870). Langerhans followed Claparède (1868) in which he recognised two tribes within the 'Serpeln'; the Sabellidae and the Serpulidae. The diagnostic difference between the two was respectively the lack or presence of a thoracic membrane. Thus, *Jasmineira* was assigned to the Sabellidae.

Subsequent to the division of the family Sabellidae Johnston, 1846 into the sub-families Myxicolinae, Sabellinae and Fabriciinae (Rioja 1923), *Jasmineira* was re-assigned to the sub-family Fabriciinae *sensu* Rioja. The main distinguishing criterion between the two sub-families was the form of the thoracic uncini, which in the Fabriciinae had long, gently curving handles whereas in the Sabellinae these took the avicular form, being z-shaped and with short handles.

The systematic position of *Jasmineira* remained unchanged for the ensuing 65 years. However, the family Sabellidae recently was revised by Fitzhugh (1989), who recognised two natural phylogenetic groups. The diagnosis of the Fabriciinae (*sensu* Fitzhugh 1989) was restricted to include only those taxa with a single cartilaginous axis within the radioles (Fitzhugh 1989) and branchial hearts (Fitzhugh 1991a). The remaining taxa, including *Jasmineira*, were recognised within the Sabellinae.

Perhaps the single most recognisable characteristic of *Jasmineira* is the reduction of the breast of the abdominal uncini to a narrow swelling (Fitzhugh 1989), although a similar state is seen in other taxa, such as *Potamethus* Chamberlin, 1919. Several other characters combine to distinguish the *Jasmineira* from other taxa, but these are not in themselves uniquely diagnostic. The extent to which the taxa currently recognised within *Jasmineira* are consistent with that diagnosis needs evaluating (see remarks in Fitzhugh 1989).

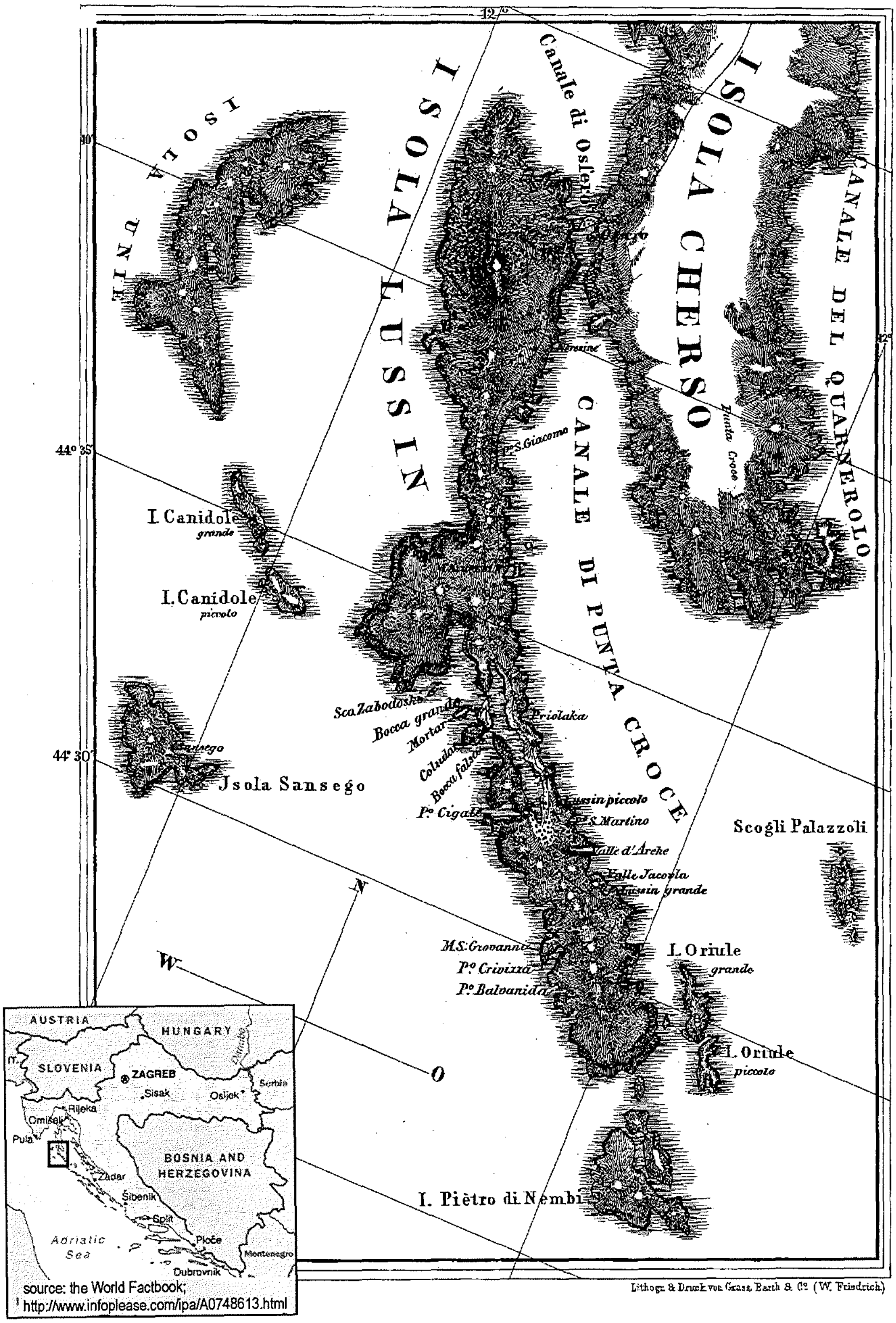
Sabella candela Grube, 1863, was described from the south-western coast of the Croatian island of Lošinj (then known as Lussin) in the northern Adriatic Sea. The specimen is reported as being from Lussin Grande (Grube 1863, see Figure 2.5.1). However, Grube (1864) stated that the specimen was collected off St. Martino, in 25-27 fathoms. Some further detective work is required to trace the exact sampling location, because the names of Lošinj settlements have undergone considerable changes during the last century. For the present purposes, it is sufficient to note that the type locality is off the south-eastern shore of that island.

Sabella candela was later assigned to *Jasmineira candela* by Langerhans (1884). Records of *J. candela* from the Adriatic and Mediterranean Seas, in addition to the type locality, include findings from Naples (Lo Bianco 1893), Istria (Fauvel 1934) and Monaco (Fauvel 1909). In Atlantic waters, *J. candela* is recorded from the Azores (Fauvel 1914), Morocco (Fauvel 1936), around the U.K. (Howson & Picton 1997) and along the Norwegian coast (Brattegard & Holthe 1997), as far north as the counties of Nordland (Holte 1998; Holte *et al.* 1993b), Troms (Cochrane *et al.* 1994) and Stjernsund, northern Finnmark (Berge *et al.* 1993), the latter two located north of the Arctic Circle. The taxon also is recorded from the Skagerak in Baltic waters (Eliason 1962).

Present taxonomic information on *Jasmineira candela* is relatively sparse and the taxon is poorly illustrated in the literature. The original description by Grube (1863) included only a drawing of the tip of two radioli. Later, Langerhans (1884) illustrated two types of thoracic notochaetae, a thoracic neurochaeta (uncinus), the pygidium with a bilateral patch of eyespots as well as a schematic view of the bilobed structure at the tip of one radiole. Langerhans noted that, in life, the two halves of the radiolar appendages usually are folded flat and are easily broken off. Fauvel (1914) illustrated some chaetal types and uncini, which later were reproduced in Fauvel (1927), but, until the present study, no illustrations of the external features of the entire animal are available in the literature.

Also in 1884, Langerhans described *Jasmineira oculata* Langerhans from Madeira, which was similar in form to *Jasmineira candela*, but of a smaller size and with fewer radioles. *J. oculata* was described as having ten pairs of radioles (Langerhans 1884), whereas the crown of *J. candela* comprises 17 pairs of (branchial) radioles (Grube 1863), hereafter simply termed radioles. *J. oculata* later was assigned as a junior synonym of *J. candela* Grube (Fauvel 1927). Therefore, at least amongst records subsequent to 1927, specimens recorded as *J. candela* also may refer to those conforming to *J. oculata.*

As far as can be ascertained, other than the original description by Langerhans (1884) and the synonymy with *Jasmineira candela* (Fauvel 1927), no further attention has been given to *Jasmineira oculata*. No records are known of the taxon, other than the holotype, which apparently is lost. The present study aimed to augment the existing information on *J. candela,* to re-examine the synonymy of *J. oculata* with the former taxon and to indicate areas for further investigation amongst the taxa currently recognised within *Jasmineira*.



source: the World Factbook;
¹ http://www.infoplease.com/ipa/A0748613.html

Lithogr. & Druck von Grass, Barth & Co (W. Friedrich)

Figure 2.5.1. Map showing type locality of Jasmineira candela *(Grube). Main map from Grube (1864), inset as marked.*

2.5.4 Materials and methods

Museum specimens and material from other collections were examined in alcohol. Study specimens conforming to *Jasmineira oculata* were obtained using a 0.1 m^2 van Veen grab, deployed from various survey vessels. These ranged from offshore supply vessels, chartered from Møkster Shipping, where sampling was carried out in the Norwegian sector of the North Sea and Norwegian continental slope on an annual basis between 1989 and 1996, to small local vessels chartered for near-coastal environmental surveys along the Norwegian coast. Specimens retained on 1 mm round-mesh sieves immersed in running sea-water were fixed in 10-15 % borax-buffered formalin in sea-water. The samples were sorted within a few weeks of fixation and further preserved in 70-75 % ethanol. An Olympus SZH zoom dissecting microscope equipped with drawing attachment and x2 objective was used for low-power work. High power observations were made using an Olympus BH2 light microscope, with a x100 oil immersion objective. Specimens for scanning electron microscopy were prepared according to Rouse (1994).

2.5.5 Results

Jasmineira Langerhans, 1880

Jasmineira Langerhans (1880): 113-114.- Langerhans (1884): 270-271.- Fauvel (1927): 330.- Fauvel (1934): 17.- Day (1967): 779.- Hartmann-Schröder (1971): 513.- Fitzhugh (1989): 68-69.- Kirkegaard (1996): 387.- Hartmann-Schröder (1996): 556.

Type species: *Jasmineira caudata* Langerhans, 1880, by monotypy.

Type locality: Madeira

Diagnosis:

Small to medium-sized sabellins with few to numerous pairs of radioles; radiolar skeleton with two rows of cells. Inter-radiolar membrane absent; radiolar flanges present. Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages absent. Ventral lips and parallel lamellae present. Few to many pairs of ventral cirri (*sensu* Krøyer) present. Anterior margin of anterior peristomial ring (hereafter referred to as the peristomium) with narrow, ventral lobe; posterior peristomial ring collar (hereafter named the collar) present. Glandular ridge on chaetiger 2. Chaetiger 1 bearing only elongate narrowly swollen chaetae with a long terminal taper, geniculate at the 'knee' area (often referred to as limbate capillary chaetae, see also Chapter 1.2.5). From chaetiger 2, inferior thoracic notochaetae present in two transverse rows or groups: anterior row(s) of shorter chaetae (also referred to in the literature as limbate capillary chaetae and in need of clarification), posterior row(s) with spatulate or chaetae with broad bilateral swellings. Abdominal fascicles arranged in two transverse rows: anterior row in anterior segments with elongate narrowly swollen chaetae, geniculate at the 'knee' area (often referred to as "limbate capillaries"); posterior row in anterior chaetigers with fine needle-like chaetae (often referred to as "needle-like capillaries"); anterior and posterior rows in posterior chaetigers containing only the latter chaetal type. Thoracic uncini acicular; teeth above main fang of equal size; hood present. Abdominal uncini with main fang surmounted by series of equal-sized teeth; breast reduced to narrow swelling; handles long. Abdominal chaetigers number several to many, depending on the taxon and/or size of the individuals.

Jasmineira candela (Grube, 1863)

Sabella candela: Grube (1863): 60, pl. vi, fig 8.
Jasmineira candela: Langerhans (1884): 270, pl. xvi, fig. 33.- Lo Bianco (1893): 68.- Fauvel (1909): 45.- Fauvel (1914): 319, pl. xxxi, fig. 26-29.- Fauvel (1927): 331, fig. 115a-f.- Fauvel (1927): 331.- Eliason (1962): 287.- Hartmann-Schröder (1971): 513.- Kirkegaard (1996): 387.- Hartmann-Schröder (1996): 556-557.

Original description (translated from Grube 1863; information in original order): Body stout, vermiform, somewhat dorso-ventrally flattened, tapering at either end, whitish, with orange gut showing through the body wall. Breadth of anterior almost 1/9th of the body length (excluding crown). As many as 18 segments[1], mid-body segments largest, approximately twice as broad as long. Pygidium triangular. Large ventral shields. Thoracic ventral shields increasing in length and breadth (down the body), with the first being twice as broad as long and the posterior shields being longer, squarish. Abdominal ventral shields divided (by faecal groove), sub-oval and tumid, distinctly separated from each other, the more anterior shields longer than broad and the more posterior shields much broader than long. Radioles of equal length, contributing 2/5th of the total body length, 17 radioles on each side, arranged in a semicircle, pinnulate, yellow tinged with orange, not interconnected by a membrane. Ends of radioles markedly dilated, greenish-yellow and rust-coloured at their tips, expanded in a leaf-like manner, distally incised at the mid-point, longitudinally folded forming two oblong halves, concave within (Figure 2.5.2.b). Some filaments lacking pinnules, longer than the radioles and in life, moving sinuously. Collar low, composed of an erect membrane, not divided into halves nor lobed. Anus posterior. Chaetae silvery, capillary chaetae projecting furthest, more than 15 per segment in the thorax, barely limbate (i.e. with very narrow borders), less than five per segment in the abdomen, spatulate chaetae[2] absent. Teeth of the uncini[3] short, less conspicuous, inserted into indistinct tori. Boundary between thorax and abdomen between segments 9 and 10.

Length 19 mm (crown 7 mm, body 12 mm), breadth 2 mm (excluding chaetae)
Sampling location: Lussin grande[4], south-east of Lussin Island, now Lošinj, northern Adriatic Sea.

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[1] See note below re-description

[2] referred to as 'paleae' in the original text

[3] tentative translation of *pectines uncinorum*

[4] most likely refers to settlement now known as Veli Lošinj

Notes:

The following additional information is based on notes in German appended to the Latin description in Grube (1863). Only one specimen was studied, which was observed to rapidly cover itself in mucus. Grube noted that prior to the description of *Jasmineira candela* (as *Sabella*), no other "*Sabella* species" (then referring to most sabellin forms) had been described that possessed similar leaf-like expansions on the tips of the radioles. Further, it was stated that the most closely related taxa, *Sabella vesiculosa* was reputed to have vesicles, rather than foliaceous appendages in this position. *Sabella vesiculosa* also lacks the filaments without pinnules, that have a greater mobility than the radioles proper. The author affiliation of *S. vesiculosa* is not stated in the manuscript and, as a result, the taxon to which the name refers is difficult to trace and has not yet been ascertained. Grube further commented that the leaf-like appendages of the present taxon (referring to *Jasmineira candela*) are easily lost and, at the time that he examined the specimen, were no longer present on all radioles.

Further descriptive records of Jasmineira candela *(Grube)*

Langerhans (1884) recorded a single specimen from Madeira and, based on its chaetal armoury that Grube (1863) did not describe in detail, reassigned the taxon to *Jasmineira.* Langerhans' (1884) specimen was smaller than that of Grube (1863), measuring 7 mm and the crown a further 1.3 mm. The specimen was colourless but with brick-red patches, in accordance with the holotype. However, Langerhans observed only 16 pairs of radioles with numerous long pinnules, the ends of which bore oval lobes (Figure 2.5.2k). These were reported as being mostly carried in a collapsed state and easily broken off.

The collar was documented as having one small mid-ventral and two small lateral incisions. The thorax had eight chaetigerous segments, of which the first contained only a dorsal bundle of simple narrowly-edged[5] chaetae. From the second chaetiger, Langerhans noted an additional row of chaetae (Figure 2.5.2g), and yet another row

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[5] Langerhans uses the term "gesäumt", literally meaning seamed or bordered. Refers to the typical narrow elongate chaetae found in the superior part of sabellid notopodia (see Chapter 1.2.5)

Figure 2.5.2h) which he described as being different from ‘usual’ paleate (spatulate) chaetae, albeit resembling these. Long-handled thoracic uncini were present from the second chaetiger (Figure 2.5.2i). The abdomen is documented as having ten chaetigers, bearing ventrally a stout bundle of elongate, “narrowly-edged” chaetae and dorsally a conspicuous row of “sabellin-like” hooks. The pygidium had several eyespots (Figure 2.5.2.j) and the anus was ventral.

A description of an unknown quantity of specimens of *Jasmineira candela* from the Azores (Fauvel 1914) was in agreement with those of Grube (1863) and Langerhans (1884), but the crown was reported as being 5 mm in length, slightly shorter than that of the holotype. The number of radioles present was not reported in detail, merely referred to as being numerous. The thoracic and abdominal uncini and thoracic notochaetae are illustrated in Figure 2.5.2c-f.

In an overview of the Polychaeta in general (relevant to French fauna), Fauvel (1927) reported the presence of two palps in *Jasmineira candela*, here interpreted as dorsal and ventral lips. In addition, the tube, which previously had received little attention in the literature, was described as being membranous, covered in *Posidonia* fibres, shell and Foraminifera debris, although this is expected to vary according to sampling location. Subsequent to this, records of specimens from Rovignio, Istria were described as having 16-17 pairs of radioles (Fauvel 1934) and appeared to lack the characteristic foliaceous radiolar appendages, which was attributed to their fragile nature. Some slight variations in the form of the collar and pygidial eyespots also were reported. Fauvel (1936) further reported findings of *Jasmineira candela* from Morocco, some of which possessed the foliaceous appendages at the tips of the radioles. In common with the previous study, these were documented as having 16-17 pairs of radioles and pygidial eyespots.

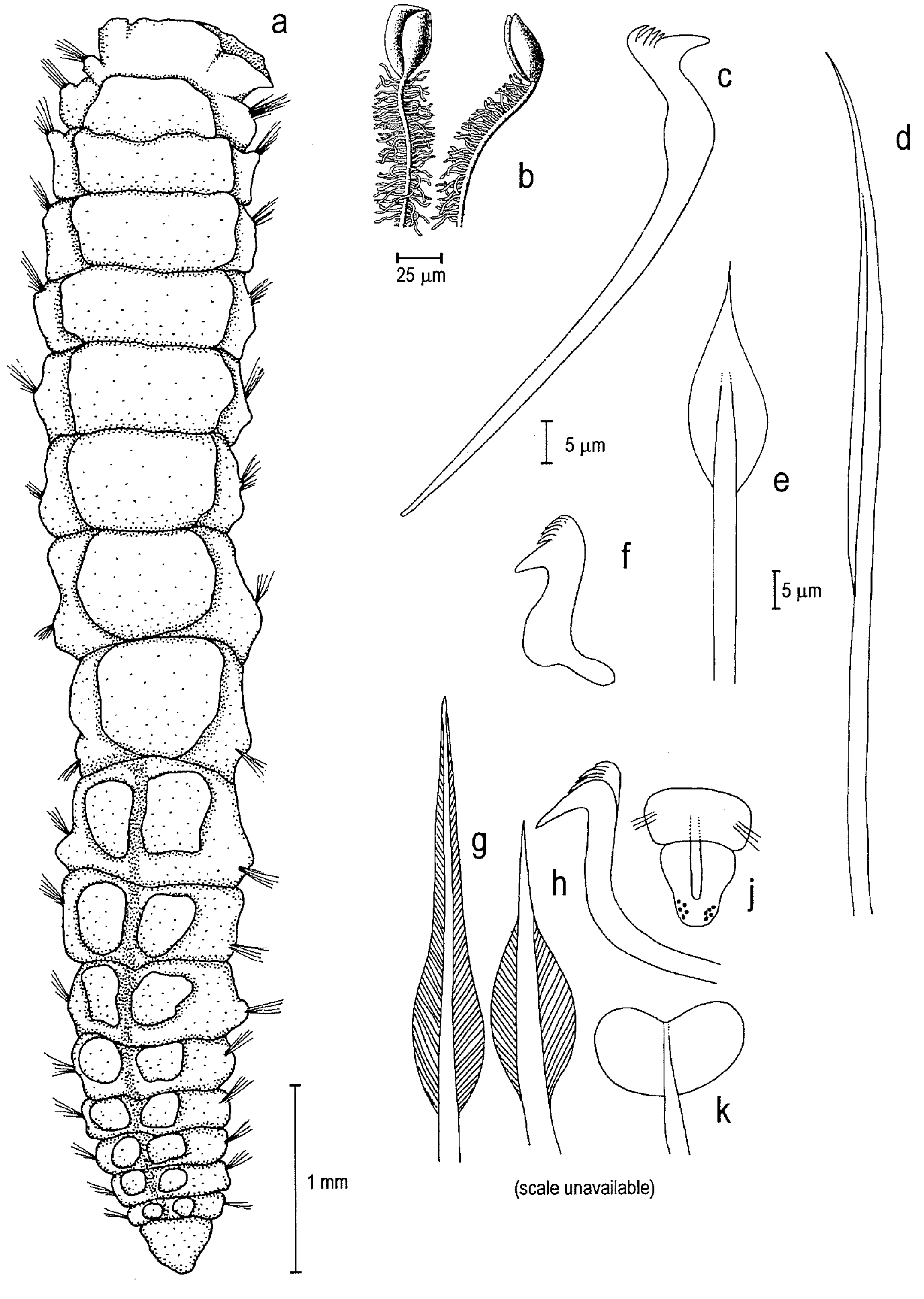

Figure 2.5.2. Jasmineira candela *Grube: external anatomical features. a) ventral view, excluding crown, b) tip of two radioles, c) thoracic uncinus, d) superior thoracic notochaeta, e) inferior thoracic notochaeta, f) abdominal uncinus, g) superior thoracic notochaeta, h) inferior thoracic notochaeta, i) thoracic uncinus, j) pygidium showing eyespots and k) tip of radiole. Illustrations a) holotype (original drawing), b) from Grube (1863), c) and d) from Fauvel (1914), e) and f) redrawn from Fauvel (1914), g) - k) redrawn from Langerhans (1884).*

Redescription of the holotype:

Diagnosis:

Ten abdominal segments, nine of which are chaetigerous, 17-18 pairs of radioli. Bilobed cup-shaped subterminal radiolar appendages. Abdominal uncini with a swollen breast and short handle, up to 21 per torus.

Redescription

Figure 2.5.2a depicts a ventral view of the holotype of *Jasmineira candela*, without crown. Specimen approximately 11.5 mm in length, excluding crown (some shrinkage of the specimen may have occurred because Grube (1863) recorded it as being 12 mm in length). The crown measured just over 5 mm; discrepancy between this and the original record of 7 mm attributed to the corkscrew-like coiling of the radioles, which were not stretched to their full length in case of damage. Alternatively, the original measurements may have been carried out on the live specimen, explaining the difference. Bilobed structures visible on several of the radiole tips, corresponding in shape to those illustrated in Figure 2.5.2b, not redrawn. Distal filamentous tip (as in *Jasmineira oculata*, see below) not observed, but its presence is not precluded. Seventeen radioles on each half of the crown, bearing numerous paired pinnules of equal length along the radiole. Inter-radiolar (palmate) membrane absent. Five pairs of ventral cirri (short, pinnule-free filaments). Excessive handling of radiolar crown was avoided, but dorsal lips appear to be elongate, ventral lips more difficult to discern, but apparently shorter. Collar low, intact ventrally, with a slight lateral fold or notch, which may or may not be a preservation artefact (see Chapter 1.3.3). Collar margins attached to the anterior peristomium, leaving narrow dorsal gap. Glandular girdle not observed on the second thoracic chaetiger, nor elsewhere. Faecal groove very indistinct in thorax, more prominent in the abdomen. Ventral glandular shields differentiated, projecting as prominent mounds, squarish in the thorax and first abdominal chaetiger; from abdominal chaetiger 2, divided by faecal groove, rounded, wart-like[6], two per chaetiger.

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[6] Reminiscent of *Euchone papillosa* (Sars)

Thoracic notochaetae present in prominent bundles. Chaetiger 1 containing elongate chaetae, narrowly swollen, slightly geniculate at the 'knee area' and with a long terminal taper, approximately 7 to 8 per fascicle. An additional row of six to seven short narrow chaetae present, without swelling. From chaetiger 2, around seven elongate superior chaetae with narrow swellings and geniculate at the knee area, with long terminal tapers (see Figure 1.2.11b). An additional row of shorter, broad chaetae, with bilateral swellings and long terminal tapers (see Figure 1.2.11f), approximately five per fascicle in mid-thoracic segments. Thoracic neurochaetae present from chaetiger 2, long-handled, acicular, with approximately five rows of teeth above the main fang (see Figure 2.5.2c, h), eight to nine per chaetiger.

In first abdominal chaetiger, seven to eight superior notochaetae similar in form to superior thoracic notochaetae, in addition to a row of six to seven short needle-like chaetae, without swellings. From mid-abdomen, only superior elongate chaetae present, these all long, needle-like forms lacking swelling or geniculate bend, seven to eight per fascicle, possibly one or two more in posterior segments. Uncini not examined.[7]

Note:

The sole specimen examined by Grube (the holotype) has eight thoracic chaetigers and nine abdominal chaetigers anterior to the pygidium (see Figure 2.5.2a). Therefore, it must be concluded that Grube included the pygidium in the total number of segments. However, Langerhans (1884) recorded the presence of ten abdominal chaetigers in a specimen from Madeira. Fauvel (1927) referred to *Jasmineira candela* as having 17-18 chaetigers, eight of which are thoracic, implying that both nine and ten chaetiger-forms were examined by that author. Other records of *J. candela* (Fauvel 1914, 1934, 1936) did not include the numbers of segments/chaetigers

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[7] Abdominal notochaetae were not removed, despite permission to do so, because the specimen examined is the only type specimen of *J. candela* currently in existence, the body of which is remarkably intact, although very soft. Perforation of the body wall during removal of uncini is expected to cause rupture and undue disintegration of the specimen. Thus, only the emergent parts of the uncini were examined. The rounded breast was clearly visible, in accordance with the illustrations of Langerhans (1884) and Fauvel (1914), up to 21 per torus).

present. Attempts to locate and examine some of Fauvel's material, and other specimens, are in progress and it is hoped thereby to investigate the extent of variation in the numbers of abdominal chaetigers present in the taxon. In so doing, the slight possibility may be eliminated that the variation reported in the literature is in fact due to a misunderstanding between documented total number of segments, as opposed to chaetigers.

Only a few of the cup-shaped appendages were clearly visible on the radioles of the holotype. This in agreement with Grube's (1863) comment that these are easily broken off and that in his specimen (the holotype), not all the radioles possessed the structures. From the holotype, it was not possible to determine conclusively whether or not there was a filiform tip extending beyond the structures. Figure 2.5.3 shows the appearance of the distal ends of two radioles where the bilobed appendages are broken off.

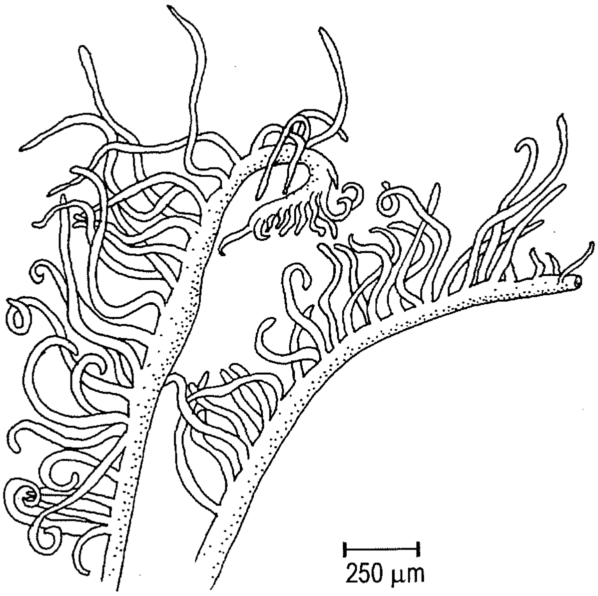

Figure 2.5.3.
Jasmineira candela *Grube. Tips of two radioles where the distal appendages are lost. Specimen from the 1933 Uppsala Expedition to the Skagerak (Eliason 1962).*

Material examined

Holotype (Grube 1863), from "Lussin Grande" (may now be Veli Lošinj), south-east Lošinj (i.e. Lussin in Grube). Lot number Q5208, Museum für Naturkunde, der Humboldt-Universität zu Berlin, Germany.

Approximately six specimens from Eliason (1962), collected 1933, Uppsala Expedition, Skagerak, Station 23. Examined while on loan to Phyllis Knight Jones.

Jasmineira oculata Langerhans, 1884

Jasmineira oculata Langerhans.– Langerhans (1884): 270, Taf. XVI, Fig. 34a-e.
Jasmineira candela Grube.– Fauvel (1927): 331 (*non* Grube).

Description (translated from Langerhans 1884):
A small animal of barely 0.5 cm in length, colourless. Ten pairs of radioli, reddish in colour and without a membrane. Collar with dorsal incision, otherwise entire. A patch of eyespots on either side of the head (i.e. collar segment). The first chaetiger bears an otocyst on either side, containing a round otolith. Thorax with eight segments, the first bearing only a dorsal bundle of chaetae with narrow wings (Figure 2.5.4a). The remaining thoracic chaetigers bear in addition, shorter chaetae with broader swellings (Figures 2.5.4b, c)[8]. In dorsal view, these resemble the chaetae depicted for *Jasmineira candela*[9]. Ventrally, a row of long-handled hooks (i.e. acicular uncini, Figure 2.5.4d) also is present. Abdomen with nine chaetigerous segments, bearing ventrally a prominent bundle of elongate, narrowly-edged[10] chaetae and short hooks dorsally (Figure 2.5.4e). Pygidium with two eyespots (Figure 2.5.4f).

Note: Langerhans (1884) further commented that the specimen merely may be a juvenile form of *J. candela* because the chaetal types appear to correspond perfectly. In that case, according to Langerhans, the radiolar appendages would have been lost and the pygidium was at an immature stage.

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[8] Langerhans (1884) did not name the short broad chaetae, merely referring the reader to Figures 34b and c in the manuscript.

[9] Referred to as Figures 33b and c in Langerhans (1884).

[10] Langerhans uses the term "gesäumt", literally meaning 'seamed' or 'edged'. Refers to the typical narrow elongate chaetae found in the superior part of sabellid notopodia (see Chapter 1.2.5)

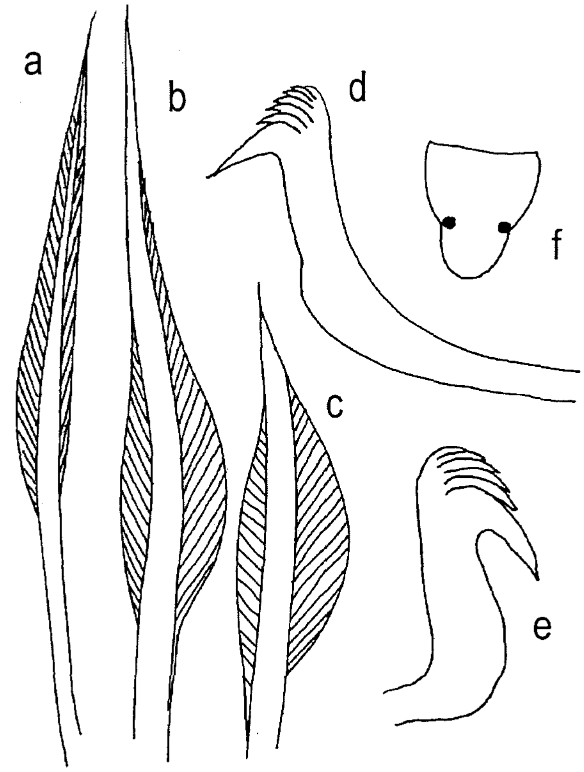

Figure 2.5.4. Jasmineira oculata *Langerhans; a), b) and c) types of thoracic notochaetae, d) thoracic uncinus, e) abdominal uncinus and f) pygidium with eyespots. Redrawn from Langerhans (1884). Scale unavailable.*

Description of specimens from the North Sea and Norwegian Sea, conforming to Jasmineira oculata Langerhans:

Diagnosis: Nine abdominal chaetigers. Ten pairs of radioli with bilobed concave foliaceous subterminal radiolar appendages. Abdominal uncini with a swollen breast and short handle, six to eight per torus.

Description: Body measuring usually 2-3 mm, excluding crown, largest specimens up to 4 mm. Crown usually between 1.5 and 2.5 mm in length. Eight thoracic and nine abdominal chaetigers (Figure 2.5.5a). Dorsal and lateral views of the anterior are shown in Figure 2.5.6. Glandular ventral shields differentiated in thorax, although not protruding as mounds as in *Jasmineira candela*; mostly visible by staining with methyl green (Hofsommer 1913); in anterior segments divided mid-segment, forming an anterior and posterior patch. Glandular shields not differentiated in abdomen.

Radiolar crown consisting of two dorsally fused lobes. Dorsal and ventral lips present (Figure 2.5.5d). Usually ten pairs of radioles each bearing approximately 30 pairs of long pinnules of approximately equal length and at least two pairs of ventral cirri (*sensu* Krøyer). Double-celled radiolar skeleton in main axis, a single skeleton in the pinnules and ventral cirri. Inter-radiolar (palmate) membrane and lateral radiolar flanges absent, leaving radioli free to the base of the crown. A bilobed foliaceous appendage present near the proximal tip of each radiole (Figures 2.5.5b, c and 2.5.8a, b), easily broken off, granular in appearance under high-power light microscopy. Short filiform radiolar tip extending beyond those structures.

Collar of posterior peristomial ring origin, intact ventrally. Collar margins attached dorsally to anterior peristomium, folds meeting dorsally when specimen preserved in tube, may be narrow dorsal gap when preserved out of the tube (see Chapter 1.3.3) Well developed collar both dorsally and ventrally, often anteriorly flared. Collar extending above and almost entirely covering the radiolar bases, very slightly higher ventrally than dorsally. The anterior part of the peristomium extends ventrally as a small ciliated triangular projection (Figure 2.5.7). Also a patch of cilia ventrally, near the anterior collar margin.

Chaetiger 1 containing only elongate, finely tapering chaetae, approximately ten per fascicle, anterior row slightly shorter than posterior row. Three types of thoracic notochaetae from chaetiger 2. Superior thoracic notochaetae elongate, tapering to a fine point, five to six per fascicle (Fig. 2.5.9a, b). Inferior anterior row short, narrow, finely tapering chaetae, four to five per fascicle (Fig 2.5.9d). Inferior posterior chaetae short, broad (Fig. 2.5.9c). Thoracic neuropodial uncini long handled (acicular), with at least three rows of smaller teeth above the main fang, usually four to five per torus. Abdominal neurochaetae narrow, longer than thoracic notochaetae, five to six per fascicle. This corresponds to Langerhans' (1884) description of the abdominal neurochaetae in *Jasmineira oculata* as being present in prominent bundles. Abdominal uncini with five to six rows of smaller teeth above the main fang, a rounded breast and a short basal handle (Figure 2.5.9e, f), six to eight per fascicle.

Intersegmental boundaries markedly constricted, particularly in the abdomen. Faecal groove in abdomen deep and very prominent. Faecal groove in thorax poorly defined, in some specimens only apparent as a broad ciliary tract without notable groove. Pygidium triangular, without appendages. Tube loosely constructed of irregular sand particles bound to mucus lining.

Material examined

Northern North Sea, between 100 and 350 m depth in silt-clay dominated sediments (co-ordinates given as petroleum field centre, or average sampling position, because an extensive network of stations were sampled and revisited at each field):
Heimdal, 59°60'N, 2°23'E, Elf Petroleum Norge a/s, approx. 165 specimens, Frøy, 59°74'N, 2°59'E, Elf Petroleum Norge a/s, approx. 120 specimens, Øst Frigg, Elf Petroleum Norge a/s, 59°87'N, 2°40'E, 25 specimens, Snorre, 61°30'N, 2°10'E Saga Petroleum, 285 specimens. Distribution records of these and other finds of the taxon are given in Akvaplan-niva reports from 1992 to 1998, recorded as "Fabriciinae A" or, latterly, as *Jasmineira candela.*

Norwegian Sea:

Smøla kommune, 63°18.50' - 63°28.89'N, 7°49.26 - 8°03.44'E, in sand-dominated sediments between 30-40 m depth, 50 specimens (recorded as "Fabriciinae A" in Larsen & Bahr, 1993). Holandsfjord, 66°45'N, 13°25'E, from silt-clay sediments at 177 m depth, 11 specimens (recorded as *Jasmineira candela* in Holte, 1998, st. 4). Stjernsundet, Finnmark, northern Norway 70°15.38'N, 22°35.42'E, silt-clay sediment, one specimen (recorded as "Fabriciinae A" in Berge *et al.*, 1993).
Study specimens from the North Sea and Norwegian Sea are pending deposition at Tromsø Museum, University of Tromsø, Norway (TNU), The Natural History Museum, London (BMNH) and the Zoological Museum, Copenhagen (ZMC).

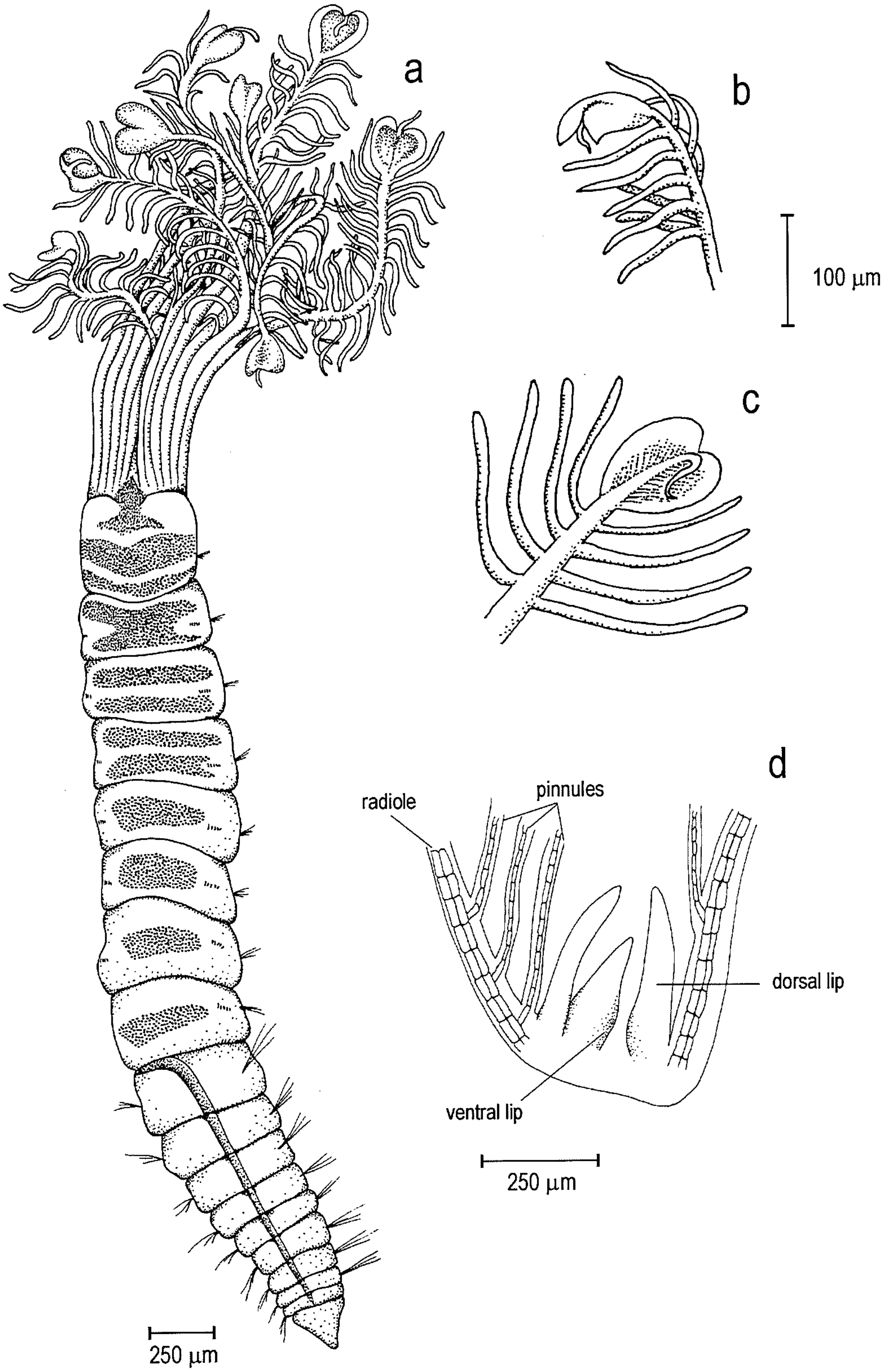

Figure 2.5.5. Jasmineira oculata *Langerhans, a) whole animal, ventral view, b), c) detail of radiolar tips, d) semi-schematic diagram of crown interior (right half) showing dorsal and ventral lips. Dark stippling indicates stained glandular areas. Study specimen from the northern North Sea, code pending.*

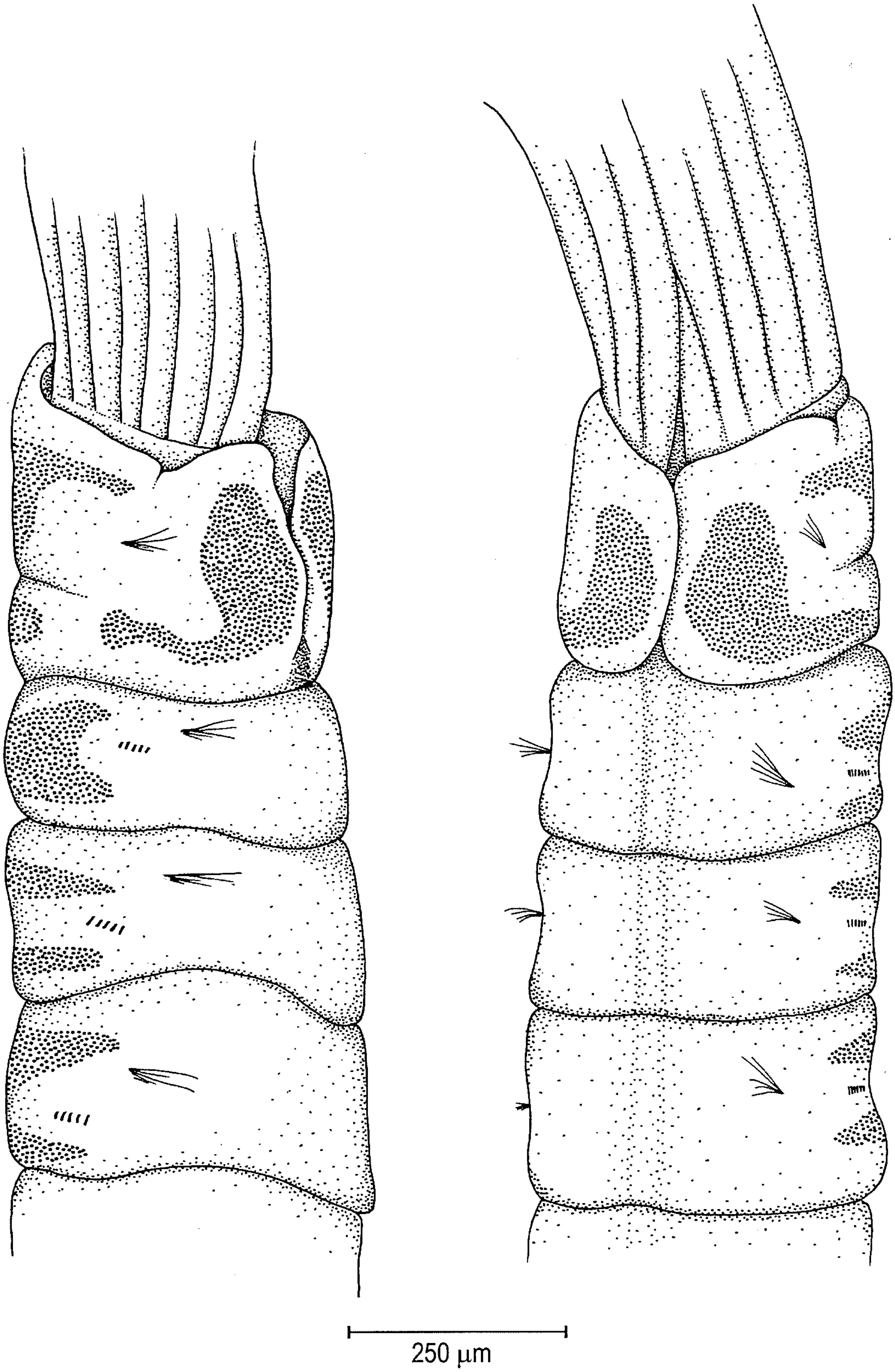

Figure 2.5.6. Jasmineira oculata *Langerhans. a) lateral view and b) dorsal view of anterior. Dark stippling indicates stained glandular regions.*

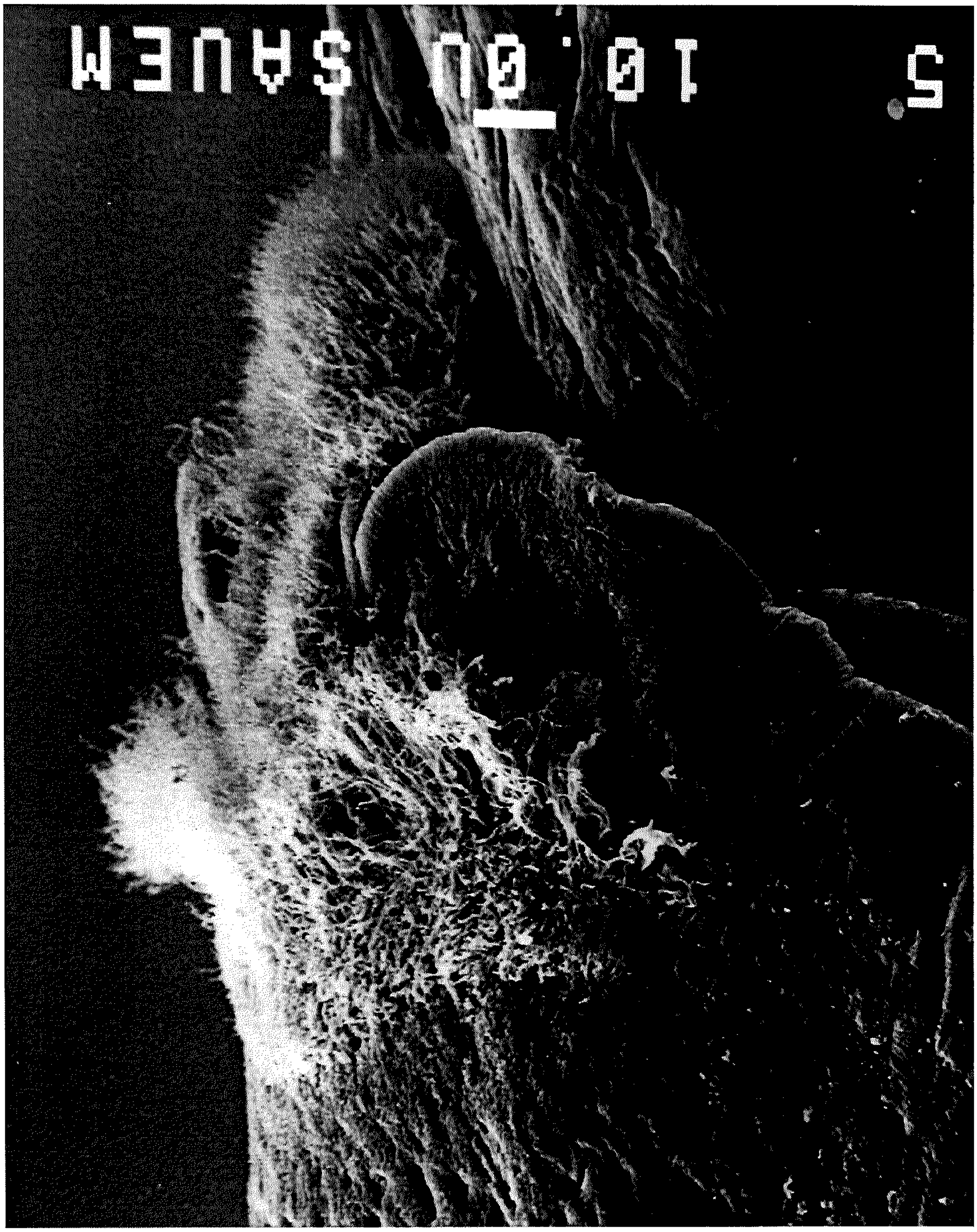

Figure 2.5.7. Jasmineira oculata *Langerhans, scanning electron micrograph: ventro-lateral view of anterior, showing ciliated triangular extension of the anterior peristomial ring. Study specimen from northern Norwegian Sea (on SEM stub).*

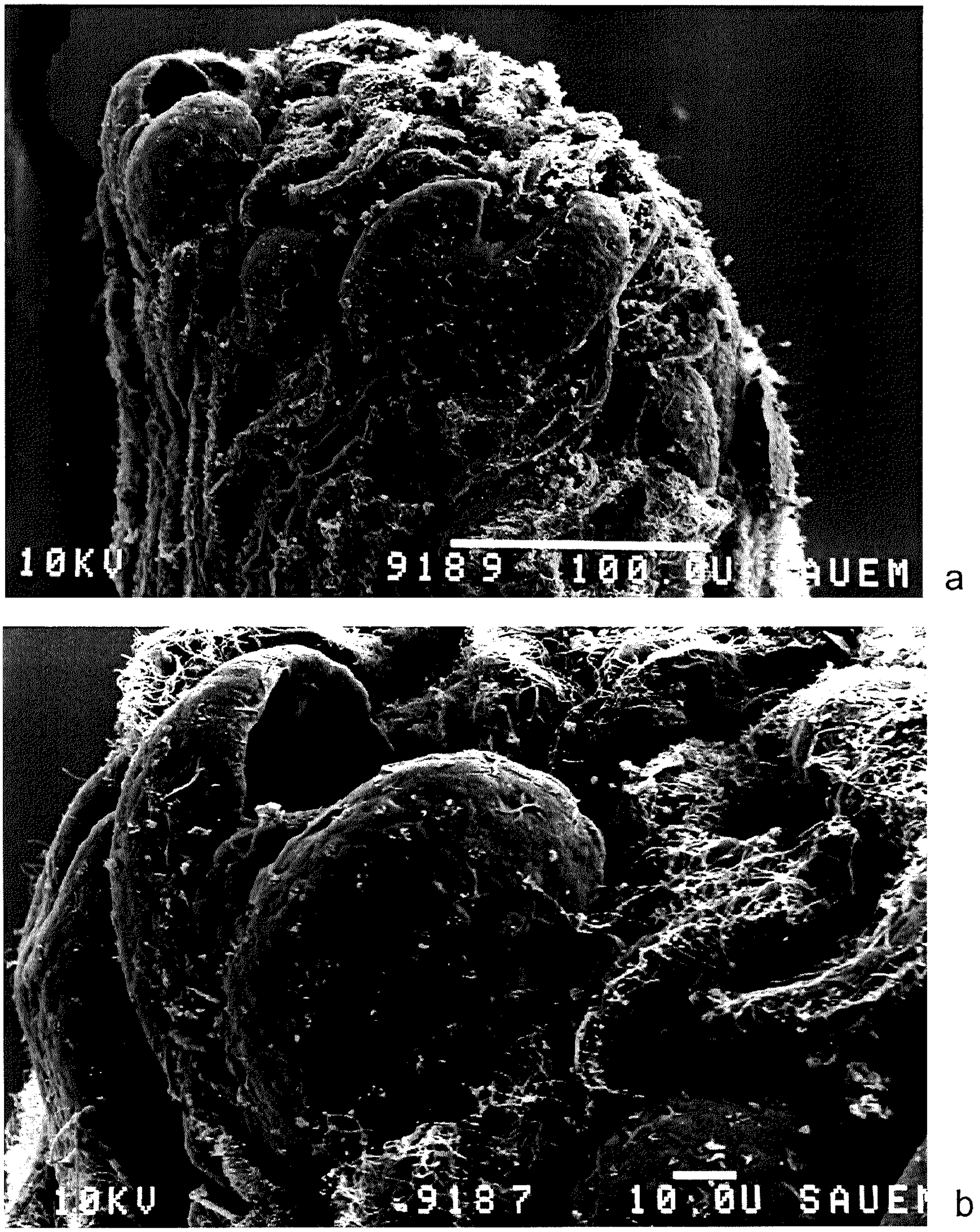

Figure 2.5.8. Jasmineira oculata *Langerhans, scanning electron micrograph of a) distal portion of radiolar crown, showing the foliaceous appendages near the tips of the radioles and b) detail of radiolar tip. Specimen as for Figure 2.5.7.*

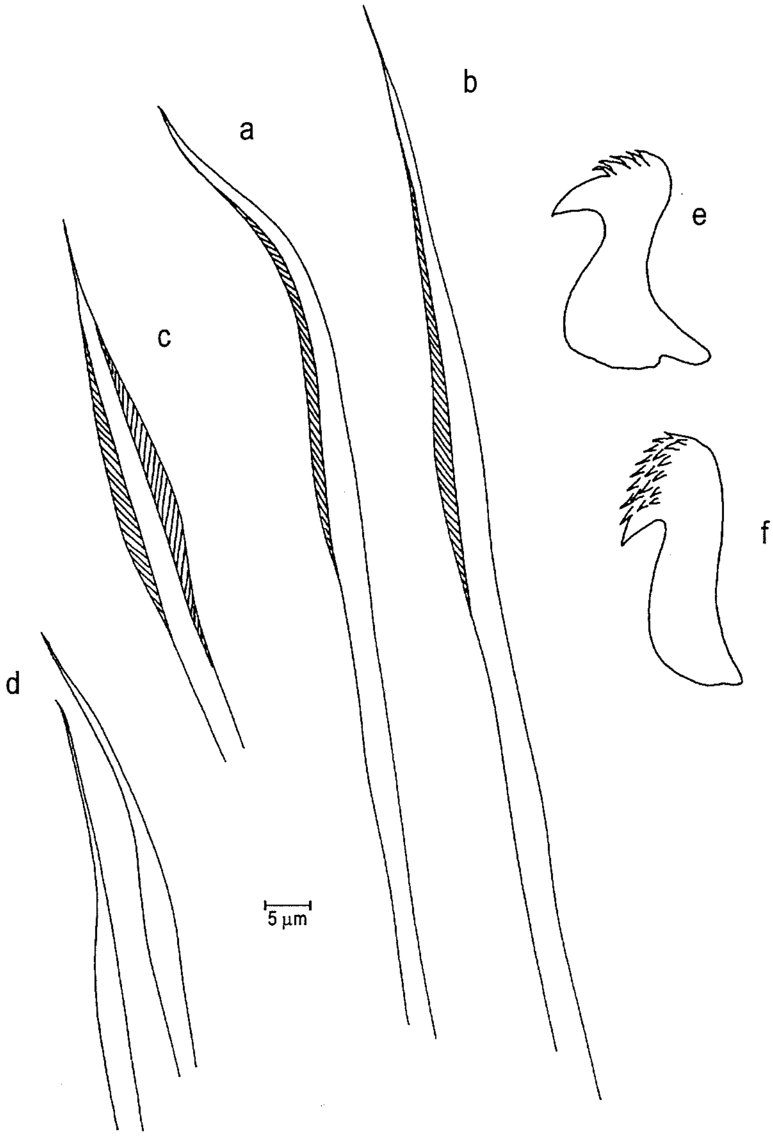

Figure 2.5.9. Jasmineira oculata *Langerhans a) and b) superior thoracic notochaetae, c) inferior posterior notochaetae, d) inferior anterior notochaetae, e) uncinus from abdominal segment 2 and f) same, oblique view.*

Distinguishing characteristics

Jasmineira candela and *Jasmineira oculata* share a number of characteristics, the combination of which enables them to be distinguished readily from other sabellin taxa commonly found in deep-water soft-bottom sediments. These are summarised as follows:

- lack of glandular girdle on the second thoracic chaetiger;
- two types of thoracic notochaetae; superior narrow elongate chaetae and inferior short and broad (as opposed to the additional presence of 'bayonet' chaetae in *Chone* and *Euchone*);
- abdominal uncini with a rounded breast and short posterior handle (as opposed to the 'square' type typical of *Chone* and *Euchone*);
- radioles with foliaceous distal or sub-distal appendages (in the Sabellidae, unique to these two taxa)
- a constant nine abdominal chaetigers[11]
- indistinct faecal groove in thorax
- marked constriction at inter-segmental boundaries, particularly in abdomen
- radioles not easily severed at their bases (as opposed to the case in several other *Jasmineira* taxa, where the peristomium projects well above the anterior collar margins and the radioles readily break off at their bases, leaving a characteristic 'stump').
- body generally of stout appearance

Although *Jasmineira candela* and *Jasmineira oculata* are relatively similar in form, a number of characteristics readily distinguish the two taxa. The crown in *J. candela* has 16-17 pairs of radioles, as opposed to the ten in *J. oculata*. In *J. candela*, the ventral glandular shields are prominently differentiated and elevated from the body. This is in contrast to *J. oculata*, where the shields are less prominent and restricted to

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[11] possibility for 10 abdominal chaetigers in *Jasmineira candela*, see comments above

the ventral surface of the thorax. In addition, *J. candela* possesses a greater number of abdominal uncini per torus than is the case in *J. oculata.* An overview of the main distinguishing characteristics between the two taxa is given in Table 2.5.1.

Table 2.5.1. Main distinguishing characteristics between Jasmineira candela *Grube and* Jasmineira oculata *Langerhans.*

Character	*Jasmineira candela*	*Jasmineira oculata*
number of radioles	17-18	10
ventral shields: thorax	prominent, elevated, squarish, one patch per chaetiger	generally not elevated, requiring stain to discern form, in anterior chaetigers, divided into discrete anterior and posterior patches
ventral shields: abdomen	rounded, wart-like, separated by faecal groove	not differentiated
number of abdominal neurochaetae (uncini) per torus	approximately 21	6-10
abdominal neurochaetae*	approximately similar length down body	longest in posterior segments

* character used informally, for recognition rather than formal diagnosis

2.5.6 Discussion

The synonymy refuted

Given the original author's doubts as to the maturity of the holotype of *Jasmineira oculata* (Langerhans 1884), and the fact that only one specimen was available, the synonymy by Fauvel (1927) of *J. oculata* with *Jasmineira candela* was, perhaps, justified.

If it were the case that *Jasmineira oculata* was a juvenile form of *J. candela,* it would be expected that there would be a certain amount of variation in the distinguishing characteristics within a given population. However, this was not observed in the material examined during the present study. These observations would support Langerhans' description of *J. oculata* as a discrete taxon in its own right.

Without suitable material from within a reasonable distance of the type locality with which to erect a neotype series, a proper redescription of *Jasmineira oculata* Langerhans is not possible. Also, without neotype material to 'fix' the taxon name, a revision of the systematic status of this taxon with respect to *Jasmineira* in its present form is inadvisable, because it carries a risk of future confusion. However, continuing to use the name of a senior synonym to refer to an apparently discrete taxon also perpetuates ambiguity in the literature, with or without a type series. In the light of the recent discovery of a large amount of material conforming to *J. oculata*, it is clear that the most appropriate action is to make a discrete taxon name available for the specimens. Therefore, the synonymy is here refuted[12]. Until evidence appears to the contrary, the specimens described in the present study that conform to *Jasmineira oculata* Langerhans are identified as such for the present purposes, despite the absence of type material.

An alternative approach would be to declare the name *Jasmineira oculata* as a *nomen dubium*, in view of the lack of type material and the sparse original description. In this case, the specimens documented in the present study would be described as a new taxon. If at some point in the future, new evidence of *Jasmineira oculata* appears, the new taxon can be synonymised as appropriate. A similar problem recently arose within *Lumbrineris* Blainville. Two taxa have been described from Arctic areas, but in both cases, the descriptions are sparse and the type material is lost. It was not possible to determine if specimens found in these areas belonged to either of the taxa and, to avoid ambiguity, these were described as *Lumbrineris mixochaeta* new taxon (Oug 1989). The issue will be addressed further before the present work is submitted for formal publication.

Because only a single specimen of *Jasmineira oculata* is known, which was described as possibly having lost the tips of its radioles (Langerhans 1884) and

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[12] Because a synonomy is not a formal action, merely reflecting the opinion of the author concerned, it may be refuted at any time, according to subsequent opinion. The term 'reinstated' is here used as such.

subsequently is assumed lost, it is impossible to know for certain whether the original *J. oculata* did or did not possess radioles with terminal or sub-terminal foliaceous appendages. However, based on the specimens from the North Sea and Norwegian Sea, the present deduction must be that also the original *Jasmineira oculata* specimen possessed sub-terminal foliaceous radiolar appendages similar to those of *Jasmineira candela.*

Shared 'atypical' characteristics

It is interesting that *Jasmineira candela* and *Jasmineira oculata* share a number of characteristics strikingly atypical of the remaining taxa within *Jasmineira.* These include 1) lack of a post-chaetal glandular girdle on the second thoracic chaetiger, 2) presence of distal or sub-distal radiolar appendages, 3) abdominal uncini with a rounded, rather than narrow, breast, 4) a fixed, rather than ontogenetically increasing, number of abdominal segments, 5) an indistinct thoracic faecal groove and 6) radioles with their bases almost covered by the collar and not easily severed (see Chapter 3.6.6 under "crown characters".

Of these characteristics, the lack of a glandular girdle on chaetiger 2 is the most interesting, from a taxonomic and systematic point of view. First, the feature is included as a diagnostic character of *Jasmineira.* Second, the presence of the thoracic glandular girdle is common to all taxa referred to as part IIa of the cladogram in Fitzhugh (1989) comprising *Desdemona* Banse, *Amphicorina* Quatrefages (then *Oriopsis* Caullery and Mesnil), *Chone*, *Euchone*, *Jasmineira*, *Panousea* Amoureux, *Fabrisabella* Hartman, *Myxicola* and *Potamethus.* Within this group of taxa the presence of transitional, or overlapping, character states, or combinations of characters, is not unusual. For example, within *Euchone* certain taxa share chaetal characteristics with *Amphicorina.* Similarly, the forms of the abdominal uncini within *Potamethus* are similar to those diagnostic of *Jasmineira.* In addition, taxa within *Panousea*, while otherwise showing chaetal characteristics similar to those of *Chone* and *Euchone*, possess companion chaetae and collar chaetae reminiscent of more apomorphic sabellins[13].

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[13] See chapter 3.3 for phylogenetic terminology

The constancy of abdominal segment number in *Jasmineira candela* and *Jasmineira oculata* is in contrast to the situation in the 'type species' *Jasmineira caudata* and *Jasmineira elegans*, which appear to have a variable number of abdominal segments, with new segments being added anterior to the pygidium as the animal grows. This comparison is reminiscent of *Euchone*, which has a constant number of abdominal segments (Banse 1972; Cochrane *in prep.*), as opposed to the related taxon *Chone*, where the segment number increases with growth. Comparing adult specimens of *Euchone* and *J. oculata* with *J. caudata* of similar sizes and collected from the same areas, the latter taxon generally has far more abdominal segments and a lower segmental length:width ratio than *J. oculata.*

The form of the peristomium, comprising the base of the radioli as well as the membranous collar, also varies between the taxa within *Jasmineira.* In *Jasmineira caudata* and *Jasmineira shaudinni* (Augener 1912), the anterior part of the peristomium (forming the base of the radioli) projects well beyond the collar (a specialisation of the posterior part of the peristomium). In both these taxa, the projection is distally flared and curiously the radioli break off very easily at their base, a characteristic not shared by the remaining taxa. The collar of *Jasmineira filiformis* Hartman 1965 is low dorsally and high ventrally, such that the peristomium is dorsally exposed, whereas that of *J. filiformis* and *J. candela* is well-developed all round, covering the peristomium.

The presence of the foliaceous radiolar appendages almost is reminiscent of the situation in the serpulid *Protis* Ehlers, 1887, emended Kuprianova (1993). Within *Protis*, one or several radioli may bear a soft, subterminal and almost transparent 'operculum', or vesicle, which may be globular or disc-shaped. By analogy with *Apomatus* Philippi, 1844, which possesses a larger, vascularised vesicle, it is suggested that those in *Protis* also may have a respiratory function, because the vesicles are too small to occlude the tube opening (Knight-Jones *et al.* 1997). It would be of interest, therefore, to examine in detail the sub-terminal radiolar appendages in *Jasmineira candela* and *Jasmineira oculata* to determine their vascularisation and thereby to obtain some insight into their function, if any.

Character inconsistencies within Jasmineira

It is important to bear in mind that the most recent revision of the Sabellidae by Fitzhugh (1989) was carried out at a higher taxonomic level ('genus'), using characters of the respective 'type species' for phylogenetic analysis. Therefore, the discovery of inconsistencies in characters between the constituent taxa is not surprising. Before further systematic work involving *Jasmineira* can be carried out, a comparative morphological assessment should be carried out amongst the taxa.

In common with many other sabellids, some taxa originally described within *Jasmineira* later have been assigned to other taxa. For example, *Chone ecaudata* (Moore 1923) originally was described within *Jasmineira* and was later assigned to *Chone* by Hartman (1942), on the basis of its having the three characteristic types of thoracic notochaetae, including spatulate and bayonet-like chaetae. Assessment of other taxa currently grouped within *Jasmineira* shows that the taxon is not free from inconsistencies. While having 'typical' abdominal uncini, *Jasmineira bermudensis* Hartman, 1965 was characterised by the presence of three types of thoracic notochaetae, rather than the two types which at that time were considered diagnostic of *Jasmineira* (compare with Fitzhugh 1989). Most of the taxa within *Jasmineira* have the typical Sabellin 'feather-like' arrangement of pinnules on the radioles (see Chapter 1.2 and 2.4). However, the crown of *Jasmineira filiformis* Hartman, 1965 appears to have the 'snowflake-like' pinnular arrangement, in which the pinnules alternate along the radioles and are longest mid-radiole, such that they terminate at the same height distally. Examination of paratype material indicates that also *Jasmineira bermudensis* possesses a 'snowflake-like' crown.

The fact that *Jasmineira candela* and *Jasmineira oculata* appear to lack the diagnostic glandular girdle and possess an atypical form of abdominal uncini suggests that *Jasmineira* in its present form may be an artificial taxon. This is supported by cladistic analyses incorporating four taxa currently included with *Jasmineira*, that indicate paraphyly of that taxon (see Chapter 3.6 and 3.9).

Ecological aspects

In muddy to fine sandy sediments, *Jasmineira oculata* has been found to be a major component of soft bottom marine environments. For example, in fine sandy-silt sediments at the Balder field in the North Sea (59°19'N, 2°39'E) *Jasmineira oculata* (recorded as *J. candela*) is found in densities of up to approximately 125 individuals per m^2. In other areas in the northern North Sea, bordering the Norwegian Sea, the taxon appears to be present in lower but consistent numbers; approximately 60 individuals per m^2 at Heimdal and Snorre Fields, 59°60'N, 2°23'E and 61°45'N, 2°18'E, respectively (Mannvik *et al.* 1998b; Pearson *et al.* 1994). The animals appear to be habitat-selective, because they are extremely rare in the somewhat coarser muddy-sand sediments in the Frigg and Oseberg Sør areas; approximately 60°N, 2°36-40'E (Mannvik *et al.* 1998a and b, respectively). Observations of live material have not, as yet, been possible, so the feeding strategy (or range of strategies) employed by the organisms is not clear. There are no clear trends in the distribution of *Jasmineira oculata*, with respect to organic enrichment or contaminant gradients and, unlike *Euchone x* (Chapter 2.4), there is no indication of opportunistic resource exploitation. The widespread occurrence of *Jasmineira oculata* in Atlantic waters supports the need for a formal clarification of its taxonomic and systematic status.

2.5.7 Conclusions

The taxon name *Jasmineira oculata* Langerhans, 1884, which was assigned as a junior synonym of *Jasmineira candela* by Fauvel (1927) is reinstated, pending availability of suitable neotype material.

Jasmineira oculata and *Jasmineira candela* share a number of morphological characters that are not shared by other members of the taxon. In addition to the characteristic foliaceous appendages near the distal ends of the radioles, the most notable common feature is the absence of a post-chaetal glandular girdle on thoracic chaetiger 2. The latter feature is shared by a group of related taxa including *Chone* and *Euchone*, such that its absence in *J. candela* and *J. oculata* is interesting. Further work in progress has indicated paraphyly of *Jasmineira*, in which case, it may be that *J. candela* and *J. oculata* should not belong to that taxon.

Features deserving of further attention in systematic and taxonomic studies of *Jasmineira* and related taxa are the form of the radioles, anterior structures of the mouth and associated appendages, growth strategies and patterns of glandularisation. The different types of thoracic notochaetae should be examined in more detail and a comparative study should be made of the various forms of abdominal uncini between the taxa included within *Jasmineira* and related taxa such as *Potamethus*. Variation in numbers of abdominal segments and crown morphology should also be assessed. In this way, a more conclusive character matrix may be compiled, which will provide the basis for a better understanding of the systematic status of *Jasmineira*.

2.5.8 Addendum

Since the completion of this chapter, a number of specimens identified as *Jasmineira candela* by Fauvel from Morocco have been examined. Because the sampling location is closer to the type locality of *Jasmineira oculata* than *Jasmineira candela*, in terms of oceanography, it was hoped that the specimens might conform to the description of the former, rather than the latter taxon.This would advance considerably the search for type material of *Jasmineira oculata*.

The material examined comprised three specimens, of which two are from the collection of P. Fauvel, dated 26.06.1923, from "Vanneau", Morocco. One specimen is from the Prince de Monaco collection, 1912, Station 0196 (reported in Fauvel 1909). Lot numbers from the Muséum National d'Histoire Naturelle, Paris, France are A449 and A310, respectively. Although the specimens appear to have foliaceous radiolar tips, close inspection reveals that these are in fact broadly flanged tips that have become curled backwards to resemble a broad canal. Although these are reminiscent of Grube's drawing of the radiolar tips of *Jasmineira candela* they do not constitute the bilobed .

Other differences between the specimens and the holotype of *Jasmineira candela* are the presence of a high inter-radiolar (palmate) web, which is absent in *Jasmineira* as a whole and far fewer pairs of radioles. There are at least 15 abdominal segments, a whole and far fewer pairs of radioles. There are at least 15 abdominal segments, compared with the constant nine in *J. candela.* Further, the specimens possess a post-chaetal glandular girdle on chaetiger 2, which is conspicuously absent in *J. candela.* The collar is well developed and high, with a small ventral incision, unlike that of *J. candela*, which is low and intact ventrally.

The combination of these features suggests that the specimens should not be identified within *Jasmineira*. Instead, the presence of the inter-radiolar web and the post-chaetal glandular girdle on the second chaetigerous segment, it is possible that the specimens might belong within the *Chone* group of taxa. This should be confirmed by examination of the abdominal uncini. In any case, it is clear that the taxonomic status of specimens with real or apparent foliaceous radiolar tips requires further investigation.

2.6 Taxonomic and systematic challenges within *Chone* Krøyer

2.6.1 Special thanks

The present chapter owes much of its starting-point to discussions with Phyllis Knight-Jones and Adriana Giangrande on the taxonomic and systematic difficulties associated with *Chone*. In particular, I am indebted to the former for allowing me the use of informative unpublished personal notes and drawings of type and study material. Both Phyllis Knight-Jones and Mary Petersen are gratefully acknowledged for giving me access to parts of Krøyer's unpublished manuscript, with the relevant illustrations and translations. I thank Greg Rouse for informative discussions of the anomalous thoracic uncini in *Chone y* and the systematic implications thereof.

2.6.2 Introduction and aims

Taxa within *Chone* Krøyer are amongst the most commonly recorded sabellids in sub-tidal soft-bottom sediments in Atlantic waters (see Brattegard & Holthe 1997). Because *Chone* is poorly diagnosed, identification at the individual level presents a number of challenges. Confounding this fundamental problem is the relatively sparse information on this taxon in the general identification literature. The taxa included in general works on the Polychaeta naturally depend on the geographic area addressed by the work in question and, to a certain degree, upon existing records from the relevant areas. Thus, mis-identifications by operators of faunal studies arising from a lack of comparative taxonomic literature are in turn perpetuated in subsequent identification guides. Although this is a potentially widespread phenomenon, the problem appears particularly relevant to *Chone*.

Because of the increasing demand for accurate biodiversity mapping studies and commercial faunal community analyses for assessment of environmental disturbance, it is clear that difficulties in identification of *Chone* has led to non-comparable faunal records between the various institutes carrying out faunal identification work. In addition to perpetuating taxonomic ambiguity, this causes difficulties when comparing the composition of faunal assemblages, both spatially and temporally. It is therefore clear that the identity of the various forms of *Chone* typically found in soft-bottom sediments are in need of clarification.

Attempts during the present work to identify the available material from Arctic and Norwegian waters proved to be an extensive task. There appear to be some discrepancies in the literature as to the descriptions of certain taxa. Some of the descriptions in the older literature, such as that of *Chone duneri* Malmgren, do not provide adequate information to distinguish taxa from each other. As a result, a range of taxa have been synonymised, the validity of which now is under question. To resolve this requires re-examination of type material as well as study material from type localities and other sampling areas. Some of the older preserved specimens are in poor condition, and study of material from various benthic collections has revealed a large degree of individual variation, such that it is difficult to determine what constitutes natural variability in characters and what merits assignment to discrete taxa.

As a result, the present work is unable to offer many conclusive solutions to the ambiguity surrounding the taxonomic status of the various *Chone* found in Atlantic waters. Therefore, it is aimed to continue the study of *Chone* in co-operation with relevant experts who have examined a wide range of type and non-type specimens of the various taxa in question. During the course of the present work, a large volume of study material has been collected and examined from various Atlantic locations, ranging from the North Sea, Norwegian Sea, Barents Sea, Pechora Sea and the Kara Sea, in addition to a variety of specimens from Iceland and Greenland, kindly lent by Elin Sigvaldadóttìr and Danny Eibye Jakobsen. In addition, a sound background knowledge of the older taxonomic literature pertaining to *Chone* has been aquired. Continuing the present work as a co-operative project will allow the matter to be resolved in due course.

Thus, the present goals are by necessity relatively modest. The present chapter aims to examine specimens and literature concerning *Chone* taxa recorded from northern Atlantic faunal records. In so doing, the taxonomic status of a limited number of taxa will be evaluated and areas for future research outlined. Because each issue addressed has revealed a wide range of inconsistencies and uncertainties, it is not aimed to provide a taxonomic review of the taxa concerned, nor to revise their status. An outline of the main taxonomic problems encountered will be given and areas to be addressed by future research will be indicated. Unless otherwise stated (see Special Thanks above regarding works by Krøyer), translations and interpretations of the various original texts examined are the responsibility of the present author. It is not aimed to provide ecological information in this chapter, simply due to a lack of data.

2.6.3 Diagnosis of *Chone* Krøyer

Chone Krøyer, 1856, emended Banse (1972), Fitzhugh (1989).
Krøyer (1856): 13.- Sars (1862): 119.- Malmgren (1866): 404.- Langerhans (1881): 111.- Saint-Joseph (1894): 250.- Bush (1905): 189.- Hofsommer (1913): 332.- McIntosh (1923): 287.- Fauvel (1927): 334.- Berkeley & Berkeley (1952): 122.- Ushakov (1955): 417.- Day (1967): 776.- Banse (1972): 460.- Hartman-Schroeder (1971): ??.- Giangrande (1992): 518.- Hartmann-Schroeder (1996): 548.- Kirkegaard (1996): 372.
Parachonia Kinberg (1867): 355
Megachone Johnson (1901): 430
Metachone Bush (1905)[1]: 190, 216.

'Type species' *Chone infundibuliformis* Krøyer[2]

Diagnosis
(modified from compiled information in Fitzhugh, 1989)
Small to large-bodied sabellins with few to numerous radioles; radiolar skeleton with two rows of cells. Inter-radiolar (palmate) membrane and radiolar flanges present. Dorsal lips present; with or without dorsal radiolar appendages[3]. Ventral lips present. Ventral cirri present, from two to eight pairs. Anterior margin of anterior peristomial ring with narrow ventral lobe (i.e. peristomial extension); posterior peristomial ring

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[1] this reference often incorrectly cited in the literature as 1904

[2] description of *C. infundibuliformis* not presented here; see Chapter 2.6.10 for remarks.

[3] feature not discussed further here

collar (i.e. the collar proper) present. Glandular ring on chaetiger 2. Inferior thoracic notochaetae in two distinct transverse groups; anterior row(s) of bayonet-type chaetae; posterior row(s) spatulate or broadly swollen[4] chaetae. Abdominal neurochaetae arranged in two transverse rows per fascicle,: anterior row in anterior chaetigers with narrow, elongate chaetae; posterior abdominal fascicles containing a modified form of those in both rows. Thoracic uncini acicular, with teeth of equal size above the main fang; hood present. Abdominal uncini usually with main fang surmounted by broad series of smaller teeth (avicular type); breast well developed, expanded; handles absent. Regional variation in abdominal uncini may occur; anterior and posterior chaetigers with uncini of the above form, or posterior chaetigers with rasp-shaped plates (as in *Amphicorina* Quatrefages). Abdominal chaetigers vary with size of individuals.

Remarks

Fitzhugh (1989) and later Giangrande (1992) commented on the lack of an unequivocal diagnosis for *Chone*. As with *Jasmineira* Langerhans (see Chapter 2.5), there is no character that is uniquely characteristic of the taxon. Instead, *Chone* is diagnosed by a combination of features. Many of the descriptive characteristics used in the diagnosis of *Chone* vary between individuals and sampling area to such an extent that these often 'overlap' with the diagnostic characters of other taxa. It remains a challenge for future research to improve the diagnosis of *Chone* and related taxa.

2.6.4 *Chone filicaudata* Southern

Chone filicaudata Southern, 1914

Chone filicaudata Southern (1914): 141.143, pl. XIV-XV, fig 32a-l., - McIntosh (1916).

Chone infundibuliformis (Krøyer). Southern (1910): 240.

Type locality - Western Ireland: Inishlyre Harbour, Ballynakill Harbour, Dingle Bay and Dublin Bay.

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[4] see Chapter 1.2.2

Description (slightly adapted from Southern, 1914; information in original order) Body short and comparatively stout. Whole body 11 mm in length; of which the crown comprised 4 mm. Width 1.5 mm in largest specimen, a female full of eggs. In a smaller specimen of 5 mm, the crown was comparatively longer, approximately equal to the trunk in length. Chaetigerous segments 26-28; eight thoracic and 18-20 abdominal chaetigers. First and last segments without chaetae. Segments biannulate and tapering abruptly towards the "tail". Body creamy-white in colour in preserved material.

Eight to nine pairs of radioles, one pair ventral "unbranched gills"[5] and several apinnate ventral cirri[6]. Palmate, or inter-radiolar, membrane approximately two-thirds of the height of the radioles. Collar resembling that of *Chone infundibuliformis*, but not quite as high or prominent. Collar entire ventrally, folding inwards dorsally and not sloping obliquely, as in *Chone duneri.*

Bifid ventral peristomial extension[7] present, which is absent in *Chone infundibuliformis*. Chaetiger 1 narrow, bearing only notochaetae; a row of long chaetae with narrow "wings" and a row of short slender chaetae with "only traces of wings". Chaetiger 2 with post-chaetigerous glandular girdle.

Thorax with one achaetous segment (the collar segment) and eight chaetigers; these are biannulate and longer than the abdominal segments, of which there are 19-21. The anal segment is achaetous and the anus is ventral. On the dorsal side of the anal segment (i.e. the pygidium) is a long filiform appendage which tapers to a fine point[8] and closely resembles the anal appendage of *Jasmineira caudata* Langerhans.

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[5] may refer to developing radioles

[6] Southern (1914) refers to these as an "inner ring of unbranched gills of varying number and length"

[7] derived from the anterior peristomial ring (see Chapter 1), referred to by Southern as the "lip-membrane"

[8] Southern (1914) stated that the pygidial filament (as "anal appendage") varies in length and curiously commented that it generally is longer and thinner than that depicted in his figure.

Anal groove dorsal in thorax, ventral in abdomen; the margins of the groove and the intersegmental grooves, or furrows, are lined by glandular cells, which also are present in a more diffused condition over the whole body.

Thoracic notochaetae of three types. Superior ones long, slender, with narrow striated "wings", 13 per fascicle. Inferior chaetae with "spatulate" tips, tapering to a fine point "more gradually than those of *Chone duneri* and *Chone infundibuliformis*". At the base of the spatulate chaetae (i.e. anterior inferior notochaetae) is a row of 13 bayonet-type chaetae. Thoracic neurochaetae (uncini) acicular, 17-27 per torus, each with a prominent main fang and two distinct and several indistinct rows of teeth. At the back of the "crown" is a "delicate wing".

Abdominal segments with long slender chaetae with very narrow "wings", 10 in abdominal segment 1 and 12 in the succeeding segment, geniculate at the base of the proximal taper. Elongate chaetae in the abdomen longer than those in the thorax. Abdominal segment 1 containing 34 uncini; 42 in abdominal segment 6. The upper uncini are small compared to the lower ones, but are of similar shape in all segments. Viewed from above, the crown of the uncini have seven or eight rows of teeth, each row comprising 5-7 teeth. In side view, the prominent main fang is surmounted by 10-12 rows of teeth. Abdominal segment 13 contains 5 elongate chaetae and 35 uncini.

Southern (1914) further commented that *Chone filicaudata* is readily distinguished from previously described forms by the presence of the pygidial filament. The exception to this is *Chone suspecta* Krøyer, which was stated as having a conical "anal appendage". *C. filicaudata* was reported to differ from *C. suspecta* in other aspects (Southern *op. cit.*). *C. suspecta* has 35-42 segments, as opposed to the 26-28 segments of *C. filicaudata*. Further, the former taxon has six pairs of radioles, whereas *C. filicaudata* has eight or nine pairs. Moreover, *C. filicaudata* has a far greater number of chaetae within each bundle. Further comments on *Chone suspecta* are given in Chapter 2.6.8.

Remarks

As might be expected considering the close proximity in terms of water masses to the type locality, *Chone filicaudata* has been widely recorded in British waters (Howson & Picton 1997). The taxon also is recorded along the Norwegian coast (Brattegard & Holthe 1997) and in certain parts of the northern North Sea (Mannvik *et al.* 1998b). Interestingly, *C. filicaudata* also has been recorded from the Mediterranean Sea (Bellan 1964; Harmelin 1969; Amoureux 1976; Drago *et al.* 1978 and Farina *et al.* 1985). However, none of these authors illustrated their specimens, or described them in detail. Further, the material from those studies is apparently unavailable, preventing further evaluation of these records. Giangrande (1992) examined a range of specimens from the Mediterranean Sea and Adriatic Sea and provided a description and illustrations. The specimens were reported to differ from the original description by Southern (1914) by the presence of fewer uncini and elongate chaetae and the "midline part of ventral collar more vestigial" (Giangrande 1992), which here is interpreted as the collar being lower ventrally. However, because the original specimen(s) of Southern (1914) were not examined for comparison (most likely due to unavailability of the material), it is impossible at this time to know for certain to what extent the material from Mediterranean and Adriatic waters conform to the original material from the type locality in the west of Ireland. In addition, *Chone filicaudata* appears in records from South Africa (Day 1967), the status of which also warrants further evaluation.

The most prominent distinguishing feature of *Chone filicaudata* is the presence of a terminal filament on the pygidium. Until recently, there was little awareness in the general literature of other *Chone* taxa that also possess this feature, such that finds of any *Chone* specimen with a pygidial filament inevitably were recorded as *C. filicaudata.* As a result, records of that taxon exist almost world-wide. Banse (1972) and recently also Giangrande (1992) have drawn attention to the existence of at least one *Chone* taxon that possesses a pygidial filament but does not conform to *C. filicaudata.* The material was not given the status of a new taxon due to a lack of intact study specimens, but a description is given below.

Chone sp. (Giangrande 1992)
as *Chone filicaudata* Southern, Giangrande (1985).

Specimens obtained from between 10 and 15 m depth, in the Adriatic Sea (Brindisi) and the Tyrrhenian Sea (Ischia, near Naples).

Description (from Giangrande 1992, in original order, some terminology changed)
A *Chone* of intermediate size, about 1.3 cm in length, of which 3 mm comprises the branchial crown, width of thorax approximately 1 mm, segments wider than long. Eight thoracic and approximately 20 abdominal chaetigers. Six pairs of radioles with a very low palmate (inter-radiolar) membrane, radioles flanged to their tips. Dorsal lips elongate, pointed. Collar high, covering the bases of the radioles. Glandularisation as indicated by Methyl Green staining uniformly distributed over body, but also weakly-differentiated glandular shields present in the thorax. Superior thoracic notochaetae elongate, narrow as in Figure 1.2.11. Inferior thoracic notochaetae in two rows; anterior of bayonet type and posterior paleate, or spatulate, with a short tip, or mucron. Thoracic uncini acicular, ten per torus, arranged in line. Abdominal uncini with five rows of teeth, 15-16 per torus. Slight variation in uncinal shape, presumably between segments as well as within torus. A filiform anal appendage, or pygidial filament, present.

Giangrande (1992) commented that the taxon differs from *Chone filicaudata* in the height of the inter-radiolar membrane, which is shorter in *Chone* sp., and the tips of the radioles, which, according to the drawings in Giangrande (1992), have an abruptly tapering free end in *C.* sp., which is not the case in *C. filicaudata*. In addition, *C.* sp. lacks the bifid ventral peristomial extensions that are characteristic of *C. filicaudata* and has fewer elongate chaetae and uncini. Finally, and perhaps most conclusively, *C.* sp. possesses true concave paleate, or spatulate chaetae, while *C. filicaudata* possesses the narrower, bilaterally swollen form, as depicted in Figure 1.2.11e, f).

Remarks

Because *Chone filicaudata* is frequently recorded from Norwegian waters, an assessment of individuals identified as such and a detailed comparison with the original description of that taxon is prudent. Features that should be given particular attention are 1) the height of the inter-radiolar membrane, 2) the form of the tips of the radioles, 3) the shape of the dorsal lips, 4) the form of the ventral peristomial extensions, if present, 5) approximate number of abdominal segments, 6) number of chaetae within each fascicle and 6) the form of the posterior row of inferior thoracic notochaetae.

This task has been initiated, the first phase of which was to locate specimens identified as *Chone filicaudata* from as wide a range of locations as possible along the coast of Norway and the northern North Sea. Figure 2.6.1. shows the external anatomy of a specimen provisionally identified by the present author as *Chone filicaudata* from the slope of the Norwegian continental shelf in the northern North Sea (recorded in Pearson *et al.* 1994). To separate these from other records of *Chone* sp., the specimens are hereafter referred to as *Chone* near *filicaudata* pending confirmation of their identity.

Chone near *filicaudata*

Material examined

Northern North Sea, between 100 and 350 m depth in silt-clay dominated sediments (co-ordinates given as petroleum field centre, or average sampling position, because an extensive network of stations was sampled and revisited at each field): Heimdal, $59^{0}60'$N, $2^{0}23'$E, Elf Petroleum Norge a/s, approx. 20 specimens, Frøy, $59^{0}74'$N, $2^{0}59'$E, Elf Petroleum Norge a/s, 60 specimens, Øst Frigg, Elf Petroleum Norge a/s, $59^{0}87'$N, $2^{0}40'$E, 25 specimens, Snorre, $61^{0}30'$N, $2^{0}10'$E Saga Petroleum, 60 specimens.

Norwegian Sea: Smøla county, Møre & Romsdal, $63^{0}18'$ - $63^{0}28'$N, $7^{0}30'$ – 8^{0}E, 55 specimens.

Description

Specimens generally small in size and stout, with a body length not exceeding 3 mm, excluding crown. Crown usually more than two-thirds of the body length, often equal in length. In this respect, the specimens conform with the description of Southern (1914). Eight thoracic chaetigers, chaetiger 1 fused with collar segment and approximately 15 abdominal segments, decreasing in length towards the pygidium.

Six to seven pairs of radioles, united by an inter-radiolar membrane for at least half their length (compared with two-thirds according to the original description). At least two pairs of apinnate ventral cirri present, possibly more. Radioles flanged almost up to their tips, with short free ends and numerous slender paired pinnules of equal length along the length of the radioles. Dorsal lips elongate, ventral lips lower, more conical in shape. Collar slightly oblique, higher ventrally than dorsally. Ventral margin distally entire, slightly rounded, dorsal margins recurved, attaching to the anterior part of the peristomium (derived from the anterior peristomial ring) to form a narrow dorsal gap.

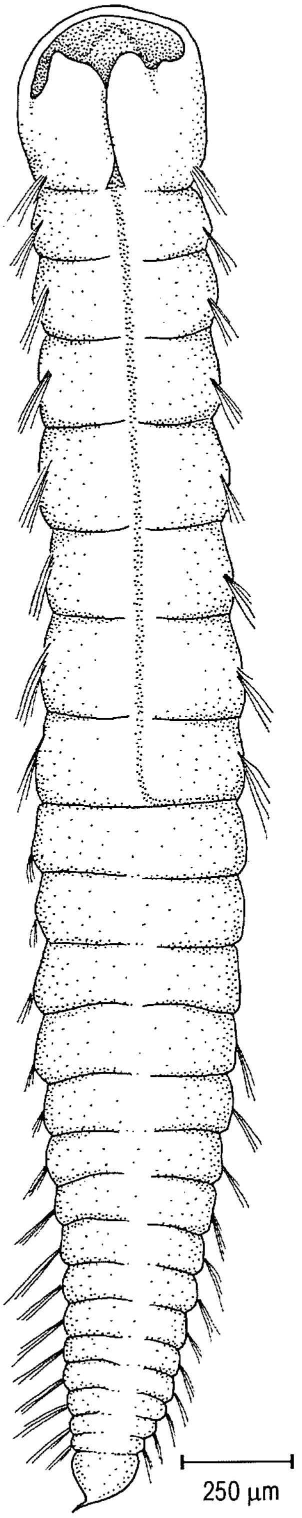
Figure 2.6.1.
Dorsal view of Chone *near* filicaudata *Southern from the northern North Sea, without radioles.*

Three types of thoracic notochaetae present; superior ones long, narrow and geniculate at the base of the proximal taper. Anterior row of inferior chaetae bayonet-type and posterior row with broad bilateral swellings. Thoracic neurochaetae (uncini) of the typical acicular form. Abdominal neurochaetae very narrow, longer than the elongate chaetae in the thorax, particularly in posterior segments. Abdominal uncini in need of detailed examination, but of the general *Chone* form, with rounded bases and a well-developed breast. Maximally 17 per torus. Pygidium conical, somewhat “bulging”, bearing a short terminal filament reminiscent of *Jasmineira caudata*.

Remarks

The main differences between the specimens from Norwegian waters and the description of *Chone filicaudata* from Ireland lie in the numbers of segments and radioles present. The Norwegian specimens generally had six pairs of radioles, whereas Southern (1914) documented eight or nine pairs of radioles. Similarly, the type specimens had 18-20 abdominal chaetigers, while those from Norway had

maximally 15. In these respects, the specimens agree more with those from Mediterranean waters described by Giangrande (1992), which had six to seven pairs of radioles and about 15 abdominal chaetigers. However, there may be regional variation in these characters. Both the Norwegian and Mediterranean specimens differed from those of Southern (1914) in having fewer abdominal uncini per torus.



Because *Chone* near *filicaudata* is frequently recorded in Norwegian waters, resolution of the doubts as to how it should be identified is a matter that should be addressed by future research. It is here proposed that the most effective means of doing so would be to examine as many specimens as possible from near the type locality, to ascertain the degree of individual variation in terms of radiole and segment number as well as the amount of chaetae present in each fascicle or uncigerous torus. Further, the chaetal morphology should be examined in further detail. Having done so, a comparative study should be carried out of a wide range of study material from the British Isles and Norway, and these in turn compared with the Mediterranean material of Giangrande (1992). Once this comparative study is carried out, it is expected that the question of whether the differences between the specimens found in Norway are within the bounds of individual variation in *Chone filicaudata* Southern, or whether they should be assigned to another discrete taxon.

2.6.5 *Chone duneri* Malmgren

Rationale

Malmgren (1867) briefly described *Chone duneri* from Spitsbergen, where the bottom water is likely to be heavily influenced by Atlantic water masses. Langerhans (1880) subsequently recorded the taxon from Madeira and Hofsommer (1913) also reported its occurrence near Jutland in the North Sea. Southern (1914) described a single specimen of *C. duneri* from Clew Bay, Ireland. Thereafter, the taxon has been reported from northern Alaska (Pettibone 1954) and Washington (see Banse 1972). Abundant records of *C. duneri* also exist from northern Norway, to the North Sea and around the British Isles (see Brattegard & Holthe 1997; Howson & Picton 1997). The taxon also is reported as being commonly found along the Italian coast in the Tyrrhenian Sea, Adriatic Sea and the Ligurian Sea (Giangrande 1992). Perhaps as a result of such abundant findings, the taxon is recorded in the general literature as having a very wide distribution.

When included in identification guides, *Chone duneri* often is characterised on the basis of having a low collar, barely concealing or slightly exposing the bases of the radioles, with an intact anterior ventral margin (not intact dorsally as stated in Knight-Jones 1990), with a characteristic crescent-shaped patch of glands and/or cilia near the anterior ventral margin of the collar. In the absence of information on other taxa that also share this characteristic, most operators dealing large quantities of material are not aware of the risk of confusion of *C. duneri* with other taxa.

Because the original description of *Chone duneri* by Malmgren (1867) was rather brief, and subsequent records contain some discrepancies in the diagnostic characters observed, a reappraisal of the status of *C. duneri* is prudent. This task recently has become of urgent importance with the increasing demands, both on a regional and national scale, for taxon lists from marine coastal habitats, as part of an overall goal of biodiversity mapping. Most faunal surveys from Norway commonly document finds of *C. duneri*. Because such records may be confused with finds of other taxa, such as *Chone longocirrata* Sars 1872, a clarification of records of *C. duneri* is timely.

Taxonomic information

Chone duneri Malmgren, 1867

Chone duneri Malmgren (1867): 225, pl. XIV, fig. 75 a-d.- Langerhans (1880): 114, fig. 44 a-e.- Hansen (1876-78):43.- Marenzeller (1878, page unknown).- Théel (1875-76): 66.- Hofsommer (1913): 336-339.- Fauvel (1914): 319, plate xxxi, fig. 10-18.- Southern (1914):141.- Fauvel (1927): 336-337, fig. 117 l-r.- Pettibone (1954): 339.- Hartmann-Schröder (1971): 517.- Banse (1972): 466, fig. 2 a-b.- Giangrande (1992).- Hartmann-Schröder (1996): 548-549.- Kirkegaard (1996): 372-374.- Dahle *et al.* (1998): 200.

Chone sp. 1. Banse *et al.* (1968): 547.

Chone bimaculata Banse & Nichols (1968): 227.- Nichols (1968): 61.

Chone duneri Malmgren, *non Malmgren*, Pettibone (1956): 577.

Diagnosis (withheld)

Because the descriptions of *Chone duneri* are variable in the literature, the most recently published diagnoses of the taxon (Banse 1972; Giangrande 1992) are not repeated here. It is here considered necessary to revise the taxon prior to providing an unequivocal diagnosis. For this reason, the various drawings found in the literature are not reproduced here.

Description(s)

Malmgren (1967) began the original description of *Chone duneri* with the comment that the taxon resembles *Chone infundibuliformis*. The original description is too brief to be informative in its own right, but the taxon was redescribed by Hofsommer (1913), providing additional details. Although Hofsommer's specimen was collected from Jutland, while that of Malmgren came from Spitzbergen, the records agree to such an extent that both specimens may be considered as belonging to the same taxon. Spitzbergen is heavily influenced by Atlantic water masses, so the occurrence of the same taxon in the North Sea is not inconceivable. Therefore, the following description is compiled from the original description, supplemented by additional information in Hofsommer (1913) and other informative records. There is some uncertainty surrounding the observations in Langerhans (1880) and Giangrande (1992, see Remarks), but some of that information is included here for comparative purposes. The information is given in anatomical order and the terminology follows modern usage. The descriptive characters are credited to the first observer, as far as can be ascertained from the literature. This extensive citation of authors is clumsy, but offers a much-needed means of tracing the observations back to the specimens to which they relate.

Material of Malmgren (1867) was 2 mm wide and 20-25 mm in total length, of which the radioles comprised 13 mm, of which the distal free ends were 5 mm in length. Numbers of segments were not mentioned by Malmgren (*op. cit.*); Hofsommer (1913) reported the presence of 75 segments, including thoracic segments (i.e. 8 thoracic, 67 abdominal segments). Langerhans (1880) and Giangrande (1992) recorded only approxinately 16 and 20 chaetigerous abdominal segments, respectively. Subsequent descriptions of *Chone duneri* generally are based on these figures. Fauvel (1927) noted the presence of approximately 75 segments, Kirkegaard (1996) cited up to 70 chaetigers and Hartmann-Schröder (1971, 1996) documented up to 75 chaetigers. Segments biannulate (Hofsommer 1913).

Radioles comprising about one third of the length of the whole animal. Long filamentous free ends devoid of pinnules, comprising approximately a third of the length of the radioles (Malmgren 1867). Number of radioles not mentioned in original description. Langerhans (1880) reported five pairs radioles, Hofsommer (1913) reported nine pairs radioles, Banse (1972) up to ten pairs and Giangrande (1992) as many as 12 pairs. Hartmann-Schröder (1971, 1996) noted 5-11 pairs of radioles. Inter-radiolar (palmate) membrane extending in height approximately two-thirds of the length of the radioles (Hofsommer 1913). Numerous paired pinnules in dense arrangement along the radioles, shortest at the radiolar bases, reaching their maximal lengths close to the terminal third of the radioles and tapering abruptly towards the free ends. Banse (1972) cited the presence of four ventral cirri, two of which are of equal length to the pinnulated radioles. However, this observation was based on Langerhans (1880) and must therefore be treated with some caution.

Collar oblique, higher ventrally than dorsally (Malmgren 1867, Figure 75a), not crenulated (Fauvel 1927). Ventral margin entire (Langerhans 1880; Hofsommer 1913). Langerhans (1880) noted a pair of otoliths in the collar segment, which Hofsommer was unable to find in his specimen. Because otoliths were not mentioned in the original description, the validity of subsequent records of the feature in *Chone* *duneri* are uncertain. Peristomium expanded ventrally to form bifid ventral peristomial extensions (derived from anterior peristomial ring), as noted by Langerhans (1880), Hofsommer (1913) and subsequent authors.

Ventral shields absent, glandular cells distributed over entire body (Hofsommer 1913). Distinctive staining pattern with Methyl Green, whereby the body stains evenly, with the exception of the anterior part of the collar, narrow bilateral patches and a post-chaetal ring on each segment, which remain pale after immersion in the dye (Hofsommer 1913; Banse 1972). Parapodial lobes prominent in thorax (Banse 1972, depicted in Hartmann-Schröder 1971, 1996).

Chaetiger 1 indistinct from collar segment, bearing only 5-7 notochaetae, not in line with the remaining thoracic chaetigers, and much shorter than those in the succeeding segments, although present in similar numbers (Hofsommer 1913). However, Hartmann-Schröder (1971, 1996) depicted long notochaetae on thoracic chaetiger 1. From thoracic chaetiger 2, an additional row of 5-7 chaetae (Hofsommer 1913), described in Malmgren (1867) as "subspatulate" and tapering, with broad bilateral swellings and a long tip. Interestingly, Hartmann-Schröder (1971, 1996) described those chaetae as "spatulate, with short tip", a discrepancy which demands further investigation. The bayonet-type inferior anterior thoracic notochaetae typical of *Chone* were not observed by Malmgren or Hofsommer, but their presence is likely. Thoracic uncini acicular, long-handled, 12-14 per torus (Hofsommer 1913), five teeth above main fang (Hartmann-Schröder 1971, 1996). Abdominal neuropodia containing 5-6 very narrow elongate chaetae (Hofsommer 1913). Abdominal uncini of the squarish form typical of *Chone*, with a wide base and five rows of teeth, each containing 2-4 teeth above the main fang (Hartmann-Schröder 1971, 1996). Pygidium without appendages (Hartmann-Schröder 1971, 1996).

Remarks

Notes and illustrations of type material from Spitsbergen (Phyllis Knight-Jones, unpublished notes) support the observations of Hofsommer (1913) in addition to the description of Malmgren (1867). Further, the presence of notopodial lobes in the thorax and a crescent-shaped patch of cilia or glands near the ventral collar margin are in accordance with Banse (1972). The specimens all have 36 or more abdominal segments and the inter-radiolar membrane unites the radioles for at least two-thirds of their length.

The confusion in the literature as to the diagnostic characteristics of *Chone duneri* is not surprising, given the sparse nature of the original description. The record of *C. duneri* from Madeira (Langerhans 1880) was reported as possibly being an immature specimen and, as such, emphasis cannot be placed upon the presence of only five pairs of radioles and only abdominal chaetigers. However, it further differs from *C. duneri* in having the (palmate) membrane uniting the radioles for only half their length, as opposed to two-thirds. Most significantly, the radioles were depicted as having short and broadly flanged tips. Because all other records of *C. duneri* describe these structures as having very long filamentous free ends, the present conclusion must be that the specimen does not belong to that taxon.

The specimens identified as *Chone duneri* in Giangrande (1992) also show some discrepancies with respect to other records of the taxon. Twelve pairs of radioles were reported, which is greater than all other records of the taxon, but their tips conformed with the description in Malmgren (1867). The same specimens possessed only approximately 20 abdominal segments, the combination of which cannot be attributed to maturity of the specimens. The posterior inferior notochaetae were described as "paleate, with long tips", but it is difficult to compare these structures directly with previous records. Irrespective, it is clear that specimens from Mediterranean waters identified as *C. duneri* should be re-examined and compared with those from near the type locality.

In the description of *Chone filicaudata*, Southern, 1914, the short broad chaetae occupying a posterior inferior position in the thoracic notopodia were stated as being narrower and more tapered than those in *Chone duneri* and *Chone infundibuliformis*. Because there are considerable subtle variations in the form of this chaetal form, a detailed comparative examination of thoracic notopodial chaetae in *Chone* should be carried out to assess the degree of individual and inter-specific variation in those structures.

2.6.6 Records of *Chone duneri* Malmgren from the Pechora Sea

Background

Chone duneri was recorded from the Pechora Sea, in the south-eastern part of the Barents Sea (Dahle *et al.* 1998), as well as in the northern Barents Sea (Cochrane *et al.* 1998). Although found at various locations, the highest densities were found in the Chernaya Bay, on the south-eastern shore of Novaya Zemlya and north-west of Vaygach Island, at the south-eastern part of the Kara Strait (approximate location 70°N, 55-57 °E), where 23 and 48 individuals per 0.5 m^2 sampling area were found, respectively. Interestingly, the sedimentology and current regimes are markedly different in the two areas. Chernaya Bay is a typical sill fjord, with restricted water exchange in the deeper layers. Sediments in which *C. duneri* were found comprised sandy mud with a high silt-clay fraction. Conversely, current flow in the Kara strait area is reputedly relatively strong and the sediments in that area comprised coarse sediments, characterised as muddy sand, but with a large amount of stones and other debris on the surface, giving a wide niche availability for benthic organisms.

A provisional study of the specimens sampled was carried out. The specimens conformed well to the original description of Malmgren (1867) and the redescription of Hofsommer (1913), as well as the unpublished observations of type material (Knight-Jones). Figure 2.6.2 shows a ventro-lateral view of the entire animal, and Figure 2.6.3 shows a detail of the anterior end, in ventral and lateral views. Figure 2.6.4 depicts two of the three chaetal types observed.

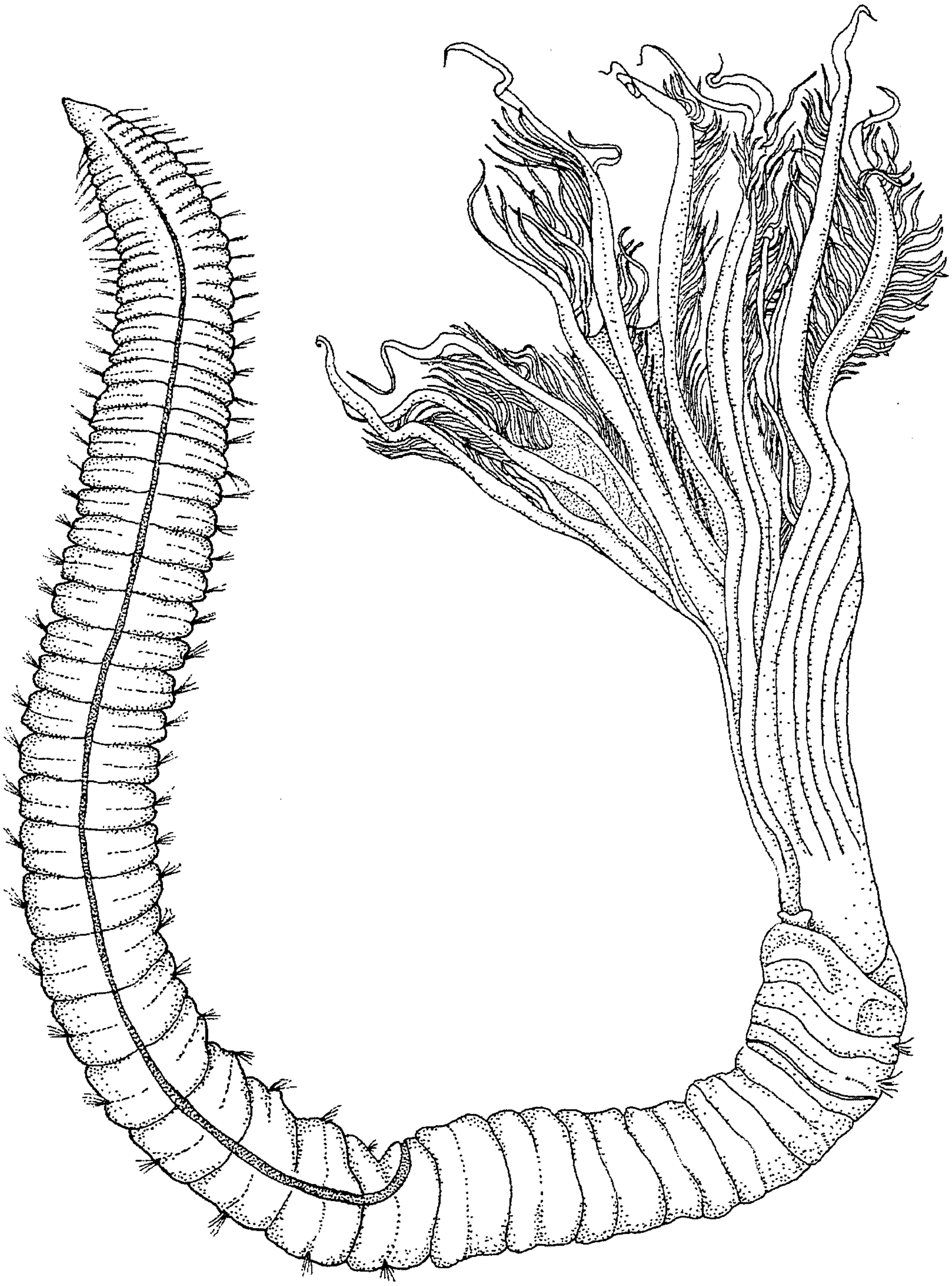


Figure 2.6.2. Ventro-lateral view of Chone duneri *Malmgren from the Kara Strait, Pechora Sea. Specimen from Akvaplan-niva collection (Station 21.4, reported in Dahle* et al. *1998). Note high inter-radiolar (palmate) membrane, low, oblique collar, bilobed ventral peristomial extensions and biannulate segments.*

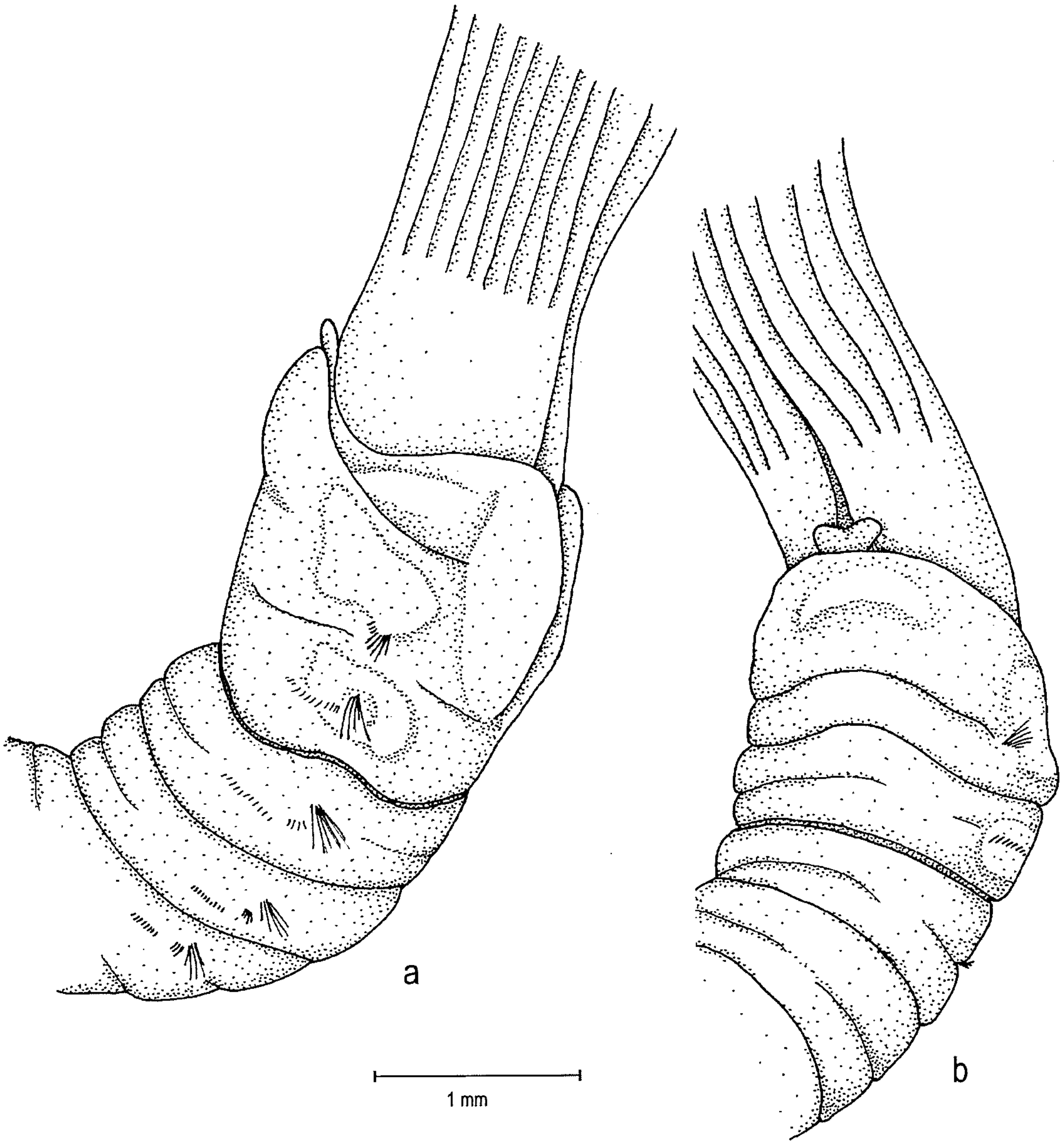


Figure 2.6.3. Chone duneri *Malmgren: anterior end (excluding radioles) in a) lateral and b) ventral view. Specimen as for Figure 2.6.2.*

Description of specimens

Eight thoracic and between 40 and 45 abdominal chaetigers, all of which biannulate. At least seven pairs of radioles, united for two-thirds of their lengths by inter-radiolar (palmate) membrane. Free ends of radioles long and filamentous; comprising up to one quarter of the length of the radioles. Radioles narrowly flanged up to the point where the pinnules ceased, thereafter radiolar tips without flange. Numerous paired pinnules thin and densely arranged along the radioles. Four pairs of ventral cirri were observed, the ventral-most two almost as long as the pinnulated radioles.

Collar intact ventrally, showing the characteristic crescent-shaped patch of cilia or glands, not concealing radiolar bases. Clearly visible ventral bilobed peristomial extensions. A curious feature was observed laterally (see Figure 2.6.3), where the ventral margin of the collar continued as a lateral fold, forming a pouch approximately 25 μm deep.

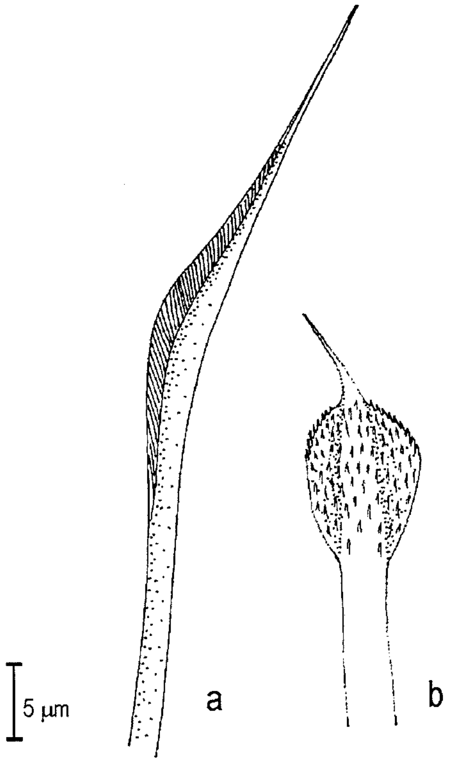


Figure 2.6.4.
Chone duneri *from the Pechora Sea: thoracic notochaetae from chaetiger 2, from a) superior and b) posterior inferior rows. Anterior inferior chaetae (bayonet-type) not illustrated.*

Chaetiger 1 only partially separated from collar segment, bearing only notochaetae which were notably shorter than those in the succeeding segments. These also had a slightly different orientation. Superior thoracic notochaetae elongate, narrowly swollen, geniculate at the base of the proximal taper. Anterior row of inferior chaetae bayonet-type and posterior row very broadly-swollen chaetae with long, geniculate tips. Pygidium conical, without appendages.

Remarks

Specimens conforming to *Chone duneri* recorded from the northern Barents Sea (Cochrane *et al.* 1998) and the Kara Sea (Cochrane *in prep.*; reported in Evenset *et al.* 1998) should be re-examined in more detail, particularly with respect to the chaetal structure. In light of the sampling location of the material to hand, comparative material from other Arctic areas should be gathered for re-examination. In particular, it would be interesting and informative to examine for comparison the specimens identified as *Chone duneri* from Novaya Zemlya collected by Théel (1875-76) as well as those from the Kara Sea (Marenzeller 1878). These issues will be given priority in the continuation of the present work.

2.6.7 Remarks on *Chone longocirrata* Sars

Chone longocirrata M. Sars, 1872
Chone longocirrata M. Sars *in* G.O. Sars (1872)
Type locality: Drobak Sound, Oslofjord, south-eastern Norway
Current status: referred to *Chone duneri* Malmgren (Fauvel 1927)

Subsequent to its description, *Chone longocirrata* received little attention in the literature, and later was listed under *Chone duneri* by Fauvel (1927). The synonymy most likely was based on the apparently intact ventral collar margin in *C. longocirrata*, resembling that of *C. duneri*, the lack of ventral shields and an approximately similar number of abdominal segments and pairs of radioles. Both *C. duneri* and *C. longocirrata* appear to possess biannulate segments.

In a recent identification guide to the Polychaeta, Kirkegaard (1996) included *Chone longocirrata* as a taxon discrete from *Chone duneri*. However, the illustrations of the anterior end and a detail of two radioles (his Figure 216 a, b) in fact appear to be redrawn from the illustration of *Chone collaris* Langerhans (Langerhans 1880, his plate V, Fig. 29a, b). This confusion may have been caused by the observation that the anterior collar margins in *C. longocirrata* are scalloped, in a manner similar to that in *C. collaris*, although apparently less conspicuous, due to the tendency for the collar margins to be turned inwards in the former taxon (Knight-Jones, unpublished drawings).

Kirkegaard (1996) illustrated in addition some of the chaetal forms present, which do not appear in Langerhans (1880) and therefore most likely refer to *C. longocirrata.* It is notable that the posterior inferior thoracic notochaetae are depicted as being short, with fairly narrow bilateral swellings and a long distal taper, in contrast with the wider form seen in *C. duneri*. The illustration is not reproduced here to avoid the risk of further confusion, until the matter is resolved conclusively.

Preliminary observations of type material from Drobak (Knight-Jones, unpublished data) show the specimens to possess six or seven pairs of radioles, whereas Sars (1872) reported the presence of eight pairs. The radioles are united by an inter-radiolar (palmate) membrane for at least two-thirds of their length, and the free ends are relatively short, tapered and not flanged. The specimens comprised eight thoracic and 40-48 abdominal segments. An interesting observation made by Knight Jones is the presence of a deep mid-ventral groove, particularly in posterior segments (see Remarks on *Chone y*, Chapter 2.6.9).

In light of the fact that *Chone longocirrata*, described from southern Norway, was synonymised with *Chone duneri*, described from Spitzbergen, and there are abundant records of the latter taxon from Norwegian waters, it is clear that the status of both *C. longocirrata* and *C. duneri* warrant further investigation. Further work therefore should clarify the characteristics that separate the taxa, with particular emphasis on the form of the posterior inferior thoracic notochaetae. In addition, the form of the anterior collar margin in both taxa should be given attention.

2.6.8 Remarks on *Chone suspecta* Krøyer

Chone suspecta Krøyer (1856):33-34, no figures.
Chone suspecta Hofsommer (1913): 339-342, fig. 13-15.

Type locality: Kristiansund, western Norway
Current status: referred to *Chone infundibuliformis* Krøyer (Malmgren 1866, p. 404), also referred to as ?*Chone suspecta* Krøyer, “juvenis?” (Hartman 1959).

Krøyer (1856) described *Chone suspecta* on the basis of a single specimen with damaged radioles, found near Kristiansund. The etymology suggests his uncertainty as to whether the specimen was representative of a discrete taxon or merely a juvenile form of *Chone infundibuliformis*. In an unpublished manuscript, Krøyer further argued that it was better to draw attention to the taxon, albeit incompletely described, rather than to dismiss it.

The following description is based on Krøyer (1856), translated by Knight-Jones, and extracts from Krøyer's unpublished manuscript translated by Mary Petersen.

Description

Body stout, width at least one-eighth of its length, flattened and narrowing posteriorly to a point. Total length approximately 19 mm, of which the "gills" (i.e. radiolar crown) comprised 7.5 mm. Width approximately 1.6 mm. Approximately 50 segments in total, not bi-annulate, flattened posteriorly. Length of anterior segments twice as broad as long; length of mid-body segments about one quarter of their width. Colour a 'dirty' yellowish-orange, radioles whitish-yellow, without markings. Tentative observation of seven pairs of radioles exceeding two-thirds of the body length, united for almost their entire length by an inter-radiolar (palmate) membrane. Only the free ends project above the membrane, and these are short, approximately 0.55 mm in length, and broad, tapering. One pair of ventral cirri observed. Faecal groove white, inconspicuous. Collar fitting closely, conspicuous dorsal gap, entire ventral margin.

Additional information

In a lecture given in 1861, Sars (1862) provided some additional remarks based on a single specimen, which subsequently was lost, such that the information was related from notes and not checked against the material. An illustration of the specimen was recorded as having been presented, but this is not reproduced in the published volume. Six of the seven pairs of radioles were well-developed and almost as long as the body. The ventral-most pair of radioles was reported as lacking pinnules, but it is not clear whether this may refer to the apinnate ventral cirri observed by Krøyer. Two "oral threads" were noted, but these may refer to enlarged basal pinnules (Knight Jones, unpublished notes). Based on two specimens tentatively identified as *Chone suspecta*, Hofsommer (1913) reported the presence of 42 and 35 abdominal segments and six pairs of pinnulated and one pair of apinnate radioles in the one specimen that was complete. The thoracic segments were reported to be of similar length to those in the abdomen, becoming narrower only in posterior segments.

Knight-Jones (unpublished notes) recorded the presence of six spatulate chaetae in the posterior row of inferior thoracic notochaetae, and abdominal uncini with a more rounded breast than is usual in *Chone*.

Remarks

Chone suspecta differs from *Chone longocirrata* in possessing fully spatulate thoracic notochaetae, with short tips. However, Krøyer (1856) recorded only "pesudo-spatulate" chaetae. The chaetal forms in *Chone suspecta* therefore warrant further examination. Further, there is no sign of biannulation in segments, as is characteristic of *C. longocirrata* and *Chone duneri*. Distinguishing between *C. suspecta* and *Chone infundibuliformis* is less clear. *C. infundibuliformis* has biannulate segments, unlike *C. suspecta,* and a greater number of radioles. However, the tips of the radioles and the presence of spatulate chaetae with short tips are in agreement between the two taxa. In light of the observation in Krøyer (1856) and Hofsommer (1913) of a very long inter-radiolar (palmate) membrane in *C. infundibuliformis*, this feature in *C. suspecta* cannot be considered to be diagnostic of that taxon. Without further study material, the status of *C. suspecta* will remain somewhat questionable. The additional information provided by Hofsommer (1913) on *C. suspecta* should be treated with some care, in light of that author's doubts as to the validity of the identifications because Krøyer (1856) did not describe the internal crown structures in any detail. It is proposed that further research should examine a wide variety of study material that could possibly conform to *C. suspecta*, focusing on variations in the height of the inter-radiolar membrane, segmental annulation (see remarks below on *Chone krøyerii* Sars, 1862 and *Chone fauveli* McIntosh, 1916) and chaetal form.

2.6.9 *Chone y* from the northern North Sea and Norwegian Sea

Background

A large number of *Chone* specimens, often misidentified as *Chone duneri* or referred to as *Chone* sp. are among the dominant soft-bottom sabellids in the northern North Sea and Norwegian Sea (Akvaplan-niva samples from the northern North Sea, between 1992-1999, most recently reported in Mannvik *et al* 1998a, b). These differ in several respects to the specimens of *Chone duneri* collected from the Pechora Sea and Barents Sea (reported in Dahle *et al.* 1998 and Cochrane *et al.* 1998). Close examination reveal these to comprise two types. The first type closely resemble *Chone longocirrata* Sars and are characterised by the presence of a faintly scalloped anterior collar margin, posterior inferior notochaetae of the broadly swollen form (see Figure 1.2.11e, f) and a marked hollowing of the faecal groove, particularly in posterior segments (see Chapter 2.6.7). Specimens belonging to the second type offer a number of taxonomic and systematic challenges primarily in terms of chaetal structure. The most appropriate strategy for identificationis not yet clear, mainly as a result of the ambiguity surrounding European Atlantic *Chone* in general. Thus, the strategy adopted here is to provide a brief description of the taxa, with emphasis on the characters peculiar to the specimens, and to highlight the areas requiring further study. Resolving this particular issue is beyond the scope of a single worker, but will be given priority as a co-operative project addressing the systematic status of north Atlantic *Chone* as a whole.

Taxonomy

Chone y

Material examined

Northern North Sea, between 100 and 350 m depth in silt-clay dominated sediments (co-ordinates given as petroleum field centre, or average sampling position, because an extensive network of stations was sampled and revisited at each field): Heimdal, 59°60'N, 2°23'E, Elf Petroleum Norge a/s, approx. 56 specimens, Frøy, 59°74'N, 2°59'E, Elf Petroleum Norge a/s, 100 specimens, Øst Frigg, Elf Petroleum Norge a/s, 59°87'N, 2°40'E, 45 specimens, Snorre, 61°30'N, 2°10'E Saga Petroleum, 120 specimens. Distribution records of these and other finds of the taxon are given in

Akvaplan-niva reports from 1992 to 1998, recorded as *Chone duneri* or, latterly, as *Chone* sp.

Norwegian Sea: Smøla, 63°18-28'N, 7°49'-8°13'E, 55 specimens (Larsen & Bahr 1993).

Description

Mature specimens approximately 11 mm in length, of which the crown comprises up to half the length of the trunk; width approximately 0.5 mm. Eight thoracic and between 28 and 35 abdominal chaetigers. Ventral shields not differentiated, but some lateral and ventral glandular patches evident on the first segment after staining with Methyl Green, using the Hofsommer (1913) method. Some glandular patches also present on posterior part of abdomen. Thoracic segments and anterior abdominal segments with mid-segmental constriction dorsally but not ventrally (Figure 2.6.5).

Five or six pairs of radioli, flanged up to near the tips, with long, tapering free ends (Figure 2.6.6a), from a quarter to a third of the total radiole length, united by a palmate membrane for at least two-thirds of the length of the radioli. Long thin pinnules, approximately 50 pairs per radiole. Pinnules of equal length along the entire length of the radiole. Four pairs of ventral cirri, two of which are almost as long as the radioles and have cartilaginous axes comprising a single row of cells. Collar deeply incised dorsally, ventrally apparently intact, rounded and highest at the mid-point. Marked ventral constriction just below the collar margin, with a marked ventral swelling of the peristomium. Collar margin higher ventrally than dorsally, exposing the base of the crown. Anterior collar margins generally involuted, usually with slightly scalloped edges. Dorsal lips elongate and pointed, ventral lips lower, more rounded.

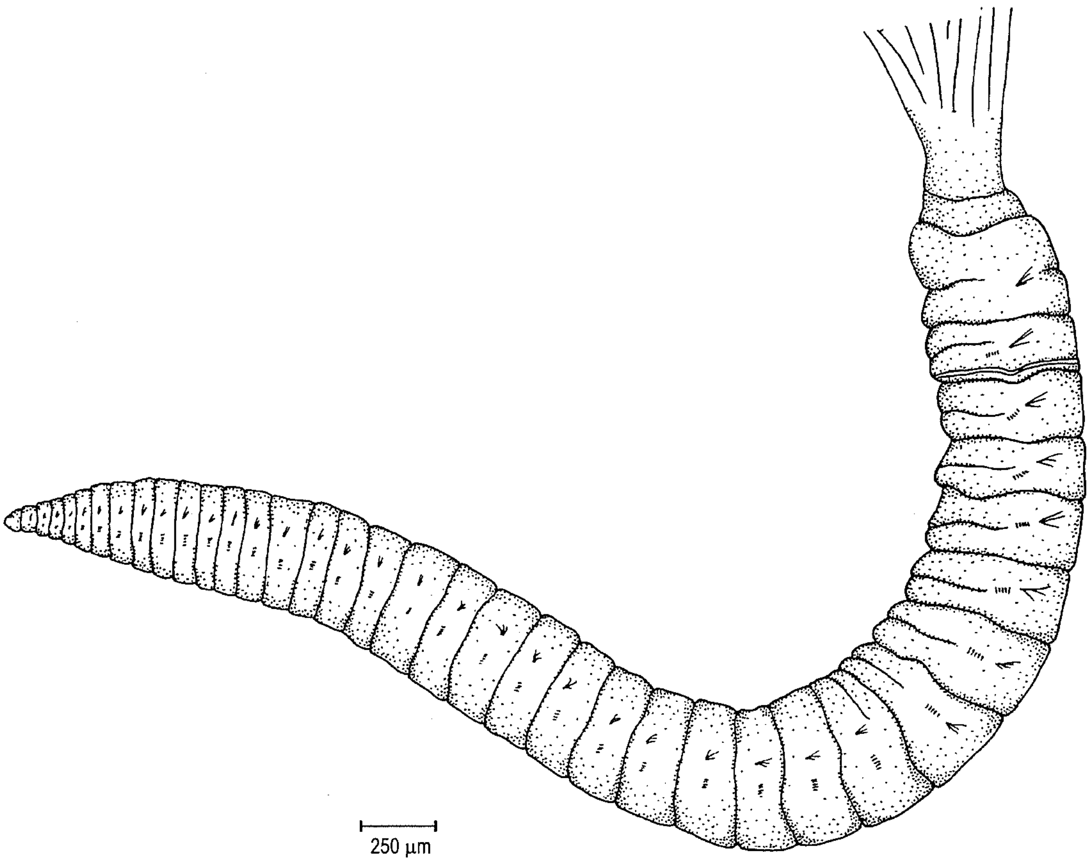


Figure 2.6.5. Chone y *from the northern North Sea. Lateral view of trunk. Note partial biannulation of thoracic segments.*

First thoracic notochaetal bundle slightly smaller than in the following fascicles. Chaetae in superior row elongate, narrowly swollen and geniculate at the base of the proximal taper. Anterior row of inferior notochaetae bayonet-type, posterior row shorter, broadly swollen, tapering with long tips (Figure 2.6.6b). Thoracic neurochaetae (uncini) acicular, long-handled, with teeth of uneven size above the main fang (Figure 2.6.6c). Abdominal neurochaetae elongate. Abdominal notochaetae (uncini) of 'typical' *Chone* form, with square bases. Single main fang below around four rows of smaller teeth. No significant variation in form of abdominal uncini observed along the length of the body.

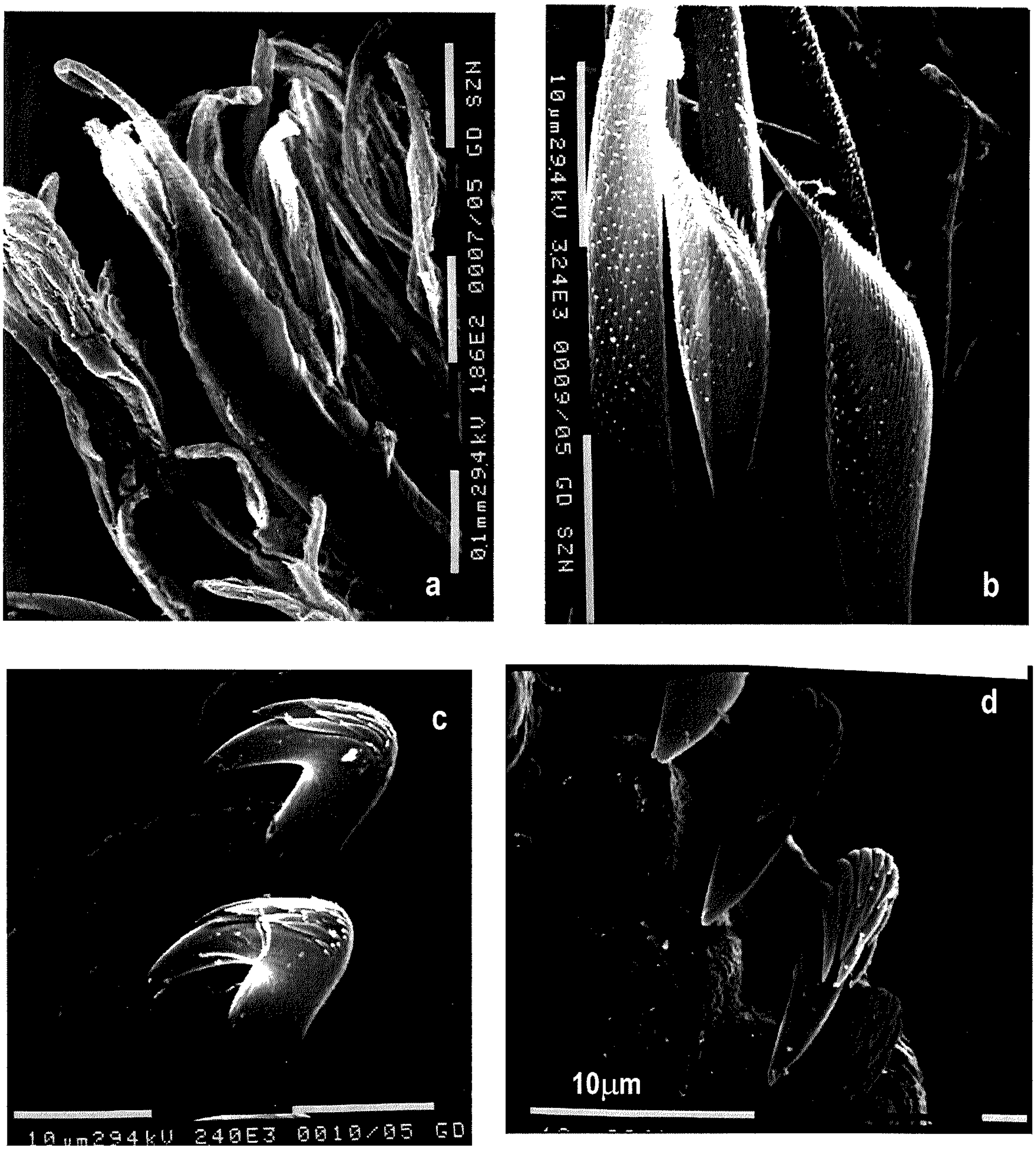


Figure 2.6.6. Chone y: *scanning electron micrographs of a) radiolar tips, note recurved tip obscuring its length, b) posterior inferior notochaetae from chaetiger 2, c) thoracic uncini from chaetiger 2, note teeth of unequal size above main fang and c) uncini from abdominal segment 2, mid-torus.*

Remarks

A number of features distinguish *Chone y* from *Chone duneri* and other related taxa. The most important of these are the presence of teeth of unequal size above the main fang in the thoracic uncini, a condition that is characteristic of *Amphicorina*, although it also is seen in some Fabriciinae. In addition, the posterior row of inferior thoracic notochaetae are markedly different from those seen in *Chone duneri*, which appear to be spatulate, or close to spatulate in form. Those in *Chone y* almost resemble the form often referred to as pseudospatulate (see Figure 1.2.12e, f). In light of the current ambiguity in chaetal terminology, this issue warrants further study. However, for the present purposes, it is sufficient to note that the posterior inferior chaetae differ from those in *Chone duneri*, *Chone infundibuliformis* and related taxa. In common with *Chone y*, *Chone suspecta* lacks biannulate segments, but the degree to which the characteristics of the posterior inferior notochaetae agree between the taxa remains to be clarified (see Chapter 2.6.8).

2.6.10 Remarks on other taxa

Records of the 'type species' of *Chone*, *Chone infundibuliformis,* described from Arctic waters, exist from a wide variety of locations, the validity of which are under question (see Giangrande 1992). Therefore, these are not cited here. Unless otherwise stated, the following description is based on Krøyer (1856), translated by Knight-Jones. Further taxonomic information on the taxon is given in Hofsommer (1913), Banse (1972), Knight-Jones (1990) and Giangrande (1992).

Chone infundibuliformis Krøyer, 1856,
Chone infundibuliformis Krøyer (1856): 33-34.

Specimens large, relatively stout, with a breadth of one twelfth to one tenth of its length, slightly flattened and narrowing to a point posteriorly. Entire worm can measure more than 87 mm in length and adult animal may possess up to 80 segments. Body relatively dark, with paler radioles, no markings. Segments biannulate in thorax and most of abdomen (Banse 1972).

Radioles numbering 14-22 pairs, in adults length of crown not exceeding one third of the body length. Hofsommer (1913) reported up to 25 pairs of radioles. Free ends of the radioles broad, leaf-shaped and included in the web margin[9]. Hofsommer (1913) noted that the radioles were united almost to their tips by this membrane, although other authors (see Banse 1972) reported the membrane to be two-thirds to three-quarters of the length of the radioles (see remarks on *Chone suspecta*). Three pairs of ventral cirri were noted by Krøyer (1856), but Banse (1972) reported up to six pairs. Pinnules numerous, long and thin.

Collar well developed, fitting closely, ventrally entire, without lobes or notches. Collar level and concealing radiolar bases (Banse 1972). Small ventral peristomial extension visible as a narrow ventral lobe (Giangrande 1992). First bundle of notochaetae on chaetiger 1 not markedly different in size or orientation to that on the succeeding segments. Notopodial lips conspicuous in thorax (Banse 1972). Thoracic notopodial chaetae of three types, as is typical for *Chone*, posterior row of inferior chaetae spatulate, with short pointed tips (Banse 1972). Glandular shields not differentiated.

Remarks

Chone infundibuliformis appears to be an Arctic taxon and records from more southern locations, particularly from Mediterranean areas, are most likely erroneous (Giangrande 1992; Knight-Jones pers. com.). Examination of specimens identified as *C. infundibuliformis* from southern Atlantic waters most often refer to *Chone fauveli* McIntosh or *Chone krøyerii* Sars. Although bearing a superficial resemblance to *C. infundibuliformis* in terms of body size and numbers of segments, those specimens possess a greater number of radioles and lack apinnate ventral cirri. An interesting feature of *C. infundibuliformis* is the very pronounced and clearly delineated faecal groove in anterior thoracic segments, almost resembling a deep mid-dorsal split or incision in the anterior part of the worm (Knight-Jones *pers. com.*). This observation is supported in specimens identified by the present author as *C. infundibuliformis* (reported in Dahle *et al.* 1998). Both *Chone fauveli* and *Chone krøyerii* were considered synonymous with *Chone infundibuliformis* by Fauvel (1927). As a result,

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[9] referring to the inter-radiolar (palmate) membrane

until recently, those taxa were not given much attention in the general identification literature, thereby contributing to the confusion.

Chone krøyerii[10] Sars, 1862

Chone krøyerii Sars (1862): 126-128, no figures

Original records from Manger, near Bergen, southern Norway, Tromsø and Vadsø, northern Norway, in gravelly sediments, between 10 and 50 fathoms (Sars 1862). Status: referred to *Chone infundibuliformis* Krøyer (Malmgren 1866, p.404).

Taxonomic notes

The following information was extracted from Sars (1862); incomplete translation from Latin.

Body cylindrical, slender, posteriorly tapering, with terminal anus. Total length approximately 40 mm[11]. Between 50 and 70 segments, biannulate, faecal groove[12] indistinct in posterior segments. Collar low, intact ventrally. Thoracic notochaetae comprising six elongate superior chaetae, six to eight shorter broadly swollen chaetae (referred to as subspatulate) and 8-10 bayonet-type chaetae. Thoracic uncini acicular, arranged in a single row, 12-14 per torus. Thoracic uncini avicular, 12-16 per torus. Radioles elongate, 8-10 pairs, connected by an inter-radiolar membrane. Apinnate ventral cirri present (Knight-Jones unpublished notes).

Remarks

Sars (1862) added (in Norwegian) that *Chone krøyerii* cannot be confused with the previous three *Chone* taxa described by Krøyer. However, Sars (*op. cit.*) stated that the specimens resembled *Chone paucibranchiata* (Krøyer) to such an extent that he was long predisposed to assume that that taxon (described on the basis of a single individual) was in fact a juvenile representative of *Chone krøyerii*, in which Krøyer may have overlooked the inter-radiolar membrane. Sars (1862) finally concluded that the two taxa were distinct as *C. paucibranchiata* possessed only three pairs of

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[10] in accordance with original manuscript, also referred to as *Chone kroyeri* in later works

[11] see Remarks

[12] tentative translation of *sulcus abdominalis*

radioles, while *C. krøyerii* specimens of the same body length possessed seven or eight pairs. Even individuals smaller than Krøyer's specimen of *C. paucibranchiata* possessed five or six pairs of radioles, which were united by only a very low membrane. Further, Sars (1862) pointed out that the segments in *C. paucibranchiata* are not biannulate (or at least this feature was not mentioned by Krøyer, 1856).

Knight-Jones (unpublished notes) noted that the larger specimens examined by Sars (1862) from Vadsø lack ventral cirri and agree well with *Chone fauveli*. The specimens from Manger and one from Vadsø should be regarded as *C. krøyerii*. The measurements in Sars (1862) therefore in part refer to *C. fauveli*.
Chone fauveli McIntosh, 1916
Chone fauveli McIntosh (1916): 36.- McIntosh (1923): 290, pl. cxxi, fig. 2, pl. cxxx, fig. 2.- Knight-Jones (1990): 275, fig. 6.20.- Kirkegaard (1996): 374, fig. 214.
Common in British waters (Knight-Jones 1990)

Taxonomic notes

Up to 120 mm in length, with approximately 80 abdominal segments. Up to 36 pairs of radioles, united for about three-quarters of their length by an inter-radiolar (palmate) membrane, with short, broad, flanged tips. Enlarged pinnules at the base of the dorsal radioles, but lacking ventral cirri. Collar entire ventrally, oblique, higher ventrally than dorsally, concealing radiolar bases.
Further details and illustrations of the taxon are given in Knight-Jones (1990) and Kirkegaard (1996).

Remarks

The lack of apinnate ventral cirri in *Chone fauveli* constitutes a diagnostic character sufficient to distinguish it from *Chone infundibuliformis*. A peculiarity of the taxon is that the anterior collar margin usually is flared distally (Knight-Jones unpublished notes). This does not appear to be a preservation artefact and is supported by examination of material from the west coast of Scotland (*pers. ob.*).

Chone paucibranchiata (Krøyer), 1856

Sabella paucibranchiata Krøyer (1856): 22-23.- *Chone paucibranchiata* (Krøyer) Dahle *et al.* (1998): 200.- Cochrane *et al.* (1998).

Type locality Finnmark, northern Norway[13]

Taxonomic notes

Based on Banse (1972), supplemented by partial translation of Krøyer (1856). Holotype with a trunk length of approximately 10mm, and a radiolar crown measuring 3.5mm. Maximum width approximately 1mm. Total number of segments approximately 50, of which eight are thoracic. Three pairs of radioles, united for at least one-third of their length by an inter-radiolar (palmate) membrane. Five pairs of slender ventral cirri, approximately one-quarter of the length of the pinnulated radioles. Thoracic uncini acicular. Thoracic notochaetae of chaetiger 1 orientated slightly more dorsally than those in the succeeding segments. Anus terminal. Krøyer (1856) did not describe the chaetae in detail and further details are not possible to determine due to the holotype having broken chaetae (Banse 1972).

Remarks

Because *Chone paucibranchiata* has a small body size and possesses only three pairs of radioles and was described from a single specimen, it often has been dismissed as being a juvenile form of another taxon. Interestingly, despite acknowledging *Chone paucibranchiata* as being distinct from *Chone krøyerii*, Sars (1862, p. 132) labelled that taxon as being uncertain. Malmgren (1866) and Fauvel (1927) considered *C. paucibranchiata* to be a synonym of *Chone infundibuliformis* (as juvenile specimen), but this judgement was not supported by Banse (1972). Until recently, specimens of *Chone paucibranchiata* have been sparsely available. As a result of recent finds of large numbers of mature individuals from near the type locality, supported by study specimens from the northern Barents Sea and the Pechora Sea (Cochrane *et al.* 1998; Dahle *et al.* 1998), doubts as to the validity of *Chone paucibranchiata* are here refuted. Future research on *Chone* will supplement the

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[13] the term Finnmark in the older literature may extend further south than in modern usage, thus including Tromsø

redescription of Banse (1972) with additional intact specimens lodged in the appropriate museums.

In a study of the benthic fauna in the Pechora Sea (Denisenko *et al.*, submitted to *Sarsia*), *Chone murmanica* Lukash, 1911 was listed amongst the Sabellidae recorded. However, the samples were taken at the same locations as those of Dahle *et al.* (1998), where the individuals in question were identified by the present author as *Chone paucibranchiata.* The illustration of the anterior end of *C. murmanica*, depicted in Lucash (1911) indeed closely resembles the drawing of *C. paucibranchiata* by Krøyer (unpublished manuscript). Both taxa have three pairs of radioles and a characteristically pronounced dorsal gap in the collar. The pinnular arrangement and structure of the free ends of the radioles also appear similar. The confusion may in part have arisen because *C. paucibranchiata* is not illustrated in the published literature. As co-operation in benthic research in Arctic areas is increasing, it is clear that further attention on this matter is timely and will be carried out during the continuation of the present work. It is anticipated that the work will be done in co-operation with the appropriate Russian taxonomists.

2.6.11 Taxa of uncertain status

Hofsommer (1913) described two *Chone* taxa from the Jutland area, which have been given little, if any, attention in the subsequent literature.

Chone gracilis Hofsommer, 1913, (not *Chone gracilis* Moore; i.e. junior homonym) was characterised as having in total between 49 and 54 segments. Hofsommer (1913) also noted that the inter-radiolar membrane, if present at all, was extremely low, almost reminiscent of the situation in *Dialychone* Claparède. The taxon was described on the basis of approximately 25 individuals.

Chone heterochaeta Hofsommer, 1913 was described on the basis of an anterior fragment comprising 12 segments. Seventeen pairs of pinnulated radioles were observed. The main distinguishing characteristic that justified its recognition as a discrete taxon was the presence of elongate chaetae in the thorax, with horizontal striations along the shaft. According to the illustration given, these are almost reminiscent of the semi-articulated chaetae in the Flabelligeridae.

In the absence of type material or further records of either taxon, their status cannot be determined.

2.6.12 Concluding remarks

As far as can be ascertained, the following *Chone* taxa have a distribution range within northern Atlantic waters, listed alphabetically:

taxon	comments on distribution
Chone infundibuliformis Krøyer	Arctic
Chone fauveli McIntosh	not Arctic
Chone krøyerii Sars	not Arctic
Chone paucibranchiata (Krøyer)	northern Norway, Arctic
Chone duneri Malmgren	Arctic, also more southern
Chone filicaudata Southern	Ireland, possibly UK, North Sea, Norway
Chone suspecta Krøyer	southern Norway, little known
Chone longocirrata Sars	southern Norway, probably wider range

The following taxa are of uncertain status:

Chone gracilis Hofsommer, 1913	Jutland
Chone heterochaeta Hofsommer, 1913	Jutland

Records of many of these taxa are confused, mainly as a result of unclear systematic status. The synonymy of taxa such as *Chone fauveli, Chone krøyerii* and *Chone suspecta* with *Chone infundibuliformis* and *Chone longocirrata* with *Chone duneri* has resulted in little attention having been paid to those taxa in the general literature. This in turn is largely responsible for the confusion in faunal records.

The information compiled in the present chapter, combined with examination of the study material collected during the course of environmental surveys carried out by Akvaplan-niva provides an excellent starting-point for a thorough revision of the status of northern European *Chone*. It is anticipated that this important task will be carried out in the near future, as a cooperative venture with the relevant authorities.

SYSTEMATIC PART

"My *name* is Alice, but——"
"It's stupid name enough!" Humpty Dumpty interrupted impatiently. "What does it mean? "
"Must a name mean something? " Alice asked doubtfully.
"Of course it must," Humpty Dumpty said with a short laugh: "*my* name means the shape I am— and a good handsome shape it is, too. With a name like yours, you might be any shape, almost. "

Lewis Carroll (1970), *Through the Looking Glass*

"The tendency has always been strong to believe that whatever received a name must be an entity or being, having an independent existence of its own."

John Stuart Mill, in Stephen Jay Gould (1990),
The Mismeasure of Man

3 Systematic part

3.1 A brief systematic history of the Sabellidae

This section outlines the major milestones in the systematic development of the present-day concept of the polychaete family Sabellidae. Further historical information on the Sabellidae and their relations is given in Fitzhugh (1989).

Classification of sabellid polychaetes dates back to the early part of the last century, when Lamarck (1818) recognised two discrete groups within the annelids: tubicolous and errant/ free-living forms. Within the tubicolous annelids, Lamarck designated two further categories: those producing calcareous tubes and those dwelling in soft tubes, the latter category including sabellid polychaetes (then partly described within *Amphitrite* Müller, 1774).

In 1822, Savigny erected the order Serpuleae, comprising three families. One of these families he named the Amphitritinae, within which three sub-groups were designated. One of these sub-groups was *Amphitrites sabelliennes*, which included the genera *Sabella* L. and *Serpula* L. This group, the *Amphitrites sabelliennes*, was established as a family by Burmeister (1837), and named the Serpulacei[1]. Johnston (1846) divided the Serpulacei into two discrete families: the Sabellidae and the Serpulidae. However, Grube (1851) continued to use Burmeister's concept of the Serpulacei, which he referred to as the Serpulacea.

Malmgren (1866) subsequently divided this family into three discrete families: Sabellacea, Eriographidae (encompassing *Myxicola* Koch *in* Reiner) and Serpulacea. Malmgren's subsequent work in 1867 named these families Sabellidæ, Serpulidæ and Eriographididæ, respectively. In 1868, Claparède continued the use of the family Serpulacea, further assigning two tribes within this family: the Sabellides (which included *Myxicola*) and the Serpulides. However, in 1870, Claparède removed *Myxicola* from the Sabellides tribe, assigning it to the tribe Eriographides. Thus, this system approximated to that of Malmgren, although the three groups were contained

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[1] spelling of the various groups follows that used by the respective authors

within the same family, whereas Malmgren considered them as families in their own right.

Langerhans (1880) discussed the systematic works of both Malmgren and Claparède and appeared to disagree with Malmgren's erection of the Eriographidea, which he claimed lacked the appropriate definition. Langerhans (1880) further disagreed with Claparéde's (1870) acceptance of this latter category, which then contained five genera. Doubting this as a natural group, Langerhans continued to follow Claparède's earlier (1868) work, in recognising two tribes within the 'Serpeln': the Sabellidae and the Serpulidae; the diagnostic difference being the lack and presence of a thoracic membrane, respectively.

Meyer (1888), whilst maintaining the use of the Serpulacea, recognised four groups within this. Fitzhugh (1989) interpreted these as four families: Serpulidae, Sabellidae, Eriographidae and Amphicorinidae (which included small sabellins such as *Fabricia* Blainville). In 1893, Hatschek recognised the sub-order Serpulimorpha within the Polychaeta, which contained the families Serpulidae and Hermellidae. Hatschek's concept of the Serpulidae contained the same groupings as Meyer's Serpulacea. Benham (1896) continued from Hatschek in recognising two main branches within the Polychaeta: the Phanerocephala and Cryptocephala, the latter being restricted to the two sub-orders Sabelliformia and Hermelliformia. True to the previous work of Meyer, the Sabelliformia comprised the four families Serpulidae, Sabellidae, Eriographidae and Amphicorinidae. The family Hermelliformia contained only two taxa: *Sabellaria alveolata* L. and *Sabellaria spinulosa* Leuk.

It should be noted that these developments in sabellid classification were not always updated in the general literature, and many textbooks failed to recognise the various sub-groups. For example, even in the fourth (1918) edition of Brehm's descriptive textbook on the 'lower animals' (1921, second printing), only the 'Serpulen' and 'Sabellen' are recognised within the family Serpulidae. The date of the first edition is unknown, but considering that the second edition was released in 1876, it is likely that Brehm followed the work of Claparède, although using the family designation reminiscent of Malmgren, just at a higher taxonomic level. It is evident that the subsequent editions of the work were published without updating the information on the Sabellidae.

Bush (1905) proposed a system of two tribes: the Sabellides and Serpulides. The former contained the Sabellidae and Eriographidae and the latter the Serpulidae. This is reminiscent of the previous work of Claparède rather than the more recent works of Meyer and Hatschek. Fitzhugh (1989) noted the lack of explanation given by Bush on the proposed arrangement.

Rioja (1923) cited the work of Benham (1896) and appeared to support the concept of the higher taxa Sabelliformia and the Hermelliformia. However, whilst recognising the contradictory opinions on the matter, Rioja decided to include within the Sabelliformia only the two families Sabellidae and Serpulidae. Within the Sabellidae he included Meyer's groups the Sabelliden, Eriographiden and the Amphicoriden (using the germanic rather than the latinised form). Rioja divided the Sabellidae into three sub-families: the Sabellinae, Fabriciinae and Myxicolinae. The main distinguishing criterion between the former two was the form of the thoracic uncini, which in the Fabriciinae have long, gently curving handles while in the Sabellinae these take the avicular form, being z-shaped with short handles. The sub-family Myxicolinae contained only *Myxicola*. The subsequent classification of Johansson (1927) was essentially similar to that of Rioja, but it did not recognise the Myxicolinae, placing *Myxicola* within the Fabriciinae. Interestingly, *Laonome* Malmgren also was placed within the Fabriciinae, despite the lack of acicular thoracic uncini in that taxon.

This fundamental recognition of the Sabellinae and the Fabriciinae was readily adopted in the subsequent literature, such as Kükenthal & Krumbach (1934, second edition). Interestingly, *Amphicorina* Quatrefages was listed under the sub-family Sabellinae, while *Oriopsis* Caullery & Mesnil was grouped under the Fabriciinae. Long, curving (acicular) thoracic uncini are present in both taxa, and *Oriopsis* recently was referred to *Amphicorina* (Rouse 1994). Thus, the appearance of the taxa under different sub-families in the literature is surprising. It is possible that the listing was in error, or that the chaetal characters were incorrectly observed.

Dales (1962) assigned the Sabellidae and Serpulidae within the order Sabellida, and placed the Sabellaridae (Hermelliformia) within the order Spionida. The influential work of Banse on selected Sabellidae (e.g. Banse 1970, 1972) followed Rioja's classification system, although using the spelling Fabricinae rather than Fabriciinae. Fauchald (1977) followed Rioja (1923) in recognising the Fabriciinae, Sabellinae and Myxicolinae within the Sabellidae, and further placed the recently described families Sabellongidae and Caobangidae within the order Sabellida.

A phylogenetic revision of the family Sabellidae was carried out by Fitzhugh (1989). The diagnosis of the sub-family Fabriciinae was restricted to include only those taxa with a single cartilaginous axis within the radioles (Fitzhugh 1989) and branchial hearts (Fitzhugh 1991a). The diagnosis of the Sabellinae was emended to include all sabellids with a radiolar skeleton comprising two or more rows of cells and mid-dorsal fusion of the branchial lobes (Fitzhugh 1989). Thus, many taxa (such as *Euchone*, *Chone* and *Jasmineira*), which previously were contained within the Fabriciinae, now are classified within the Sabellinae. Further details on this major revision of the Sabellidae are given in Chapter 2.4.

Two general works on the Polychaeta have been published subsequent to the 1989 review of Fitzhugh (Hartmann-Schröder 1996; Kirkegaard 1996). Although credit certainly is due to both authors for their wealth of compiled information on the Polychaeta as whole, it should be noted that the sections dealing with the Sabellidae are not updated. Hartmann-Schröder (1996) still used Rioja's (1923) distinction between the Fabriciinae and the Sabellinae, based on the form of the thoracic uncini. In Kirkegaard (1996), perhaps more correctly in cases of doubt, the sub-families simply were omitted and a key and diagnoses were given of the relevant taxa.

3.2 Willi Hennig and phylogenetic systematics[1]

3.2.1 Methods for systemising[2] taxa

The need for a system for ordering biological organisms into a logical system is deeply rooted, dating back to Aristotle (350BC). Hennig (1966) offered a broad explanation of systematics as being "all scientific activity that aims at ordering and rationalising the world of phenomena" with taxonomy, some workers have considered the role of systematics to be to provide "as complete and accurate a catalogue as possible of plant and animal species" (von Bertalanffy 1932). Zimmermann (1953) responded by claiming that "such a functional grouping is a technical, not a scientific, problem". This viewpoint was later supported by Hennig (1966), who considered hypotheses of descent to be essential to systematics. Borgmeier (1955), on the other hand, rejected the necessity of discussing how a systematic ordering of taxa might have arisen.

In any case, subsequent to evolutionary thinking, three main approaches to biological classification, or systemising taxa have been adopted. These are the traditional evolutionary approach, as used by, for example, Mayr (1969) and Mayr *et al.* (1953), phenetic taxonomy, presented as numerical taxonomy by Sokal & Sneath (1963) and the most recently developed phylogenetic systematics, also known as cladism (Zimmermann 1953; Hennig 1966). The present thesis adopts a phylogenetic approach to systematics, the main principles of which are outlined in this chapter. A brief comparison with evolutionary and phenetic methods is given in Chapter 3.2.14.

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[1] Chapter 3.2. is based on a review of the concepts expressed in Hennig (1966). Although the basic concepts are retained, some are used in a slightly different form in the discussions in Chapter 3.3 or the interpretations of the phylogenetic analyses presented in Chapter 3.5.

[2] preferred term, as used by Pleijel (2000), moving away from the rigid concept of ordering organisms into 'classes'

3.2.2 Background to phylogenetic systematics

Hennig (1966) gave a more precise interpretation of systematics as being "the investigation and presentation of all relations that exist among natural objects". Hennig's emphasis therefore was on devising a "general reference system and investigation of the "relationships between this and other possible systems" (Hennig 1966). Whereas ontogeny is the entire sequence of events involved in the development of an individual organism, phylogeny is the sequence of events involved in the evolution of organisms. Therefore, a phylogenetic system is one that expresses the evolutionary relationships between organisms at the chosen hierarchical levels, which may include the relationships between individuals within a population.

It is often falsely assumed that phylogenetic systematics is a 'new' means of systemising taxa but in fact the fundamental ideas were expressed already by the German workers Zimmermann (1937, 1943, 1953), Hennig (1950) and Remane (1952). Over the subsequent years, Hennig's 1950 manuscript was extensively revised, rewritten and translated into English, later issued as *Phylogenetic Systematics* in 1966. The availability of that work in English formed a turning point in systematic biology, and the principles of phylogenetic systematics steadily have become more accepted.

At the time of his writings, the ideas Hennig expressed were somewhat controversial, because they opposed the established principles of classifying organisms in terms of morphological similarity, without reference to an evolutionary hypothesis. In certain scientific circles the ideas were rejected by those who failed to see the potential in the approach, but they formed the inspiration for other workers. Latterly, however, Willi Hennig has become something of a legend in the field of systematics, and an active society for phylogenetic systematics, the Willi Hennig Society, has been founded in his name.

Phylogenetic systematics aims to offer a solution to the instability and uncertainties that mar traditional biological classifications by revealing natural, existing relationship groupings between organisms (Hennig 1966). This re-directs the focus of systematics towards biological information, and eliminates the frustration of purely nomenclatural arguments. Ultimately, this may help to stabilise taxon names. Because all disciplines that involve the study of organisms require a knowledge of systematics (Simpson 1961; Mayr 1969), research into phylogenetics has application throughout almost all fields of both botany and zoology.

The main structure of biological systematics in use today has its origins in the 10th edition the *Systema Naturae* (Linné 1758), published well over a century and a half before the writings of Lamarck and Erasmus Darwin, and still 100 years before Darwin published his theory of natural selection. Therefore, the main structure of present day systematics was devised against a background fundamental belief in discretely created entities called species. As a result, little concession is made for the possibility that, through time, different species may evolve from their ancestors, and that traits, or characters, may appear or equally likely disappear over time. With this in mind, it is not unlikely that some organisms exist that cannot easily be classified under a single taxon, but which bear a striking similarity to one or more taxa.

With the discovery of more and more species, the existing higher taxa became inadequate to encompass all the new species, requiring the erection of new genera, families, orders and classes, or at least rearrangement of existing ones. If we accept that species continually evolve from each other, this systematic difficulty will always be present as long as the higher taxa are not able to take this into account. Over the last two or three decades, polychaete taxonomists and systematists have begun to re-structure the higher taxa on the basis of phylogenetic systematic principles and, in time, it is hoped that the problems gradually will be resolved.

Subsequent to Hennig (1966), a wide range of reference works concerning the principles of phylogenetic systematics have been published, including Farris (1983), Ridley (1986), Wiley *et al.* (1991), Maddison & Maddison (1992), Quicke (1993), Kitching *et al.* (1998) and Lipscomb (1998). These have formed the backbone of the phylogenetic analyses carried out in the present work. However, because these use the translated volume of *Phylogenetic Systematics* (Hennig 1966) as their fundamental basis, the following is largely an interpretation of this text, using some examples relevant to the systematics of the Sabellidae.

The most important terminology used in Hennig (1966) is presented and clarified using concepts relevant to the Sabellidae. As in Chapter 1, the aim is to provide sufficient background knowledge of the subject to allow the results in Chapter 3.6 to be comprehended by the non-specialist. The most important terminology is summarised in the glossary in Chapter 1.5.

3.2.3 The fundamental units of phylogenetic systematics

In nature, the individual organism may undergo considerable variation in form during the course of its life, such as during development from larval to adult stages, or during sexual maturation. Such individuals may therefore exhibit remarkably different morphologies, or characters, at different stages of their lives. The term given to the individual at a certain point in its life is the "character bearing semaphoront" (Hennig 1966). In the case of a single sabellid individual undergoing development, the semaphoront of the three day old larva may have a crown of budding radioles, and only few segments, whereas the adult semaphoront will have a full radiolar crown and numerous segments. The process of changing semaphoronts in the individual may be termed ontogeny and thus the semaphoronts themselves are ontogenetically related.

The semaphoronts have obvious morphological attributes, but also may be described in terms of behaviour (feeding, locomotion etc.). This total consideration of the characteristics of the semaphoront is referred to as the 'total form', or 'holomorphy' (Hennig 1966). The holomorphy of a hypothetical adult sabellid semaphoront might therefore be described as sedentary, suspension feeding, broadcast spawning, with 20 pairs of radioles, 70 segments and so forth. Those attributes that describe the semaphoronts are referred to as characters. Some characters may be constant throughout the life of an individual while others may undergo considerable change. Individuals may be seen as semaphoront complexes, but Hennig (*op. cit.*) considered it to be the semaphoronts themselves, rather than the individuals, that form the fundamental elements of systematics.

3.2.4 Species and speciation[3]

A species may be considered as a complex of individuals interconnected by complex genealogical relationships, which are capable of reproducing only with each other. These genealogical relationships are known as tokogenetic relationships (Hennig 1966). An entirely separate species will have no members which are tokogenetically related to another species. However, species are not static entities and can evolve from each other, for example by geographic and reproductive isolation. This leads to a hierarchical relationship between the species, as shown in Figure 3.2.1, where the circles represent species and the arrows the direction of evolution (phylogeny).

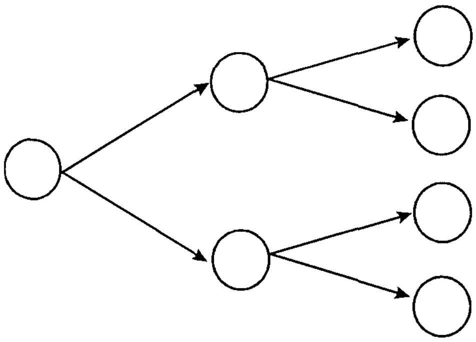

Figure 3.2.1.

Structure of the relationships among the elements of a hierarchy (after Gregg, 1954, modified from Hennig, 1966).

In such a hierarchy, the relationships are clearly unidirectional, and there is one, and only one, element from which arrows emanate, but to which no arrow leads. In the above example, the species are derived from a single common ancestor. This is the fundamental concept of the phylogenetic 'tree'. The genetic relationships which connect the species with each other are known as the phylogenetic relationships. Three main types of relationship are recognised in Hennig (1966):

- *Ontogenetic relationship* - the relationship between the semaphoronts;
- *Tokogenetic relationship* - the genealogical relationship between individual members of the same species;
- *Phylogenetic relationship* - the genetic relationships which interconnect species.

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[3] Because the present chapter is based on Hennig (1966), the use of the word species is retained, bearing in mind the inherent flaws (see Chapter 3.3 and subsequent chapters).

The total consideration of all these relationships is known as hologenetic relationships. Holomorphic differences among individuals within a single species are referred to as polymorphism. Polymorphism is particularly evident in the Sabellidae, where the number of radioles and abdominal segments may vary considerably between individuals of the same species.

For example, a hypothetical sabellid species generally has 15 pairs of radioles. However, some members have only 10 and others have more than 20. At a certain point in time, the numbers of radioles present in members of that species followed a unimodal distribution about the norm of 15 pairs. If, however, this distribution changed with time, such that it became increasingly bimodal, there would come a point at which two separate curves arose. At that point, the two conditions may belong to a pair of newly-evolved daughter species. This split from one parent species to two daughter species is known as speciation by cleavage.

As a result of this variability and continual process of change, there will always be individuals, which do not conform to the general species norm (or description). In the words of Hennig (1966) - “If absolute certainty of perceptions were a condition and sole justification for scientific effort, there could be no science at all. A characteristic of any science is the ‘endless task’ and the knowledge that its final goal will probably never be reached. This is also true of phylogenetic systematics.” Thus, our goal in creating a phylogenetic tree of interrelationships between groups of organisms is not to reach a finite endpoint. The goal is to resolve the main evolutionary pathways which have occurred in the past, and create the possibility for our descendants in the future to place those species which are evolving now, into a continuation of the same main framework.

3.2.5 Transformation

In theory, a pair of daughter species arising from a parent species by cleavage both differ from their parent in some way. However, species may also be formed by transformation, in which only a small part of the species population splits off from the parent population (Hennig 1966, see Figure 3.2.2). In this case, the parent species theoretically is unchanged, whereas the daughter species, which has split from the main population, is changed, or transformed. The series of changes in characters which occur during the course of phylogeny is known as the transformation series.

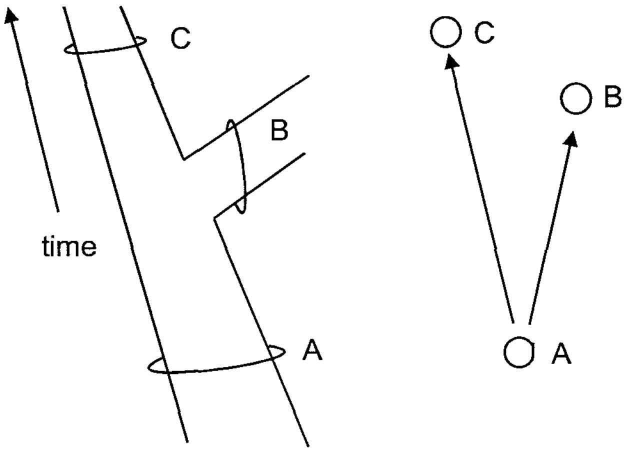

Figure 3.2.2.
Schematic representation of speciation by transformation of a portion of the population (modified after Hennig 1966).

This may be visualised in the Sabellidae by considering the morphologically similar genera *Chone* Krøyer and the 'larger' *Euchone* Malmgren (i.e. those with 'feather-like' radioles). For example, it is often debated whether a portion of the ancestral *Chone* species developed an anal funnel, to become the ancestral *Euchone*. This issue is addressed further in Chapter 3.6.

In most cases, 'splitting' of a new species from a parent species involves a change in the polymorphic range of that parent species (Hennig 1966). Thus, the scope of that species is changed by the transformation of a part of its members into a new species. This is indicated by the letters A, B and C in Figure 3.2.2.

3.2.6 Plesiomorphy, apomorphy and character polarisation

During the process of transformation, which ultimately results in speciation, features, or characters, change from their ancestral state to that of the daughter species, often involving a series of intermediate stages. Variations in the form of a character are termed character states. The state of the ancestral species is known as plesiomorphic while subsequently evolved states are termed apomorphic (Hennig 1966).

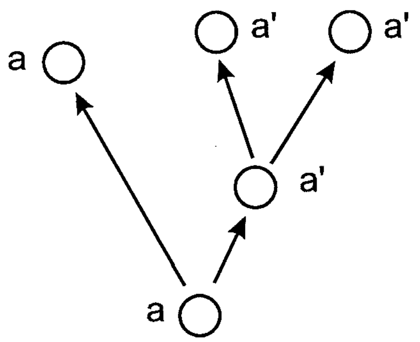

Figure 3.2.3. Illustration of the concepts of plesiomorphy (state a) and apomorphy (state a').

This may be illustrated in Figure 3.2.3, where the ancestral state of a particular character is a. Through transformation, the character assumes state a'. State a therefore is the plesiomorphic condition, and state a' is apomorphic. The direction of transformation of a character is termed its polarity or phylogeny (Hennig 1966). The actual process of determining which of the character states in a given transformation series represent the plesiomorphic and which the apomorphic conditions is termed character polarisation and is discussed in Crisci & Stuessy (1980). See also Chapter 3.3.8 on rooting trees).

An autapomorphy (Hennig 1966) is a characteristic of a monophyletic group which is not shared by other groups. Indeed, an autapomorphy may be visualised as being the 'fingerprint' of that monophyletic group (Kitching *et al.* 1998). A synapomorphy is a character which is shared by all members of that monophyletic group (Hennig 1966). In the case of the Sabellidae, one synapomorphy of the sub-family Fabriciinae is the mid-dorsal fusion of the branchial lobes. The sole synapomorphy of the genus *Amphicorina* Quatrefages (sub-family Sabellinae) is the presence of unequal sized teeth above the main fang (Fitzhugh 1989). However, this is not an autapomorphy, because this same characteristic also appears in some members of the Fabriciinae (see Chapter 3.2.8 on homoplasy).

3.2.7 Homology

The term homology was first used by Owen (1843), as a more precise form of the term analogy, as used by Saint-Hillaire (1818). Homology refers to character states that are derived from the transformation series of one and the same plesiomorphic, or ancestral-state, character. Therefore, homology may be defined as a trait shared by several taxa, that is derived from a single common ancestor. In this respect, homology may be seen as synapomorphy, at the chosen level in the phylogenetic hierarchy (see Patterson 1982, 1988; Brooks & McLennan 1991; de Pinna 1991).

In Figure 3.2.3, both states are homologous because the two character states a and a' have arisen from the same transformation series (i.e. by immediate common descent). For example, the branchial crown of the Sabellidae is homologous to the paired palps in groups such as the Spionidae (Orrhage 1980). A further review of homology in phylogenetic systematics is given in Nelson (1994).

3.2.8 Homoplasy

Homoplasy (see Harvey & Pagel 1991), or homoplastic character states, refers to morphologically similar features which are not due to immediate common ancestry, or characters that have reverted to their ancestral condition through the course of evolution. In general, homoplastic character states may arise through convergence, parallelism in a broad or narrow sense, or by reversalism.

Convergence occurs when a given character state is reached by transformation of another quite different character i.e. the same character state is reached by two different transformation series (a a' a" and b b' a" in Hennig, 1966). Parallelism occurs when the same transformation series occurs in different monophyletic groups, or evolutionary lines, described in Hennig (1966) as $\begin{matrix}a\ a'\ a''\\ a\ a'\ a''\end{matrix}$. The transformation of characters is not static, or even strictly unidirectional. Through the course of evolution, features that appear may subsequently be lost or even re-appear in the successive daughter taxa (Remane 1952). This phenomenon is known as reversalism (a a' a" a' a in Hennig, 1966).

The recognition of homoplasy is by no means simple and it is not possible to assess how frequently these actually occur in phylogenies (see reviews in Ridley 1986; Donoghue 1989; Moore & Willmer 1997 and references therein). For phylogenetic analyses, a character is treated as a homoplasy if it shows more changes on a tree than the minimum possible amount of change (Ridley 1986; Maddison & Maddison

1992). This implies that where the minimum amount of change is shown, homology is assumed.

3.2.9 Latent homology

The term homoiology, as used by Plate (1928) refers to non-homologous character states that ocur in closely-related taxa but which nonetheless developed independently in their bearers. In this respect, homoiology is a form of parallelism. Sæther (1979) argued that parallelism may be a result of either parallel selection pressure or common inherited genetic factors, including genetic mutations. The latter concept was termed inside parallelism (Brundin 1976) or underlying synapomorphy (Sæther 1977, 1979). Previously, this type of resemblance was referred to as orthogenesis (de Beer 1971). Nelson (1994) simply referred to the issue as latent homology. The concept may be visualised in terms of a larger clade, within which a smaller group of taxa possesses a character that is lacking in the other members of the main clade. Latent homology would be if all members of the clade were genetically capable of possessing the character, but the gene was only expressed in a sub-set of the clade. Sæther (1979) considered underlying synapomorphies to be equivalent to Hennig's (1966) concept of homoiology, i.e. parallelism amongst closely related taxa.

Determination of latent homology is not possible without the relevant gene being recognised. If the gene is recognised, it becomes included in the data set as a viable character, such that the concept of latent homology often is considered of little importance in phylogenetic systematics (Nelson 1994). In the present context, the issue is borne in mind, but not further addressed.

There appears to be some residual confusion surrounding these concepts in the literature, because Kitching *et al.* (1998) misleadingly defined homoiology as being a result of convergent evolution, rather than parallelism (see Hennig 1966 and Chapter 3.2.7). In any case, it is clear that the possibility of homoplasy within a data set should be given due attention (see Chapter 3.3.4 on homology testing).

3.2.10 The question of the higher taxa

Throughout the older literature, the status of the various taxonomic categories (taxa) has been debated. Some of the older literature (e.g. Uhlmann 1923) argues that the concept of the species is real, as it comprises a group of inter-reproductive individuals, but that the higher taxa are abstractions created by man. Thus, the species were considered 'objective' categories, whereas the higher taxa were considered 'subjective' (Rensch 1934).

In phylogenetic systematics, it is argued that the relationships between taxa exist, whether or not they are recognised by science (Hennig 1966). Phylogenetic systematics aims to recognise and describe the existing groups of inter-related organisms, rather than to create systematic categories, within which to place known organisms. Whereas traditional systematics places organisms into higher taxa on the basis of their similarity in appearance (without reference to a phylogeny hypothesis), phylogenetic groups are revealed by referring to the relevant tree. Therefore all phylogenetic groups, regardless of their inclusiveness, or level in the hierarchy of relationships, are equally 'real'. Providing systematic taxa are equivalent to monophyletic clades (see Chapter 3.2.11), higher taxa are not more subjective than lower taxa.

3.2.11 Monophyly, paraphyly and polyphyly

Hennig (1966) conceptualised individuals in terms of semaphoront complexes. Similarly, he regarded species as a collection of genealogically inter-related individuals. Therefore, individuals may be grouped together and termed 'species' and likewise 'species' may be grouped together into higher taxa. The central dogma in phylogenetic systematics is that for every higher taxon in the phylogenetic system, a 'stem' taxon exists from which all individuals included in the taxon have arisen. In other words, a higher taxon includes members that share a common ancestor and does not exclude any of its descendants. Such a group is termed monophyletic. A monophyletic group therefore represents a natural taxon. Providing the group fulfils the requirements of monophyly, the level at which the group is designated is not defined (see Figure 3.2.4). Hennig's (1966) concept of monophyly differs from that used in evolutionary taxonomy (see Chapter 3.2.13).

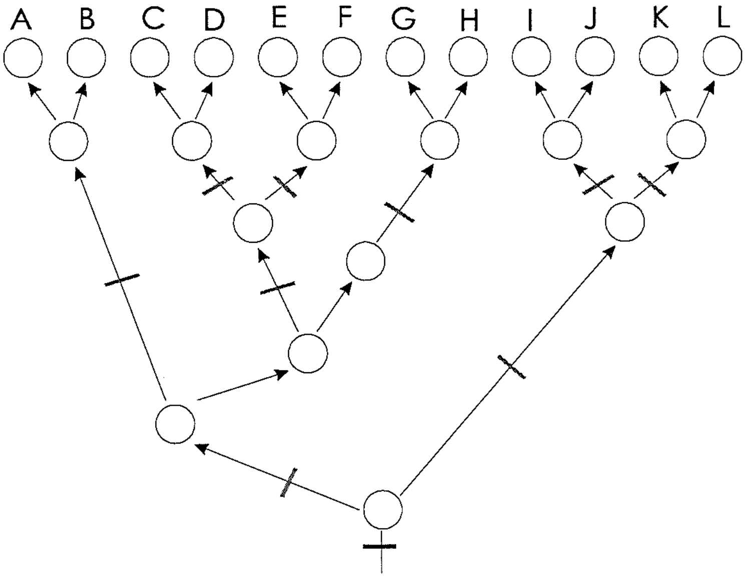

Figure 3.2.4. The concept of monophyly at several chosen levels. All taxa arising subsequent to each of the intersecting lines on the phylogenetic tree represent a monophyletic group.

Thus, in the case of the terminal taxa indicated by the letters A - L, A and B comprise a monophyletic group; likewise taxa C and D, E and F and so on. At a lower level on the tree, taxa C, D, E and F form a monophyletic group. Still lower, taxa C to H form a monophyletic group, as do I to L, and so forth. A paraphyletic group is one in which one (or more) of the descendants of the ancestor is (are) excluded from the group. A polyphyletic group is one where the ancestor is included in another taxon. In this way, both paraphyletic and polyphyletic groups can be considered to be artificial taxa. These concepts are illustrated in Figure 3.2.5.

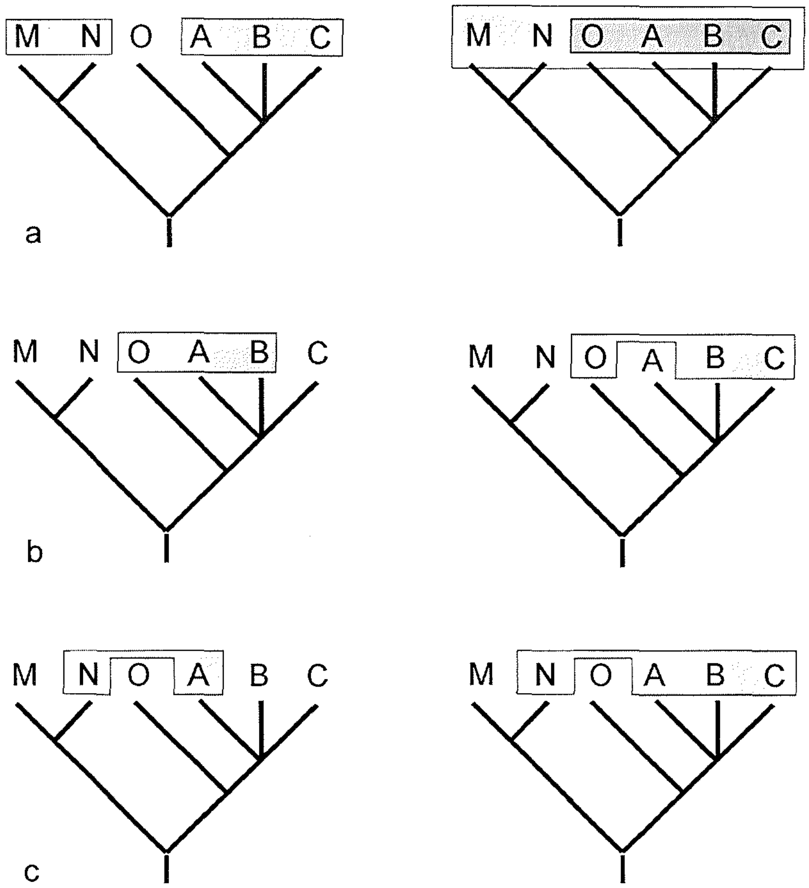

Figure 3.2.5. Examples of a) monophyletic, b) paraphyletic and c) polyphyletic groups (modified after Wiley et al. 1991).

Many of the traditional taxon names currently in use today are defined in terms of a few selected characters that are considered 'important', without carrying out analyses to determine at what point in the phylogeny these characters appeared (see Chapter 3.2.14). As a consequence, in phylogenetic terms, many of those taxa may be paraphyletic or polyphyletic. This applies to taxa at all levels of the systematic hierarchy, from phylum, through order and class to genus. For example, in recent years there has been much discussion on the validity of the Annelida as a taxon. Most authors agree that the traditional concept of the Annelida (segmented worms) represents an artificial taxon (e.g. Barnes 1980). In recent years, several workers have addressed the problem and proposed alternative systematic arrangements of the constituent taxa. There has been much debate as to the systematic status of various other taxa traditionally outwith the Annelida, such as the Echiurida and Pogonophora. A review of this broad and still somewhat controversial issue is outwith the scope of the present work, but the main arguments and discussions may be followed in the following publications (in chronological order): Rouse & Fauchald (1995), Eibye-Jakobsen & Nielsen (1996), McHugh (1997), Rouse & Fauchald (1997), Kojima (1998), Siddall *et al.* (1998) and most recently, McHugh (1999).

Fitzhugh (1989) addressed the issue of monophyly of the constituent sub-families within the Sabellidae. As mentioned in Chapter 1.2.5, prior to this study, the criterion used to group the Sabellinae was the form of the thoracic uncini. Phylogenetic analysis revealed this to be a homoplasy, rather than a synapomorphy, resulting in an extensive rearrangement of the taxa within the two sub-families, the Fabriciinae and the Sabellinae. The main arguments and conclusions of this revision are presented in Chapter 3.5.

3.2.12 Hennigian argumentation

Using the concepts described above allows a hierarchical cladogram, or 'tree', to be constructed wherein the taxa are arranged in terms of their relative apomorphy. The cladogram is constructed using a series of polarised characters (i.e. where the direction of transformation is known before constructing the cladogram). The information contained within each polarised character is treated individually, and monophyletic groups, or clades, are recognised in terms of possession of shared apomorphies. This use of *a priori* recognition of apomorphy is known as "Hennigian argumentation" (reviewed in Kitching *et al.* 1998).

In practice, the most widely used method of character polarisation is the 'outgroup method', whereby the characters possessed by a group of taxa under investigation (the 'ingroup') are compared with those possessed by one or more known ancestors (the 'outgroup'). The character state of the outgroup is always the plesiomorphic condition. This is also known as 'rooting' the cladogram, or tree and is discussed further in Chapter 3.3.8).

Hennigian argumentation thus allows groups of taxa to be represented hierarchically in terms of their transformation history, as well as revealing sister-group relationships. However, because characters are prone to reversibility, parallelism and convergence (see Section 3.2.7), there is seldom only one tree that represents all possible evolutionary scenarios (reviewed in Ridley 1986; Maddison & Madison 1992). Where the data set comprises several species and many characters there may be hundreds or thousands of cladograms representing possible relationships between the taxa.

In order to process this information into a meaningful entity, the least likely scenarios are rejected, leaving one or several cladograms as the most plausible hypotheses. The present work uses parsimony for cladogram selection (see Chapter 3.2.12). Other methods for cladogram selection exist, such as the principle of maximum likelihood (see Felsenstein 1973; Goldman 1990 and references therein). This approach uses frequency probability to arrive at phylogeny hypotheses and will not be considered here. Further insight into the use and logical difficulties associated with probabilism in phylogenetics is given in Siddall & Kluge (1997). A discussion of parsimony compared with other methods of cladogram selection is given in Felsenstein & Sober (1986) and Sober (1988).

3.2.13 Cladogram selection using parsimony

Parsimony analyses have been presented as providing a reasonable assumption of character evolution (Maddison 1991; Maddison *et al.* 1984) and may be thought of as the most simple solution to the problem in hand. In the context of multiple cladograms, the most parsimonious would be the one containing the least amount of convoluted transformation series, such as reversals, convergences and parallelisms (reviewed in Farris 1983; Kitching *et al.* 1998). This is easily illustrated by a simple three-taxon statement (Nelson & Platnick 1991), wherein two taxa are most closely related to each other than they are to a third. Table 3.2.1 shows a hypothetical character matrix for three taxa, A, B and C. Characters 1, 2 and 3 are coded as states 0 or 1, with 0 being the ancestral state. Therefore, the characters are polarised, but the ancestral taxon is not shown on the data set.

	A	B	C
1	1	0	1
2	1	1	0
3	1	0	1

Table 3.2.1.
Hypothetical data matrix for a three taxon statement of taxa A, B and C. Characters 1, 2 and 3 are coded as states 0 or 1, where 0 is the ancestral, or plesiomorphic state.

Where the ingroup comprises only three taxa, only three possible scenarios could express the relationships between the taxa. Either A and B are more closely related to each other than they are to C, or B and C are more closely related than they are to A, or C and A are the most closely related.

Figure 3.2.6 shows these three cladograms, with each step in the three transformation series (characters) marked as slashes on the appropriate branch of the trees. Each slash is referred to as a 'step'. In this example, each step represents a transition from the ancestral state 0 to the apomorphic state 1.

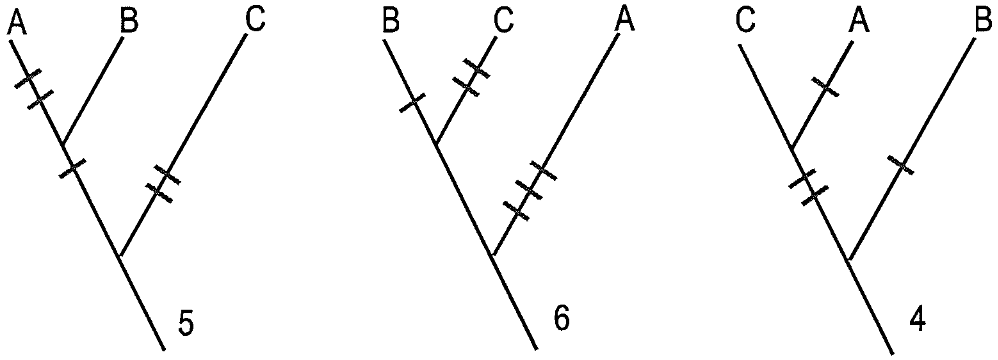

Figure 3.2.6. Demonstration of the principle of parsimony; step numbers are shown at base of cladograms. The cladogram comprising 4 steps is the most parsimonious.

Where the apomorphy is shared by the two most closely related taxa (on each of the cladograms), there is only one step. Where it appears in only one of the 'paired' taxa and the third taxon, the transformation is marked as two independent steps (parallelisms). Note however that this could equally well be represented by a single transformation at the base of the tree (i.e. shared by all three taxa) and a reversal back to the ancestral state in the appropriate taxon. In either case, this would represent two steps, such that the choice of representing the steps as parallelisms or reversals is somewhat arbitrary.

In the above example, the right-hand tree would be selected as being the most parsimonious, as it comprises the lowest number of steps. Had a different set of transformation series, or characters, been used, the results may have been such that there were two equally parsimonious trees, in which case, both would be considered as equal hypotheses of the evolutionary scenario.

This same method of tree construction is used for larger data sets, comprising numerous taxa and characters. Because the number of possible cladograms increases logarithmically with increasing numbers of taxa, computing these manually soon becomes a monumental task. As a result, various computer algorithms have been developed to construct the possible cladograms, trace the steps entailed by the transformation series and to retain the most parsimonious trees (see Maddison & Maddison 1992). The fact that these algorithms are based on a very simple principle dissipates the mystery of computerised phylogenetic analysis, or 'cladistics'.

Having arrived at one or several parsimonious trees, it is essential to bear in mind that parsimony does not necessarily reflect the correct evolutionary scenario (Felsenstein 1978, 1983a, b; see also Ridley 1986). Because we have no direct knowledge of the speciation processes that took place long ago, the absolute 'truth' always will elude us. Choosing the most parsimonious trees as reflecting the most likely pattern of relationships assumes that evolution took place along the simplest route of character transformation. This must be regarded as no more than a working assumption, but for the sake of research, it may be accepted as being plausible. As a result, parsimonious cladograms never can be more than most plausible hypotheses to explain patterns of shared apomorphies between a set of taxa. Providing these limitations are borne in mind, phylogenetic analysis using parsimony offers an informative means of exploring relationships between organisms.

3.2.14 Comparison with evolutionary and phenetic approaches

Subsequent to evolutionary thinking in the 19th century, taxonomists and systematists aimed to produce a natural, rather than artificial, systematic hierarchy that reflected the course of evolution. In this respect, the aim, if not the method, of evolutionary systematics is similar to that of the phylogenetic approach. The main principles of evolutionary systematics are outlined works including Mayr *et al.* (1953), Mayr (1969), Simpson (1961) and Mayr & Ashlock (1991). The approaches are further discussed in Ridley (1986), Holthe (1987) and Quicke (1993).

Evolutionary taxonomy aims to provide a hierarchical grouping of taxa, based on the distribution of character states and their phylogeny (reviewed in Ridley 1986). However, Simpson (1961) considered evolutionary classification systems not to express phylogeny, nor even to be based on it (except in a very broad sense), but merely as being consistent with it.

In evolutionary taxonomy, it is recognised that only homologous characters can be used. Thus, shared characters resulting from convergence must be recognised and excluded from the classification scheme. One means of doing so is to exclude characters of adaptive value, using only 'selectively neutral' characters (see Ridley 1986). The relative taxonomic value, or weight, of characters is sought, in order to ensure that groups are recognised on the basis of informative, taxonomically important characters. Examples given by Mayr (1969) of highly weighted characters include those that are highly complex, fit a broad range of environments, non-adaptive, resistant to ecological shifts and characters that co-occur but are independent of each other. In addition, characters that are consistently present in one group but consistently absent in another are highly-weighted. A major criticism of this technique is the subjectivity it allows in designation of character importance (reviewed in Ridley 1986).

A fundamental difference between evolutionary taxonomy and phylogenetic systematics is the interpretation of monophyly. Mayr (1969, p.75) stated that "cladists sometimes claim that their theory of classification is the only one that can lead to the establishment of monophyletic taxa. This claim is based on a misinterpretation of the concept monophyly". Mayr (1969) supported the definition of monophyly being "the derivation of a taxon through one or more lineages, from one immediately ancestral taxon of the same or lower rank" Simpson (1961). As shown in Chapter 3.2.10, Hennig (1966) restricted the concept of a monophyletic group as one comprising organisms that share a common ancestor and which does not exclude any of its descendents. This definition was rejected by Mayr (1969) as being "contradictory to common sense". Thus, a character shared by all members but one of a group would be considered paraphyletic in Hennigian terms (see Figure 3.2.5b), but would still satisfy the criteria of monophyly in evolutionary taxonomy.

Numerical (phenetic) taxonomy aims to remove the subjectivity associated with character weighting by removing it altogether such that all characters are weighted equally (Sokal & Sneath 1963). Phenetic methods are further discussed in Farris (1983), Ridley (1986) and Holthe (1987). The main advantages of such procedures were considered to be objectivity and repeatability (Sneath & Sokal 1973). Phenetic classifications produce hierarchical clusters of taxa based on numerical assessment of similarity (or dissimilarity) between the taxa, without consideration of phylogeny. However, despite the claims of repeatability, Johnston (1970) showed that different statistical calculations of dissimilarity produced different clusters. In addition, different means of measuring distances between taxa also produced discrepancies in results. Because there is no means of objective selection of computational method, the results of phenetic classification may be said to be subjective. Thus, the argument of objectivity and repeatibility in phenetic taxonomy becomes circular. In the present work, numerical taxonomy is used to discern spatial trends in faunal structure across a sampling area, using a species by station frequency data-set. The method is not considered further.

In conclusion, phenetic and phylogenetic methods of systemising taxa arose from a desire to address the problem of subjectivity in assigning relative importance to characters in evolutionary taxonomy. Phenetic methods aimed to remove the subjectivity, while phylogenetic methods aimed to improve the methods for inferring the path of evolution (Ridley 1986).

As outlined in the foreword, taxonomy and systematics of the soft bottom sabellin taxa that inspired the present research presents a number of challenges. The characters are in some cases difficult to quantify and show a great deal of variation both within and between taxa. In many cases, the characters previously considered 'important' to traditional sabellid classification systems did not appear to be consistent in terms of the groups involved. To avoid the risk of subjectivity in assigning character importance, a phylogenetic approach was chosen. Because the most recent revision of the Sabellidae (Fitzhugh 1989) was carried out using phylogenetic analyses, with parsimony as the cladogram selection method, the present work is directly comparable with and supplementary to previous research, only focusing on smaller, less inclusive groups of taxa.

3.3 "Tree thinking"[1] - some current issues in cladistics

3.3.1 Background

This chapter has been much inspired by lectures and discussions between and with (in alphabetical order) Kristian Fauchald, Kirk Fitzhugh, Fredrik Pleijel and Greg Rouse. To these I owe my 'tree-thinking' and for this I am eternally grateful. I do not claim originality; most of the ideas have occupied the above and other workers for many years. Further, I have discussed the concepts merely as I have perceived them. Therefore, any errors and misconceptions are my own entirely.

Further, I beg forgiveness for some sections, particularly those relating to faunal community analyses, which may appear over-laboured in point. This came about because the issues are not widely discussed amongst those commercially involved in such activities, at least not in Norway. My aim was to create a simple awareness of the pitfalls, to allow me to influence the studies carried out by myself and my colleagues, in any small way possible or appropriate.

3.3.2 The overall aims of phylogeny reconstruction hypotheses

Before carrying out cladistic, or phylogenetic, analyses, it is important to establish the overall aims of the technique. Cladistic analyses might be thought of as aiming 1) to infer the phylogeny of the group in question or 2) to reveal a natural hierarchical order between a group of organisms, from which a classification system can be derived. In fact, both these interpretations are correct, but the fundamental aim may be stated more simply. Phylogenetic analyses aim to present an explanatory hypothesis of relationships to account for observed shared similarities between taxa.

Shared similarities are expressed as homologies. Therefore the issue of homology is fundamental to cladistic analyses. Each coded character represents an elemental hypothesis of homology. Parsimony analyses produce a cladogram, or tree, which may be thought of as a composite hypothesis. Where several equally parsimonious

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[1] term coined by O'Hara (1988)

trees are produced, a consensus tree is no more than a composite hypothesis of all the composite cladograms.

3.3.3 Trees as explanatory hypotheses

Because phylogenetic analyses are concerned with shared similarities derived from a common ancestor, it is impossible to observe all the components of the hypotheses. We observe organisms existing in the present time, take note of their features and form sets of characters. On this basis, a series of elemental hypotheses of homology are formed. A cladistic analysis carried out on such data produces a composite hypothesis of relationships between the taxa under investigation. This composite hypothesis of relationships includes hypotheses of common ancestors. Because these common ancestors existed in the past, the truth will never be known for certain.

Just as it is important to recognise that a common ancestor cannot be seen (except in some instances as fossil remains), it is essential to remember that the Linnean higher taxa are artificial concepts in a phylogenetic sense. A genus does not evolve as a unit, nor can a genus as such be examined. All that can be seen of a genus is a set of shared characteristics between a set of included taxa, commonly referred to as 'species'. At the risk of inducing controversy, the same statement also might be applied to the 'species' concept. The only real single entity is that of the individual. A group of individuals sharing similar characteristics are grouped together, and it is this collective unit that is commonly referred to as the 'species'.

It has been argued that the aim of science is merely to find a satisfactory explanation (rather than a firm conclusion) for whatever phenomenon appears to need explaining (Popper 1979). In the present context therefore, it may be accepted that cladistic analyses need not be more than acceptable phylogeny hypotheses. Abduction may be thought of as inference to the best explanation, or looking for a pattern in a phenomenon and suggesting a hypothesis (Peirce 1878). In this sense, abduction is not falsification in the sense of Popper (1965) but rather the process by which hypotheses are generated (Rescher 1978). Abductive inferences are not based on experimentation, nor do they lead to immediate conclusions, but may be seen to advance the present understanding in the form of new hypotheses.

Cladistic analyses allow abductive inferences to be made, selecting the hypothesis or hypotheses which best explain the observed phenomenon, based on the available evidence. Thus, cladograms, being abductive inferences, do not necessarily present the truth, only the most plausible hypothesis based on the information currently available. New information can (and frequently does) change that hypothesis and lead to a new hypothesis. In this way, cladistic analyses of groups is constantly evolving, as more evidence becomes available. Thus, an abductive cladogram cannot be 'tested' in the statistical sense. The homology statements may be 'tested' (see Chapter 3.3.4) or comparative statistics may be applied to sub-sets of characters (see Chapter 3.4.8 under 'the comparative method'). However, the actual hypothesis of phylogenetic relationships cannot conclusively be proved or disproved.

3.3.4 Homology testing

As shown above, the principle of homology is fundamental to systematics and comparative biology. An important concept is the equation of homology with synapomorphy (Patterson 1982; reviewed in de Pinna 1991 and Nelson 1994), confirming that homology statements must be treated as hypotheses rather than known facts. Thus, a transformation series of a single character is a hypothesis of homology, which must be borne in mind during character coding.

A hypothesis of homology is the recognition of the equivalence of characters between taxa (de Pinna 1991), although these need not necessarily be morphologically identical. However, because characters may diverge in form and /or function during the course of evolution, or apparently similar features in two taxa may be the result of convergence or parallelism (see Hennig 1966; Chapter 3.3.8), the homology of characters should be 'tested' for congruence before drawing conclusions.

The most widely-used and logically reliable tests of homology are empirical methods, which depend on acceptance of homology as synapomorphy. These are discussed in de Pinna (1991). Empirical homology testing is achieved after or during cladogram construction, a process known as character congruence testing. Characters are deemed homologous (and therefore synapomorphic) between two or more taxa if, and only if, they fit to a cladogram with the same number of transformation steps. Characters requiring more steps are revealed as homoplastic. Homology testing becomes more rigorous the more characters that are included in the analysis. Thus, a large character inclusion set will give the most confidence in the homology hypotheses, relative to a more restricted character matrix.

3.3.5 "Total evidence" or partitioned analysis?

Willi Hennig's concept of holomorphy was outlined in Chapter 3.3. Holomorphic characters comprise ecological, morphological, genetic or any other attributes pertaining to the organisms in question. An as yet unresolved debate has ensued as to whether the different types of characters should be analysed separately, and the resulting cladograms then combined into a consensus tree or whether all such characters should be included in a single analysis. These approaches are known as taxonomic congruence and character congruence or total evidence, respectively (Mikevich 1978; Kluge 1989).

Nixon & Carpenter (1996) preferred to use the terms partitioned analyses and simultaneous analyses, because the two approaches both use all the available information, but differ in the way that information is processed. In partitioned analyses, the available data is partitioned into different 'types', for example genetic, morphological, ecological etc., and analysed independently. After the best-fitting cladograms for each of the partitioned data sets have been selected, a consensus method is used to obtain the overall best-fitting cladogram. On the other hand, in simultaneous analyses, all characters, be these ecological, morphological or genetic, are included in a single phylogenetic analysis. The main arguments are reviewed in Kluge & Wolf (1993), de Queiroz *et al.* (1995) and Nixon & Carpenter (1996). Figure 3.3.1. shows a schematic comparison of the approaches.

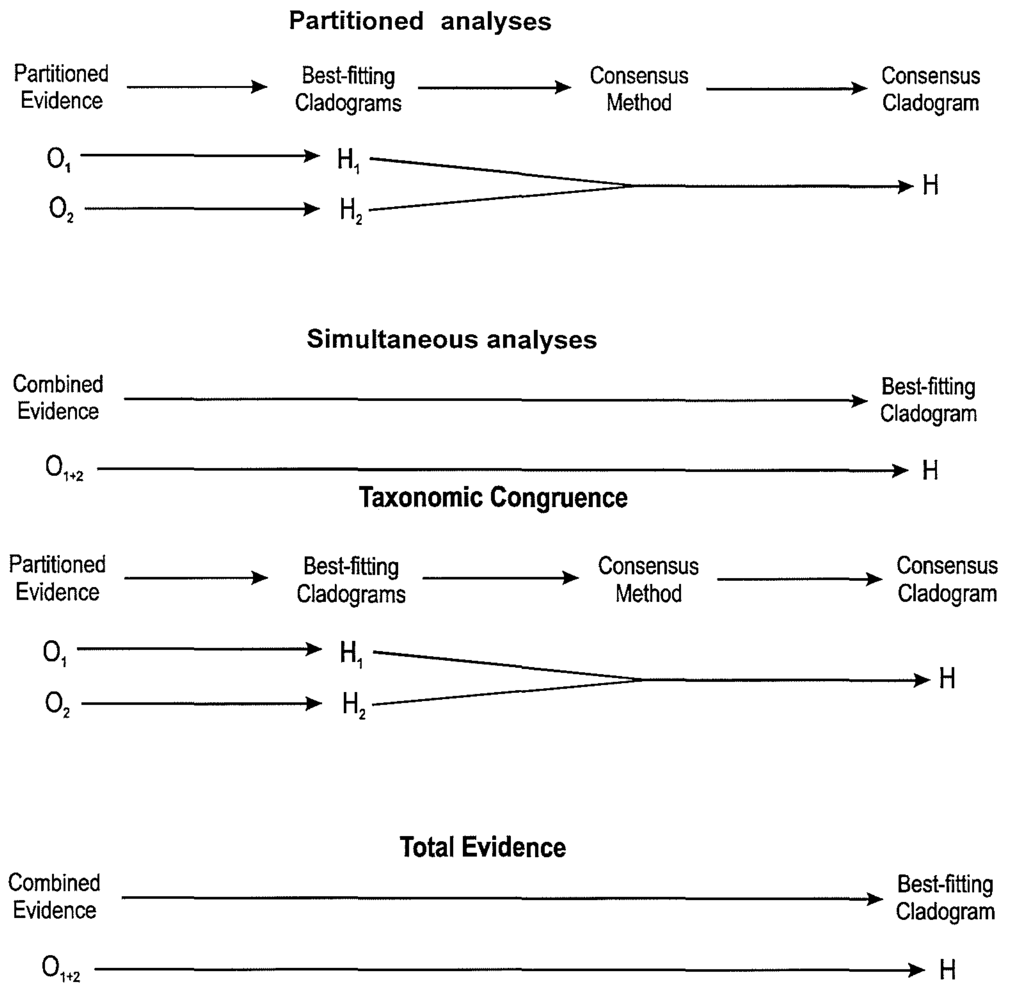

Figure 3.3.1. Comparison of analytical approaches used in taxonomic congruence (partitioned analyses) and the total evidence method (modified after Kluge & Wolf 1993).

It might reasonably be argued that organisms comprise living entities which possess morphological, genetic, behavioural and a host of other attributes simultaneously. Each of these attributes becomes a character (regardless of 'type'), and thus is a hypothesis of homology (see Patterson 1982; Nelson 1994). Each of these elementary hypotheses contribute to the overall composite hypothesis, the cladogram.

Cladograms, being abductive inferences, may be changed by the addition (or subtraction) of premises. Thus, splitting up a data set and conducting separate analyses on the constituent parts may not result in the same composite hypothesis. In other words, a cladogram based on morphological attributes may produce a different homology hypothesis than one based on another set of premises, or characters. The differing cladograms then form mutually exclusive hypotheses of ancestry to explain different sets of observed features.

If cladistic analyses are a form of abductive inference, then so also is the concept of homology. Homology statements (the characters) form the basis of phylogenetic systematics, and, being abductive inferences, all the available evidence is required to arrive at the most plausible phylogeny hypothesis. Because morphological, behavioural and ecological traits are present simultaneously in organisms, it is plausible that to obtain the best fitting homology hypothesis, all available evidence should be used simultaneously.

The choice of strategy is not free from debate and a full discussion of the arguments for and against both partitioned and simultaneous analyses are outwith the scope of the present work. De Quieroz *et al.* (1996) pointed out a range of arguments for and against both methods and concluded that in some circumstances, it might be justifiable to partition data, while in other cases a simultaneous approach would be more appropriate. They advocated a careful scrutiny of the data sets involved, in the context of the particular method of tree selection used before deciding on the analytical strategy.

The total evidence approach, by dealing with all known characters in a single analysis, is said to maximise cladistic parsimony and can, on these grounds, be argued as being the preferable method (Kluge & Wolf 1993; Nixon & Carpenter 1996 and Zrzavý 1997). A common criticism of combined analyses is that the analyses may become biased towards the most numerous 'type' of character (see Kitching *et al.* 1998). For example, genetic characters as a rule are more numerous than morphological characters, which in turn tend to outnumber ecological characters. However, this criticism makes a fundamental, and arguably unjustified, assumption of the existence of discrete types of premises in nature, which appears to contradict the concept of organisms as holistic entities. Instead, it might be argued that evolution should be recognised as an integrated process, whereby the differential possession of genes, morphological and ecological attributes of organisms evolve together and thus should not be treated separately in phylogenetic analyses.

In many instances, the discussion moves into a theoretical rather than a practical realm. The act of separating form and function becomes arbitrary, rather than a logical procedure. A morphological feature may or may not have an ecologically significant function. A gene may or may not be expressed in the form of a visible trait. Partitioning data therefore can lead to subjective and operator-dependent data sets. Individuals do exist in the present, and these individuals possess a myriad of characters simultaneously. The viewpoint taken here is that individual characters possessed by an individual cannot be considered in isolation of the other characters of that same individual. Having said this, however, the independence of characters must be considered. A behavioural pattern may co-vary with a morphological feature; for example long-beaked birds may be precisely those that feed on nectar and the two observations could be construed as inter-related, rather than independent characters.

Luckow & Bruneau (1997) argued that such co-varying characters, whether arising through one or a combination of adaptation or hereditary processes, do not necessarily constitute non-independence of characters. Before them, Wilkinson (1995) distinguished between logical and biological independence of character, and compared and contrasted different methods of character construction aimed to resolve the dependence issue. Finding different logical traps in different methods, he advocated a careful scrutiny of the individual character (or set of characters) before choosing the appropriate analytical strategy. Like the subject matter, arguments of circularity and character independence often end almost where they began. The matter is acknowledged here, but the arguments are not represented in any detail, apart from some further relevant issues which are discussed in Chapters 3.3.7 and 3.3.10 (under 'Ecology meets systematics').

In summary, therefore, the aim of cladistic analyses is to use homology hypotheses to explain shared similarities amongst taxa existing in the present, by way of inferring evolutionary events which occurred in the past. The criticism of inadvertent weighting, or 'bias', by including different 'types' of characters in a single 'total evidence' analysis may be countered by questioning the logic of treating characters as discrete classes of homologies. The concept of organisms as holistic products of evolution is embraced, and, at the present point in time, the logic behind the 'total evidence' approach is supported. At the same time, an appreciation for the inherent problems of character linkage is maintained.

It is likely that a balanced approach to the "to combine or not" question is advisable. As pointed out by de Queiroz (1996), there are likely to be instances where combining data causes certain logical problems, which may not apply to other cases. Perhaps the approach that carries the greatest risk of all would be one of fixed adherence to one or the other strategy. Ideally, the cladistic analyses carried out in the present work would experiment with the different approaches, using both the partitioned analyses and the total evidence methods and comparing the results. In this way, the theoretical preference for total evidence expressed above may be seen in a practical context. However, because the analyses use preserved material as the basis for constructing the data matrix and DNA extraction is outwith the financial scope of the work, the analyses are based on morphological characters. Future work on the Sabellidae should address the issue of combined and partitioned analyses, and compare and contrast the results of the different methods, as a more advanced set of characters becomes available.

3.3.6 Character mapping and the 'circularity' issue

Cladograms (as composite hypotheses of homology) can be used to trace the (hypothetical) development of a particular character through time. This can be achieved by tracing a particular character on the various branches of the cladogram. However, even this practice is not free from debate. Some authors have argued that to include a character of interest in the analyses leads to circular reasoning, and may bias the analyses. Brooks & McLennan (1991) stated "never bias your analysis by using the ecological information you want to study to build your phylogenetic tree". Instead, it is argued that the character should be removed from the data set prior to parsimony analysis, and then subsequently mapped onto the resulting cladogram(s).

The logic of that approach is questioned by once more returning to the fundamental aim of cladistic analyses, which is the causal explanation of shared features i.e.

homologies. As shown above, the abductive nature of cladistic analyses demands that all elemental homology hypotheses are maintained during compilation of the composite hypothesis. To remove a character is to remove a homology hypothesis and the resulting cladogram does not include all available information. In other words, fragmentation of a data matrix does not comply with the concept of homology. If a cladogram arising from analysis of a data set from which one or more characters have been removed is considered incomplete, then so an eventual consensus tree of these cladograms might be thought of as merely a compilation of incomplete hypotheses.

It might be counter-argued at this point that a complete set of homology hypotheses never will be possible, as not all characters of an organism are ever known at any point in time. The closest to perfection that will ever be achieved at any point in time is to present all the evidence known at that time. Therefore, a data set for parsimony analysis should comprise all known homology hypotheses. The resulting cladogram will be a composite of this 'best available' evidence, and therefore will represent the most plausible hypothesis, based on the total known evidence. Characters for cladistic analyses should be treated as homology statements rather than functional statements (Luckow & Brunneau 1997). They also supported the view that fragmentation of a data matrix by character exclusion may lead to weaker phylogeny hypotheses and concluded that the practice should be avoided. This approach is in agreement with Deleporte (1993) and Zravý (1997).

The cladistic analyses carried out in the present work do not subscribe to the practice of character mapping. Instead, all characters are included into the matrix for parsimony analysis. Examination of causal relationships of shared similarities of particular features is carried out simply by tracing the behaviour of these characters on the cladogram(s) generated by a single parsimony analysis. Logical problems are minimal in the present analyses because all characters analysed are based on external morphology and no attempt is made to compare pattern and process.

3.3.7 Character independence, linkage and coding strategies

When coded, each character, or transformation series, represents a statement of homology. Therefore, particular care must be taken to ensure that all states within each character really are homologous (to the best of one's knowledge). In theory, to minimise operator bias, all characters ideally should be assigned equal weights during analysis, such that no *a priori* assumptions are made as to the relative 'importance' of any particular character in the developmental history of the organisms in question. To avoid inadvertent weighting by overrepresentation of a particular character, each transformation series should be independent of the other characters in the matrix. Whilst seeming perfectly logical, these requirements pose a number of fundamental and often controversial problems when coding characters for cladistic analyses.

The first issue to address is that of homology statements. In the absence of absolute knowledge of the developmental history of the study organisms, it is difficult to be entirely certain of the homology of the character states within a transformation series. As seen in the previous sections, apparently similar features may have arisen through convergence or parallelism. Therefore, when coding the morphological variations within a particular character, there always will be a risk that not all states share the same evolutionary history (see below). This risk logically would increase with the number of character states within each transition series. In cases of doubt, Hennig (1966) advocated assuming homology rather than convergence or parallel evolution, in the absence of contrary evidence. This important guideline is known as 'Hennig's auxiliary principle'. In any case, careful morphological observation usually keeps the risk to a minimum, but the possibility of non-homology within transition series always should be borne in mind when scrutinising data sets. This is exemplified by the peristomial collar in sabellids. An uninformed observer might, for example, code the various conditions seen within the Sabellinae and Fabriciinae as different states within a character termed "collar". However, having established that the fabriciin collar arises from the anterior peristomial ring and the sabellin collar from the posterior peristomial ring, it is evident that any approach assuming homology of this externally similar feature will be incorrect.

There are two types of error that may occur when making homology statements (see Pleijel 1995). First, two taxa may be scored in the same way, even though the character is not homologous and second, one multi-state character may contain states that are non-homologous. These risks are minimised where each transformation series comprises only two states, for example 'absent' or 'present', an approach known as 'binary coding' (Pleijel 1995). Binary coding is ideally suited for characters that exist in only one of two possible states. For example, one might simply record the simple presence or absence of ventral cirri within the Sabellidae. In this case, the transformation series might be as depicted in Table 3.3.1. In this example, taxa A and E lack ventral cirri, while the feature is a shared apomorphy between taxa B, C and D. However, this binary approach becomes problematic if the operator wishes to record not only the presence of ventral cirri, but also the number of these structures.

Table 3.3.1. Example of binary coding of a simple character that either is present or absent, without intermediate states.

Taxa	**Character: ventral cirri**
A	0
B	1
C	1
D	1
E	0

where:
0 = absent
1 = present

Two options exist; the feature may be treated as a single character with several states as follows. In this case, the statement is made that possession of single or multiple pairs of ventral cirri is homologous. This approach is known as "multi-state" coding and is illustrated in Table 3.3.2.

Table 3.3.2. Illustration of the multi-state coding approach, for a character that displays a number of morphological variations between taxa.

Taxa	**Character ventral cirri**
A	0
B	1
C	3
D	2
E	0

where:
0 = absent
1 = one pair
2 = 2 pairs
3 = 3 pairs

A comparative discussion of these coding approaches is given in Pleijel (1995). The advantage with multi-state characters is that, having assumed homology, the feature is treated once, and only once, within the data set. Difficulties might arise where a character displays continuous rather than discrete variation. An example from the Sabellidae might be the number of abdominal segments or pairs of radioles. In some taxa, the numbers are clearly defined and invariant, while in others, the numbers may vary considerably between individuals, even within the same population. Because Fitzhugh's (1989) study dealt with higher taxonomic levels, such continuous characters as numbers of radioles or abdominal segments were omitted because, in many sabellins, the characters appear to vary according to body size. Knowledge of the extent of variation at the lowest taxonomic level is advocated before using these characters (Fitzhugh 1989). In any case, the most objective approach for multi-state coding of a character that has many possible character states between taxa would be to assign a single state to each of the possible variations, rather than grouping the values into 'blocks' of a pre-determined range.

Alternatively, if there was doubt as to the homology of the different character states, a binary approach might be taken, whereby a complex character is decomposed into a series of characters which have only two states: either the character is absent or present. The principle of this approach of 'additive binary re-coding' (Sokal & Sneath 1963), or A/P coding (Pleijel 1995) is illustrated in Table 3.3.3.

Table 3.3.3. Example of the binary coding approach (A/P coding) for a character that displays a number of morphological variations between taxa.

Character: ventral cirri

Taxa	**1 pair**	**2 pairs**	**3 pairs**	**4 pairs**
A	0	0	0	0
B	1	0	0	0
C	0	0	1	0
D	0	1	0	0
E	0	0	0	0

where:
0 = absent
1 = present

By using A/P rather than multi-state coding, a single transformation series comprising five states becomes four separate characters. A/P coding offers the clear advantage that the characters coded are entirely unambiguous, and there are no instances where more than one character state is applicable to a taxon.

Using A/P coding, unless otherwise specified during analysis, each character is treated as an independent unit with a weight of one. Therefore, the character 'ventral cirri' coded in multi-state form is given a weight of one, while the same feature, coded as a series of binary characters, assumes a total weight of four. In this case, the weight of the four binary characters could be reduced such that their combined weight equals one (see Pleijel 1995). This resolves the immediate problem of inadvertent weighting by establishing a series of characters instead of one multi-state character, but might in turn be open to further criticism. By reducing the influence of each of the binary characters such that their combined weight equals that of a single multi-state character, it might be argued that this affects the homology statements being made.

The four characters in the above example of the binary approach cannot be considered as independent units - presence of two pairs of ventral cirri logically precludes any of the other possible combinations. Therefore, such A/P characters are very much linked, another justification for down-weighting. In the example shown, the state 0 (absence) is used in each case, whether presence of that particular character is physically possible or not. For example, taxa A and E completely lack ventral cirri. Coding each state as zero means that the information about the lack of ventral cirri is stated three times in the matrix. An alternative reasoning might state that all three characters are inapplicable to taxa A and E, because they lack the feature, making it physically impossible for them to possess any of the variations. It is possible to code inapplicable characters as '?' in the data sets, and these are treated as equivocal under analysis. However, this approach may be criticised for causing loss of information.

The problems of inadvertent weighting, character linkage and missing information, together with recent opinions on these and other controversial issues, are discussed in publications including Maddison (1993), Pleijel (1995) and Wilkinson (1995). While recognising that A/P coding offers a simplicity in dealing with characters that is not possible with multi-state characters, the other problems of character linkage and duplication/ loss of information are acknowledged. It is generally concluded that the matter of character coding deserves further assessment.

Deliberate differential character weighting is an issue that also remains controversial. In the older literature, particular characters were given preferential weightings, based on an intuitive knowledge of the organisms concerned. However, this practice is rejected by those wishing to retain objectivity. Arguments for and against various means of differential character weighting are reviewed in Kluge (1997).

Despite the fact that problems related to character coding and weighting strategies have been recognised for several years, there still is no absolute solution available, nor is there any set of recognised guidelines on the subject. As with the taxonomic congruence versus total evidence debate, the most thorough approach would be to try different approaches of coding the same data set and to assess the respective results for congruence. If different methods produce similar cladograms, or trees, then the choice of coding method becomes unimportant or arbitrary in that instance. However, this may not be the case for all data sets. Where incongruent results are achieved by different coding systems, close examination of the transformation series on the different cladograms will provide some insight into the nature of the incongruity. For decision-making, the phylogenetic relationships supported by the largest number of traits should be chosen (reviewed in Brooks & McLennon, 1991).

The viewpoint taken here is that it is logical to ensure that a consistent coding strategy is used within a given data matrix. In other words, binary-coded complex characters should not occur in the same matrix as multi-state characters. Operators should not fear incongruence between different coding strategies. The more constructive approach would be to present any incongruities openly, and then to offer these for discussion. As with other areas within phylogenetic systematics, the debate surrounding coding strategies is expected to continue, as more options are constantly being developed, as both the techniques and available characters improve and as more potential logical traps are encountered and dealt with. As expressed previously in the context of incongruent cladograms, the coding debate should be treated as an interesting challenge, rather than a potential analytical mine-field.

3.3.8 Rooting trees - outgroups and hypothetical ancestors

Rooting of trees, or cladograms, is among the most debated and disputed areas of cladistic theory. A full discussion of the various arguments is outwith the scope of the present work, but a brief outline is given of the fundamental principles and the main approaches used in recent phylogenetic analyses. As seen in Chapter 3.2.6, characters are polarised by specification of the ancestral state. Using the example given in Table 3.3.2, if the state 0 represents the outgroup condition, all character states shown in taxa A and E are the plesiomorphic condition.

Hennigian argumentation requires the *a priori* recognition of plesiomorphy and apomorphy (see Chapter 3.2.12). While cladograms may be constructed without defining the ancestral conditions (unconstrained analyses), most workers agree that a meaningful phylogeny hypothesis requires a clear prior notion of relative apomorphy. However, opinions diverge on the precise method of defining polarity.

Nelson (1978) recognised indirect methods of character polarisation as those which require information from a source external to the study taxa. Direct methods allow character polarity to be assessed by using the information contained within the study taxa. Some workers have argued that, within a given group of taxa, the most common or general state within each transition series must be the ancestral condition (e.g. Nelson 1978), a practice known as the ontogenetic criterion. The method represents a direct means of inferring character polarity by assessing the group of taxa under investigation, without prior knowledge of its phylogeny (Weston 1988). This and other methods of state order analysis are discussed in Lipscomb (1992).

An alternative approach to character polarisation is to analyse the chosen group of taxa, known as the ingroup, in the context of one or more pre-defined ancestral taxa, or co-descendant(s) of a common ancestor, referred to as the outgroup (Farris 1972; 1982; Watrous & Wheeler 1981; Maddison *et al.* 1984). This taxon or group of taxa, is known as the outgroup. Because the outgroup determines character polarisation, it is essential to ensure that an appropriate taxon, or group of taxa, is used as an outgroup. It is not usually possible to find the ancestor of any given organisms alive today. Therefore, it is generally thought that the most appropriate comparative outgroup is the sister group of the ingroup (Maddison *et al.* 1984; Wiley *et al.* 1991). Unless the sister group of the taxa under investigation is revealed by a prior study, it will be necessary to conduct a range of phylogenetic analyses to find the most appropriate outgroup. The outgroup should be sufficiently closely related to the ingroup such that the majority of characters are relevant to both in- and outgroups, but still show sufficient synapomorphies to polarise the characters of the ingroup.

Because the character states shown by the outgroup are treated as the plesiomorphic condition, the direction of the transformation series is determined. Outgroup comparison is thus an indirect means of character polarisation. Phylogenetic analyses based on Hennigian argumentation, where the characters are polarised prior to analysis by outgroup analysis and where the shared synapomorphies combine to build the cladograms, are referred to as simultaneous, constrained analysis. The analyses are simultaneous, because both ingroup and outgroup are analysed together, and constrained because the polarity is determined prior to analysis.

Nixon & Carpenter (1993) dispelled as a myth the assumed necessity of using the sister group as the outgroup and presented a rather more flexible approach to outgroup selection. They reasoned that, in such cases where the data are highly divergent (as may occur when using molecular sequence data), it may be “necessary to estimate a hypothetical ancestor”. Because a hypothetical ancestor is likely to affect ingroup analysis in a manner different to a real outgroup, an unrooted ingroup analysis is advocated. The ingroup root is determined as “occurring along the internode that provides the overall most parsimonious tree length for the hypothetical ancestor + unrooted ingroup cladogram” (Nixon & Carpenter 1993). The viewpoint taken here is that constructing hypothetical ancestors carries a high risk of making unfounded assumptions and, as such, may contradict the aim of developing objective phylogeny hypotheses.

Some workers further claim that it is essential that the outgroup should contain more than one taxon (Donoghue 1983; Brooks & McLennon 1991). Nixon & Carpenter (1993) again consider this to be a "propagated myth". It is likely that the choice of one or several outgroups will depend on the taxa being analysed. If a single outgroup is chosen, such as the sister group to the ingroup, and it adequately polarises the characters of the ingroup, then it may not be necessary (or even desirable) to include another, more distantly related taxon within the outgroup. The more distant the relationship of the outgroup to the ingroup, the more likely it is that some characters of the outgroup will be inapplicable to the ingroup and vice versa. In such cases, multiple outgroups may serve only to obscure rather than reveal relationships.

In conclusion, as in other areas of phylogenetic systematics, outgroup selection is not free from controversy and debate. The present work subscribes to the use of real taxa as outgroups. The analyses carried out in the following section benefit from the previous work of Fitzhugh (1989), where the sister-group relationship of the Serpulidae and the Sabellidae was explored, as is that between the Fabriciinae and the Sabellinae. In the absence of previous knowledge, it is advisable to experiment with a variety of different approaches to outgroup selection before drawing firm conclusions.

3.3.9 The implications of "tree thinking"

The discovery of relationships

The transition from 'traditional', *Linnean* systematics to phylogenetic systematics offers a number of possibilities. Observations of individuals are interpreted in a new light, and discussions of phylogeny replace often tedious arguments of generic designation. The existence of organisms with sets of characters, some of which 'belong' to one 'genus' and others 'belong' to another area of the Linnean hierarchy, is widely recognised by any careful observer and previously has been a constant source of frustration. Phylogenetic systematics allows these idiosyncrasies to be regarded in a new light: that of inheritance of characters, rather than rigid adherence to 'species'- or 'genus'-specific features. Characters no longer are constrained to ‘belong’ to a particular level of systematic hierarchy. Instead, characters are expressed as differentially shared homologies.

The difference between considering animals in terms of relationships rather than systematic categories may be visualised in terms of a worker engaged in ‘species’ determination of a sample of benthic invertebrates. Following the Linnean system, the worker divides the sample into groups based on marked differences, first determining the generic affiliation of a particular animal, then striving to find the most appropriate ‘species’ description. The worker who subscribes to phylogenetic systematics first regards the animals as a collection of individuals, and then groups them on the basis of shared traits.

Seen in tree-form, the Linnean worker begins at the bottom of the tree and works upwards, looking for differences. The Hennigian worker begins at the level of the individual and works down the tree, looking for similarities. In most instances, both workers will arrive at the same result. The main differences are seen amongst systematists, in cases where the ‘generic’ diagnosis allows less morphological variation than seen in the constituent ‘species’ and likewise, where the variation seen between individuals is outwith that of the ‘species’ diagnosis. The Linnean worker is left with no other choice than to use intuition and personal experience to rearrange the taxonomic and systematic categories, a process not without frustration. The Hennigian worker is less concerned with having a discrete hierarchical category within which to place the individuals concerned, but is more engaged in examining the phylogenetic relationships between these individuals and other known taxa.

Faunal diversity indices

> ' "Alright" said Deep Thought (the biggest computer in the universe, after calculating for several generations).
> "The Answer to the Great Question.... of Life, the Universe and Everything..."
> "yes..."
> "is..."
> "YES..."
> "Forty-two," said Deep Thought, with infinite majesty and calm.'
>
> *Douglas Adams 1979: The hitch-hiker's guide to the galaxy*

Large-scale analyses of benthic faunal communities have been widely used over the recent decades and serve a variety of important purposes. The most commercially applicable use is as a tool in monitoring environmental change in areas exposed to contamination and various effect studies. Analyses of community composition also are useful in determining recovery of previously disturbed areas after cessation of industrial activities. Conflicts between industry and nature conservation issues in coastal areas frequently employ benthic surveys to assess the situation. In recent years, much attention has been paid to the need for assessment and mapping of the biodiversity within pre-defined geographical zones. The aim of such programmes is to determine 'vulnerability' or to carry out 'sensitivity mapping', as well as to document the occurrence of taxa found in the areas concerned. Recent examples of such catalogues of invertebrate organisms are published for the coast of Norway Brattegard & Holthe (1997) as well as Spitsbergen and Jan Mayen (Gulliksen *et al.* 1999).

As a result of these applied studies, a wealth of benthic material from often hitherto little investigated areas has become available to taxonomists. A positive result of this has been an increased interest in taxonomy, and the description and categorisation of a wide range of taxa new to science. A negative side to this is that commercial operators concerned with obtaining many hundreds of quantitative samples cannot treat the specimens with the same care as a taxonomist engaged in qualitative collection of particular taxa of interest. Highlighting the difference between commercial and non-commercial sampling techniques and moving towards an increased co-operation between museums and environmental monitoring agencies are likely to improve the situation in the future. As with many other conflicting activities, this is a long-term aim, requiring diplomacy, creative marketing and financing and a broad evaluation of the various cost-benefit relationships involved.

Most commercial benthic analyses in Western Europe are based on the Petersen (1914) strategy of assessing numerical taxon dominance and diversity within "communities", or faunal assemblages. This process is time-consuming and requires the participation of a team of specialists in the various processes, from sorting the animals from sediment residue, through identification, statistical analysis and finally assessment and interpretation. In the past, operators of commercial surveys generally have acknowledged the labour-intensity of the method and made the appropriate allowances. However, in recent years, as financial resources become increasingly limited, attention has been given to finding less expensive methods of assessing environmental change by benthic faunal analyses.

The first change noted by many workers in the field is the reduction in time-budget allowed for faunal identification work. Although not formally documented, this often results in a higher degree of identification error and inconsistencies in taxon determination. Particularly in the case of the polychaete fraction of the samples, the need to process a large volume of material in a short space of time usually entails engaging several workers to share the task of identification. Without proper quality control and ring-test procedures, the risk of inconsistencies in 'high-speed' identification is high, even amongst experienced workers. Failure to correct errors and discrepancies can lead to erroneous inflation of the numbers of taxa recorded across the sampling area at large. Even more serious, such errors can result in a false grouping of sampling stations, based on phenetic methods of dissimilarity analysis. Because there are no established national or international ring-testing procedures in Norway, this problem is in urgent need of attention. Recently implemented national guidelines for sampling and analysis of soft-bottom benthic macrofauna have specified that operators should participate in ring-testing, when such facilities become available (NS 9423 1998).

When identification time is limited, many operators are forced to restrict identification to higher taxonomic levels. Seen from a phylogenetic point of view, this trend is alarming. Because many of the existing Linnean genera may paraphyletic, identifications at the level of genus are of restricted use in intercomparison of temporal data series. Any practice that treats an artificial taxon as a single entity violates the concept of homology, which is the fundamental 'building block' of systematic classification.

The following example illustrates the potential ambiguity. At a fixed sampling station, Station 1, twenty individuals of three discrete morphological groups of individuals (putative 'species') are found, all of which appear to correspond with the traditional diagnosis of 'Genus X'. These are noted in the taxon list of Station 1 as 20 representatives of 'Species X'. At Station 2, five individuals are found, also corresponding to 'Genus X', but thought to be different to those found at Station 1. Because identifications are carried out at the genus level, these five individuals also are recorded as 'Genus X' in the taxon list of Station 2. During phenetic faunal diversity analyses, all these entries are regarded as a single taxon.

Suppose that, during the following year, a systematic revision has been carried out of 'Genus X', which is found to be paraphyletic. Some of the taxa previously assigned to 'Genus X' are now contained within 'Genus Y' and 'Genus Z'. The operator faces a dilemma when Stations 1 and 2 are revisited. Either the former, now incorrect approach of recording all four morphological types as a single taxon may be adopted in order to ensure comparability of the data set with that from the previous year. In this case, three real taxa are treated as a single, artificial taxon and any differing responses to environmental change between the three taxa are masked.

The alternative approach would be to acknowledge the systematic changes, and record the individuals as differentially belonging to the three 'new' taxa, 'Genus X' (revised), 'Genus Y' and 'Genus Z'. While this approach provides a more correct representation of the faunal community, the numbers of taxa recorded is higher than in the taxon list of the preceding year. Unless properly corrected for prior to statistical analysis, this will appear in the results as an increase in faunal diversity, when in fact it is unchanged in terms of the animals present. Of course, the same scenario is applicable at the 'species' level.

In recent years, various workers have questioned the need for 'species' identification in routine environmental monitoring (e.g. Rutt & Pickering 1993; Warwick 1988; Warwick & Clarke 1995). These authors claim that identification to 'genus', or even 'family' level is sufficient to reveal spatial and temporal trends in faunal diversity, as a function of anthropogenic disturbance. This notion was tested by subjecting various data sets to standard statistical analyses at different taxonomic levels, and the hypothesis appeared to be supported. However, these studies inspire several criticisms. First, the data sets used all were in the vicinity of known sources of environmental impact, largely organic, and thus a strong gradient of faunal community composition might be expected, seen as very marked differences in the resident infauna across the sampling area. For example, the deep-burrowing *Maldane sarsi* (Maldanidae) is common in stable glacio-marine sediments across large areas of the Arctic Basin, including some fjord systems. Less stable environments, such as those close to human settlements or influenced by other natural disturbance, preclude these large burrowing animals, and tend to be occupied by smaller, rapidly colonising taxa (see Pearson & Rosenberg 1978; Dahle *et al.* 1998). In such cases, inter-station differences are likely to be apparent at the 'genus' or even 'family' level. However, in areas of more diffuse natural or anthropogenic disturbance, the gradients may be less evident, and may be revealed only at lower taxonomic levels.

Another aspect to consider is the loss of ecological information which may occur by ignoring lower taxa in environmental surveys. If sampled individuals are grouped into single Linnean higher taxa, which turn out to be paraphyletic, treating these as a single statistical unit may not have any ecological meaning whatsoever. For example, studies operating at the 'family' level will group all the sabellid 'subfamilies', 'genera' and 'species' under a single entity, called "Sabellidae". As seen in Chapter 1.4, McHugh & Rouse (1998) and Rouse & Fitzhugh (1994), a wide range of behavioural and reproductive strategies is seen among the many members of the family Sabellidae. Some sabellids are exclusively suspension-feeders, while others are capable of additional deposit-feeding strategies (see Chapter 4). Some sabellids brood their young, either within or outside their tubes, while others display no parental care at all. Some may have a (non-feeding) planktonic phase in their development (Rouse & Fitzhugh 1994), while others may settle close to the parent.

Grouping all sabellid individuals as a single entity masks this ecological information. Even worse, there is a subsequent risk of misinterpretation, as sabellids in many general contexts are classed as being suspension feeders. In many cases, the person who interprets the statistical analyses is not the same person that carried out the faunal identifications. In the above example, an operator faced with a taxon list dominated by "Sabellidae" may interpret this as a dominance of suspensivorous organisms, which in turn is indicative of good water exchange. Pearson *et al.* (1996) found a small sabellid member of *Euchone* Malmgren to be numerically dominant in certain parts on the Norwegian continental slope (see also Chapters 3.4 and 4). Because attention was paid to the type of animals present, the populations were not interpreted as being dominated by suspensivores. Instead, attention was drawn to the possibility that these animals may represent a deposit-feeding assemblage operating at the sediment-water interface. Abandoning observations at lower taxonomic levels therefore carries a high risk of misinterpretation of the ecological conditions prevalent in a given area.

'Tree thinking' highlights yet another fundamental criticism of conducting faunal diversity and community analyses at higher taxonomic levels. Within the Linnean system, there are no currently recognised 'upper limits' as to how many taxa should be contained within any given higher systematic category. For example, both maldanids and chaetopterids are common in the Norwegian Sea and the Arctic Basin. Fauchald (1977) recognised 4 genera within the family Chaetopteridae Malmgren, while all of 30 genera were listed within the Maldanidae Malmgren. Similarly, at the level of genus, there may be great variation even within a single family, such as the Ampharetidae Malmgren. Some genera, such as *Eclysippe* Eliason, common in soft bottom sediments in the North Sea and Norwegian Seas, contain only a single lower taxon, while *Ampharete* Malmgren is noted as containing 27 taxa.

Several different taxa within *Ampharete* are known to co-occur in Norwegian and Arctic waters (Holthe 1986, Gulliksen *et al.* 1999) and *Eclysippe* was among the numerically dominant taxon in several areas of the North Sea and Norwegian Sea (Pearson *et al.* 1996). Recording these taxa at 'genus' level therefore leads to under-representation of *Ampharete* in statistical analyses, because several real taxa are recorded as a single entity, while *Eclysippe* is still treated as the single taxon it was at a lower level. This inherent flaw is expected to be magnified at the 'family' level. Figure 3.4.2 uses a checklist of polychaetes recorded from Spitzbergen and Jan Mayen (Gulliksen *et al.* 1999) to illustrate this issue.

It is immediately apparent that some 'families'[2], such as Apistobranchidae Mesnil & Caullery, Chaetopteridae Malmgren, Onuphidae Kinberg and Orbiniidae Hartman, all of which are numerically dominant in Arctic areas (Cochrane *et al.* 1998, Dahle *et al.* 1998), are represented by only a single 'species' within a single 'genus'. On the other hand, 'families' such as the Polynoidae Malmgren, Terebellidae Malmgren, Ampharetidae Malmgren and Phyllodocidae Oersted, which also are numerically abundant in these waters, are represented by more than five 'genera' and up to more than 25 'species'. Particularly in the case of the Polynoidae, Phyllodocidae and Spionidae Grube, it is clear that treatment of these taxa at 'genus' or 'family' levels will lead to a disproportionate underestimation of the different taxa present, relative to those shown to the right of the plot.

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[2] The concepts of 'family' ,'genus' and 'species' are here referred to in the same way these are currently used in phenetic faunal analyses, i.e. as statistical units. It is recognised that these often artificial categories are used for statistical convenience and do not necessarily represent meaningful biological groups that reflect relationships between taxa.

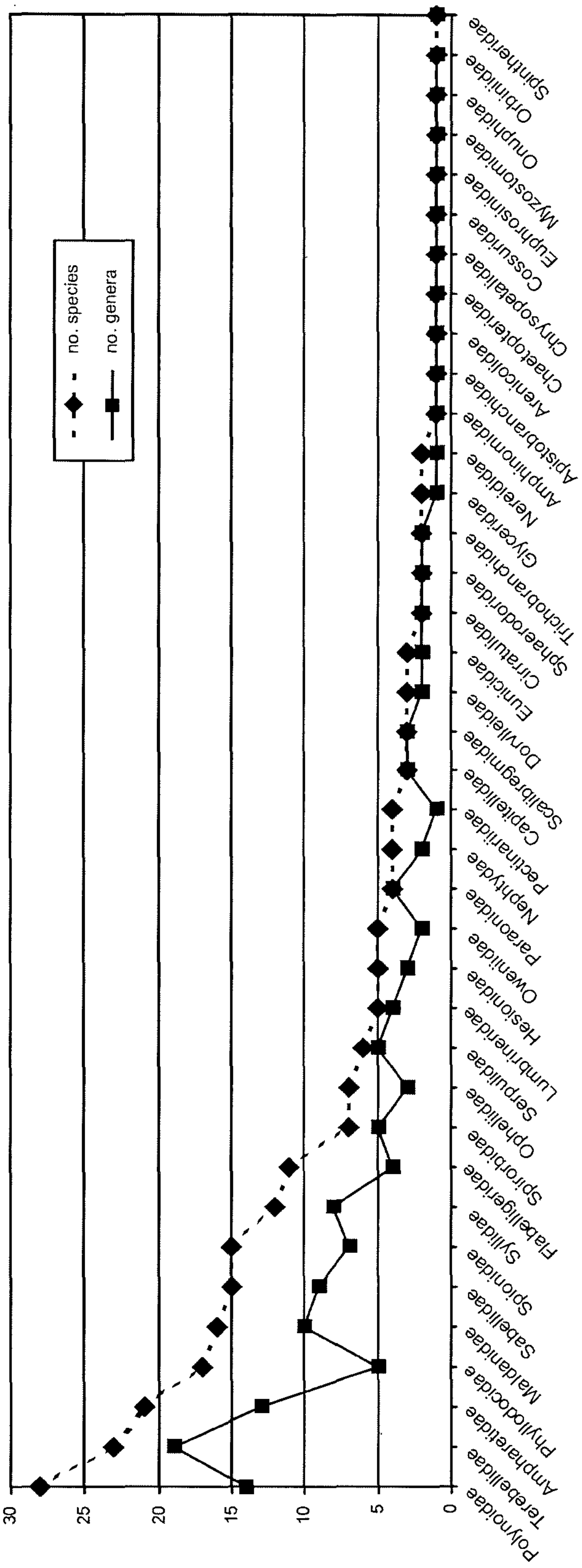

Figure 3.3.2. Plot of polychaete 'genera' and 'species' within' families' recorded from Spitsbergen and Jan Mayen (data taken from Gulliksen et al. 1999).

In areas of marked organic gradients, the infaunal assemblages become poorer in taxa (Pearson & Rosenberg 1998). Interestingly, whereas certain 'genera' tend to be represented by several 'species' in pristine areas, this decreases markedly with increasing sedimentary enrichment (see data from sediments around fish farms in Cochrane *et al.* 1994). This also applies to the number of 'genera' represented within 'families'. Therefore, in areas where strong enrichment gradients are seen, the main ecological trends may be apparent in the data despite faunal analysis at higher taxonomic levels. However, it is expected that doing so in pristine areas, where trends are not so clear, will mask the faunal information by preventing analysis of similarities and differences between and within assemblages.

The viewpoint adopted here is that statistical analyses at higher taxonomic levels should be avoided. While perhaps being of some use for cost-cutting in areas of marked organic gradients, this advantage is considered to be outweighed by the risk of erroneous conclusion as a result of the flaws inherent in the practice. Where a "rough guide" to environmental conditions is sought, for example under and around an aquaculture installation, it is considered preferable to conduct a qualitative or semi-quantitative assessment of the organisms present in the sampled populations rather than risk an ecologically flawed numerical analysis. Although a theoretically objective number is better suited to categorisation of environmental conditions than is a series of qualitative remarks, the above arguments show that statistical faunal analyses are by no means objective in terms of phylogeny, relationships and ecology. Sometimes, one is forced to accept that some aspects of 'life, the universe and everything' just cannot adequately be described in terms of numerical units.

Ecology meets systematics - the comparative method

Statistical analyses of the co-variation of traits across a sample set of taxa, known as the comparative method, are widely used as a means of assessing adaptation and other ecological and ethological hypotheses. Such comparative studies are by no means new. Already in 350 B.C., Aristotle documented taxon-specific habitat selection as well as shared traits or behaviours between groups of similar organisms. Most ethologists working from the end of the 19th century to the mid-20th century acknowledged that not only morphology, but also behavioural characters, provide a means of assessing kinship, and that morphology, behaviour and phylogeny are inextricably linked.

A full discussion of the comparative method is not possible here, but the issue is widely discussed in works including Ridley (1983, 1989), Felsenstein (1985), Pagel & Harvey (1988), Coddington (1990), Harvey & Pagel (1991) and Harvey & Purvis (1991). The arguments for and against use of the comparative method on phylogenetic hypotheses rage on. Unlike many aspects of science, it is not possible to conduct experiments to reconstruct phylogeny - the processes took place long ago, and we must be content with a 'most plausible explanatory hypothesis'. Having achieved a parsimonious phylogeny hypothesis, the comparative method entails conducting statistical analyses to assess the extent to which one or more characters co-vary with each other. For example, having produced a phylogeny hypothesis of polychaete worms, the co-occurrence of reduced parapodia and a tubicolous lifestyle could be assessed statistically.

The lack of absolute certainty of the 'correctness' of tree topology is the basis for the first major criticism of the comparative method. The tree, or cladogram, is only as reliable or complete as the data that went into its construction (see Coddington 1988; McHugh & Rouse 1998). Therefore, trees should not be equated with phylogenies (Eggleton & Vane-Wright 1994). Any subsequent changes in the tree structure, for example with the addition of more characters, may render the original comparative analysis invalid. Pagel (1998) advocated that until a method is available for simultaneous construction of both phylogenetic and comparative hypotheses, phylogeny reconstructions and comparative results should be presented as inter-dependent hypotheses.

Some authors argue that the inter-relatedness of the characters of an organism and its phylogeny causes circularity in the comparative method. Felsenstein (1985) argued that "species are part of hierarchically structured phylogeny, and thus cannot be regarded for statistical purposes as if drawn independently from the same distribution". While being an important factor to bear in mind when drawing conclusions from any comparative analysis, the issue of phylogenetic similarity does not necessarily preclude the utility of such studies. Providing the phylogeny (hypothesis) of the study taxa is known, then contrasts between groups of taxa which shared a common ancestor, not shared by any member of another group can be compared. These contrasts may then be regarded as independent (see Felsenstein, 1985) and useful in statistical analysis, providing the appropriate technique is chosen.

Although the phylogeny hypothesis itself cannot be tested for absolute accuracy, some workers use cladograms as a means of 'testing' *a priori* adaptational hypotheses (e.g. Coddington 1988). Even *ad hoc* hypotheses of adaptation usually state a null hypothesis; i.e. the direction of evolution of the trait(s) in question is inferred. Statistical analysis of the co-occurrence of these traits on a cladogram indeed help to reveal whether the organisms are phylogenetically constrained to show the traits, or whether they are more likely to have occurred as a result of convergent or parallel evolution.

As a relevant example of a possible future application of the comparative method to the taxa in the present work, the feeding strategy of sabellids (strict suspension-feeding or multi-trophic suspension/deposit feeding) could be incorporated into a matrix which also includes crown morphology ('snowflake-like' or 'feather-like'). Tracing these characters on the resulting parsimonious tree(s) (after simultaneous analysis of all characters) may show a similar distribution pattern. Purely hypothetically for example, all the taxa noted as utilising deposit feeding may have snowflake-like radiolar crowns, whilst those apparently constrained to suspension-feeding may possess the 'feather-like' radiolar arrangement.

The viewpoint taken here is that, once sufficient data are available to allow the above comparative analyses to be carried out, the 'try it and see' approach is the most appropriate. Providing the results are never taken for more than the hypotheses they are, and a healthy respect is maintained for the possible statistical pitfalls of the technique, the comparative method seems to offer a more informative means of exploring the holomorphic phylogeny (hypotheses) of taxa of ecological interest.

3.3.10 Phylogenetic taxonomy

Classification and taxonomy as a communication tool

From antiquity to the present day, organisms have been named upon discovery. Biological names, both those in common usage and the formal binomial nomenclature, are neither more nor less than a means of conveying information about organisms informatively and concisely. Without nomenclature, the observer must rely on description. In this case, the observer would report sighting a stout four-legged mammal with cloven hooves, greyish fur, a black shiny nose and a pair of branching antlers. Common nomenclature allows the observer simply to say "I saw a reindeer" and immediately be understood. The attributes of the animal are implicit in the name reindeer. Because this label is shorter than the description, yet retains the biological information, the name becomes an effective communication tool. It is important to recognise that a taxon name functions as a shorthand label for a group of organisms, identified by a set of characteristics associated with that name. The characteristics themselves do not define the taxon.

Single, or uninomial, common names offer no explicit hierarchical information. As with the characteristics evoked by the name label 'reindeer', the observer must rely on prior or external knowledge to know that the reindeer is a mammal. Thus, hierarchical information in common names also is implicit. On the other hand, the binomial system of nomenclature offers explicit hierarchical information. The 'species' name is given as well as an affiliation to 'genus'. The fundamental problem with the Linnean binomial system in the light of phylogenetic systematics is outlined in Chapter 3.1.3. As 'genera' increasingly are found to be paraphyletic, the 'generic affiliation' of lower-level taxa must be subjected to tedious revision and re-revision.

Prior to the mid 18th century, species were considered to be invariant objects of creation. Therefore, at that time, the Linnean system was the most informative communication tool available. Species were categorised according to similarity and the higher systematic taxa appeared to be real entities. In the absence of evolutionary thinking, any other approach would be illogical. In summary, the Linnean system of binomial nomenclature aimed to categorise biological organisms into a series of discrete hierarchical units, each unit being morphologically distinct. Phylogenetic systematics, on the other hand, is concerned with revealing relationships between different groups of taxa, based on hypotheses of common ancestry. Natural groupings of taxa are of more importance than rigid hierarchical levels.

It is acknowledged that the only real units available to the phylogenetic systematist are the individuals that physically can be examined. Linnean taxonomic categories, from species, genus, family and upwards in the present systematic hierarchy are erected for convenience. These categories might be thought of as labels, created as communication tools. Do Linnean categories still function as such, two and a half centuries after their conception?

The present work supports a systematic hierarchy based on natural phylogenetic groups. Therefore, a paraphyletic family, sub-family or genus must be rejected as being an artificial taxon. Because many Linnean taxa are paraphyletic, the present standpoint must be to reject these. Without having carried out a phylogenetic analysis of all the traditional Linnean taxa, we cannot be sure which taxa are monophyletic and which are artificial. Because of this uncertainty, the present opinion must be to consider the Linnean system in its present form to be a potentially misleading communication tool. The traditional Linnean categories are somewhat comforting in their familiarity and deeply-rooted history. These should be accorded the respect they deserve, as representing an admirable classification system for discretely created entities. However, in terms of phylogenetic systematics, the same categories should be treated with caution.

Following the logic of taxonomy as a means of conveying information, the concept of 'species' also must function as an effective communication tool if it is to be embraced. Considered independently of its binomial 'generic' affiliation, a 'species' label refers to a least-inclusive group of individuals sharing a set of similarities. As outlined above, the traditional concept of genus and the higher systematic categories are rejected on the grounds of risk of paraphyly. To be consistent, the 'species' label also should refer to a monophyletic group, in this case individuals. If monophyly of 'species' cannot be guaranteed, then logically, the concept fails to be an informative communication tool.

This demand for consistency and integrity of information contained within taxon labels forms the basis for the concept of phylogenetic taxonomy. At present, the issue is extremely controversial and discussions thereof usually provoke strong sentiments among followers and opponents alike. Because the reasoning behind phylogenetic taxonomy has arisen through the practice of phylogenetic systematics, an understanding of the main arguments is important, regardless of whether the approach is adopted or not. For more detailed information and discussion of the proposed means of defining phylogenetic taxon names, the reader is referred to de Queiroz & Gauthier (1992, 1994), Sundberg & Pleijel (1994), Schander & Thollesson (1995), Lidén & Oxelman (1996) and Dominiguez & Wheeler (1997).

Some workers have explored the idea of abandoning the Linnean concept of species and higher taxa altogether, concentrating instead on the 'least inclusive taxonomic unit (LITU)' (Pleijel 1999; Pleijel & Rouse 2000). The reasoning behind the LITU concept, and how it might function as a communication tool, whilst still acknowledging two and a half centuries of taxonomic research, is outlined below.

Phylogenetic taxonomy outlined

Phylogenetic taxonomy is stated as being "... the branch of phylogenetic systematics concerned with the representation - rather than the reconstruction - of phylogenetic relationships. The objective of phylogenetic taxonomy is to present relationships of common descent using a system of names" (de Queiroz & Gauthier 1992).

As pointed out previously, a Linnean genus does not evolve, nor can it exist as such in nature; it exists only in the mind of those concerned with systematics and taxonomy, as a convenient (if sometimes misguided) conceptual tool. Phylogenetic taxonomy recognises a clade as a taxon, whose members all share a common evolutionary history. Therefore, a phylogenetic taxon might be perceived as existing in nature, whether we as scientists have discovered it or not (Sundberg & Pleijel 1994).

The definition of phylogenetic taxon names is achieved on the basis of common ancestry. Because traditional taxon diagnoses are based only on presence of features, without consideration for any potential losses, a diagnosis does not necessarily describe a monophyletic group. The aim of phylogenetic taxonomy therefore carries no mystique; the goal quite simply is to describe a monophyletic group using an unambiguous name label (see Sundberg & Pleijel 1994).

Because a taxon name merely is a means of communicating biological information, such a label must have a point of reference. Neither a taxon nor its members can be defined; it is the name itself that can and must be defined in order to secure its meaning. Three means of defining phylogenetic taxon names have been proposed (de Queiroz & Gauthier 1994). First, definition of a phylogenetic taxon name may be node-based, the reference point being the most recent common ancestor. Second, the definition may be stem-based, where the reference is to the clade that shares a more recent common ancestor with one taxon than with one (or more) other taxon. Third, the definition may be apomorphy-based, where the clade in question stems from the first ancestor to possess a particular apomorphy. These three alternatives are illustrated in Figure 3.4.3.

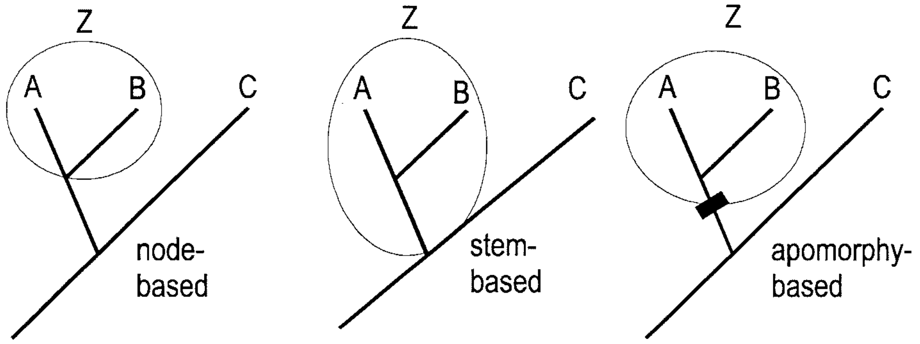

Figure 3.3.3. Three means of defining phylogenetic taxon names (after de Queiroz & Gauthier 1994).

When devising a method to define taxon names, it is essential to consider how any organism discovered in the future will be incorporated within a phylogenetic taxonomic system. Sundberg & Pleijel (1994) discussed the stability of each of these three definitions. Node-based taxon names will exclude subsequently discovered taxa that arise from the branch leading to the main clade. In apomorphy-based definitions, the ancestor plus the descendants are defined by the apomorphic character, such that a group arising along the branch between the first and second nodes may or may not appear within the taxon, depending on whether or not it possesses the apomorphy. In stem-based definitions, all taxa arising from the branch leading to the named clade are incorporated within that named clade. This reduces potential name changes relative to the other two definitions. However, because it is based on the closest known neighbouring group (in this case, the sister group), stem-based relationships are subject to change with changes in the known ingroup-outgroup relationships.

Phylogenetic taxon names are singular, rather than binomial entities. In this respect, phylogenetic taxonomy functions in a manner similar to the use of common names for organisms, because the hierarchical information is implicit in the name label. Common names rely on external information, whereas phylogenetic taxa refer to the most recent tree available at the time of writing. Further, a clade that previously could be equated to genus might, under revision and publication of a new explanatory hypothesis, become enlarged to encompass the original clade, along with a range of new members.

Because the spelling of the phylogenetic taxon names remain unchanged, opponents claim loss of rank and hierarchical or structural information (Dominiquez & Wheeler 1997). Other opponents claim that the Linnean system of hierarchical categories is "perfectly compatible with phylogenetic systematics .... yet completely independent of it" (Lidén & Oxelman 1996). However, this argument becomes circular if one agrees that a hierarchical taxon such as genus or family cannot exist but in the mind of the observer and that relationships between taxa exist whether or not these are recognised. Linnean categories can be compatible with phylogenetic systematics if, and only if, the criterion of monophyly is fulfilled.

This has been expressed by the statement that "(p)araphyletic taxa have long been avoided in the Linnean system by referring to a cladogram and naming monophyletic taxa" (Dominiguez & Wheeler 1997). Based on the comments of Fitzhugh (1989) and personal experience with certain sabellid taxa, the existing Linnean system certainly is not free from paraphyly. The above statement simply could be modified to note that Linnean taxonomists aim to avoid paraphyletic taxa by revising the inclusion sets of existing categories to promote monophyly. However, it is necessary to bear in mind that inclusion sets of monophyletic groups, and indeed tree topology, are subject to radical change as new information arises. Maintaining Linnean taxa as monophyletic groups will be a seemingly endless and labour-intensive task.

It seems that the main debate for and against phylogenetic systematics can be distilled to a cost-benefit analysis of nomenclatural stability versus the need for hierarchical information. The traditional need for a structured hierarchy, within which to place the names of identified organisms are deeply rooted. Such a hierarchy was firmly in place by the time of Aristotle in 350 B.C. Systematics and taxonomy are by their nature hierarchical disciplines. Perhaps the difference between traditional and phylogenetic taxonomists is simply that the former wish the hierarchy to be indicated by the spelling of the taxon name and to be defined by a fixed and observable point (the 'type specimen', or 'type species'). Phylogenetic taxonomists, on the other hand, are content to look to an ever-changing tree to gain an understanding of the relationships concerned. Phylogenetic taxonomists accept a reference point they cannot see. A proposed transition from the realms of the 'real' to the conceptual requires a major change in the thought processes of systematists and taxonomists. This being the case, an extended period of debate can be expected, not unlike that experienced by Willi Hennig himself, whose work took several decades before being incorporated into general research practices.

LITU – least inclusive taxonomic unit

Traditional taxonomy embraces the concept of species as a group of discretely recognisable individuals. However, the means of delineating this group has been the subject of controversy and discussion for many years. Instead of entering into this debate, Pleijel & Rouse (2000) proposed an alternative approach whereby 'species' are not given any particular role in taxonomy and only monophyletic groups are recognised by formal Latin names. In the opinion of those authors, the diversity of biological organisms can adequately be represented without reference to 'species' as such. Instead, the term LITU (Least Inclusive Taxonomic Unit) was introduced to refer to a smallest known clade of which the current knowledge base does not allow further subdivision. LITU taxa are uninomial and rank-free, although they are part of more inclusive taxa 'higher' up on the tree.

LITU taxa are identifiable in being italicised with a lower case initial letter, whereas all other taxa are italicised with a capital initial letter. Using a group of hesionid individuals that in traditional terms would have been described as a "new species", Pleijel & Rouse (*in press*) introduced the LITU *capricornia* as a new taxon. Affiliation to more inclusive taxa was indicated in parentheses (*Hesionidae, Polychaeta*). Should future research allow the LITU clade to be further subdivided, the original taxon becomes capitalised, i.e. *Capricornia* and the sub-groups become the new LITUs, denoted by the absence of capitalisation. The synapomorphies that described *capricornia* (as a LITU) still remain unchanged if that group later becomes sub-divided. In this way, phylogenetic taxon names are stable in that their meaning never changes; it is merely the inclusion set within the taxa that changes. Once given, the actual names denoting LITUs and more inclusive taxa are permanent.

The utility of the LITU concept in revising higher taxa was demonstrated by Pliejel (*in press*), using the well-confirmed hesionid group *Heteropodarke* (*Annelida, Polychaeta, Hesionidae*[3]). A monophyletic sub-group within *Heteropodarke* comprising four taxa was named *Crassichaetae*, as an informative means of distinguishing these from the remaining members of the group. Such a system provides hierarchical information of the taxa concerned, but does not make assumptions of rank.

Current status

Because science deals with individuals existing in the present, phylogeny hypotheses always will be open to dispute, discussion and further development. It is reasonable to expect that groups of organisms exist that have not yet been revealed to science. Because each newly-discovered taxon adds further information to and may change a phylogeny hypothesis, the quest for absolute taxonomic stability may be futile. Some authors even claim that taxonomic stability is undesirable, and that changes in names

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[3] note all taxon names italicised; capitalised first letter denotes a more inclusive taxon

are a positive effect of increasing phylogenetic knowledge (Dominguez & Wheeler 1997). Supporters of phylogenetic taxonomy might further claim that taxonomists would be better served by using their resources for biologically meaningful pursuits rather than arguing about organism names.

The issues surrounding phylogenetic taxonomy remain controversial within the taxonomic scientific community. Further, it is only very recently that the first phylogenetic taxonomic studies have been accepted for publication. The use of LITU and phylogenetic taxonomy is not (?yet) accepted by the international code of zoological nomenclature (ICZN). No worker can dispute the ideal wish for monophyletic units to describe groups of related organisms. Development of the means by which this is to be achieved will provide interesting and lively 'food for thought' both in the literature and at gatherings of systematists and taxonomists for some time to come. Whether the ideas recently proposed by Pleijel and Rouse (2000) will be adopted in future taxonomic research, or whether these will remain dormant for an indefinite period is yet uncertain.

What is certain, however, is that the disciplines of both taxonomy and systematics currently are in a dynamic and changing phase. The most constructive approach in all cases is for scientists to maintain an open mind to proposed changes, experiment with ideas in the context of their own particular research field, and to document and discuss the advantages and pitfalls encountered. Rejecting or accepting ideas on the basis of pre-conceived notions or prejudices is to perpetuate the flaws and inconsistencies that mar the current system of biological nomenclature.

The approach adopted here is that, while subscribing to the logic of phylogenetic taxonomy, it will not be used conclusively in the present taxonomic and systematic work. Mostly, this is because, while the debate on how the phylogenetic taxonomic system should operate in detail rages on, it would be presumptious of the present work to use a technique that still requires a great deal of thought and skill in its development. However, the results obtained in Chapter 3.6 will be used to investigate the potential utility of phylogenetic taxonomy for the group of taxa in question.

3.4 Current phylogenetic status of the Sabellidae

3.4.1 Background

Discussions of the monophyly of various sub-divisions[1] within the Sabellidae are not new (see Banse 1972, 1970, 1957). However, much of these arguments are subjective and, while offering insight into a previously little-researched subject-matter, will not be discussed further here. However, some of the arguments regarding the phylogeny of *Euchone* Malmgren are examined in Chapter 3.5. A brief historical account of the systematics of the Sabellidae as a whole is given in Chapter 3.2. The Sabellidae, together with the Caobangiidae Jones and Sabellongidae Hartman (Fitzhugh 1989) were recently revised using phylogenetic analyses. The present chapter is a brief outline of this work and the later emendments to the sub-family diagnoses (Fitzhugh 1991a). Because the present thesis is concerned mainly with selected Sabellinae and the Fabriciinae for comparative purposes, the systematic and pylogenetic status of the Sabellaridae Johnston, Caobangidae, Sabellongidae and Serpulidae are not discussed in detail.

3.4.2 Taxa and characters

A total of 34 sabellid taxa were analysed, comprising the recognised 'genera' within the Sabellidae. *Caobangia* Giard and *Sabellonga* Hartman, which previously were assigned to separate families within the order Sabellida; the Caobangiidae and Sabellongidae respectively, also were included. For practical reasons, the analyses were largely based on descriptions of 'type species', or reference specimens.

Polarisation of the transformation series, or character phylogeny, was achieved by outgroup comparison (Hennig 1966, Wiley 1981, Watrous & Wheeler 1981) with the Serpulidae. This choice of outgroup was based on a series of cladistic analyses of the "orders" Spionida and Sabellida, which consistently showed the Serpulidae to be the sister taxon of the Sabellidae.

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[1] The various categories as used by Fitzhugh (1989) are retained in this chapter.

Characters were not weighted *a priori*, that is, all characters were ranked of equal importance in the analyses. Most of the analysed characters were those widely used in descriptions of sabellid taxa, such as segmentation, number of radioles and chaetal morphology. However, also included in the analyses were characters which only recently have been given attention, such as the structure of the branchial crown, lip morphology and finer chaetal structure (Knight-Jones 1983; Perkins 1984; Knight-Jones & Perkins 1998).

In total, 43 morphological characters were used in Fitzhugh's analyses. Most of the characters were coded in binary-state form, i.e. with only two character states (presence/ absence). Some characters, however, were coded in multi-state form (transformation series comprising more than two states), in which case the character states were presented as an unordered series. In all cases, character state 'a' corresponds to the pleisiomorphic condition (in this case, that of the Serpulid outgroup), while states 'b', 'c' etc. refer to the apomorphic conditions. Since the character states were unordered, coding of characters other than state 'a' makes no assumptions of relative apomorphy or character phylogeny. A full character list and a useful description of characters are given in Fitzhugh (1989).

3.4.3 Monophyly of the Sabellinae and Fabriciinae

After branch-swapping using Hennig86 version 1.5, developed by J.S. Farris, 16 minimum-length cladograms were produced, each with a treelength of 154 steps (Fitzhugh 1989). The Adams consensus tree[2] (a composite representation of the 16 most parsimonious cladograms obtained) obtained is shown in Figure 3.5.1. The systematic groupings of taxa by four different workers are shown at the top of the cladogram. Note that '?' refers to taxa that were not described at the time and therefore cannot be assigned to any category.

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[2] note that in Chapter 3.5, the strict consensus technique is used to obtain composite cladograms, rather than the Adams consensus method as used by Fitzhugh (1989)

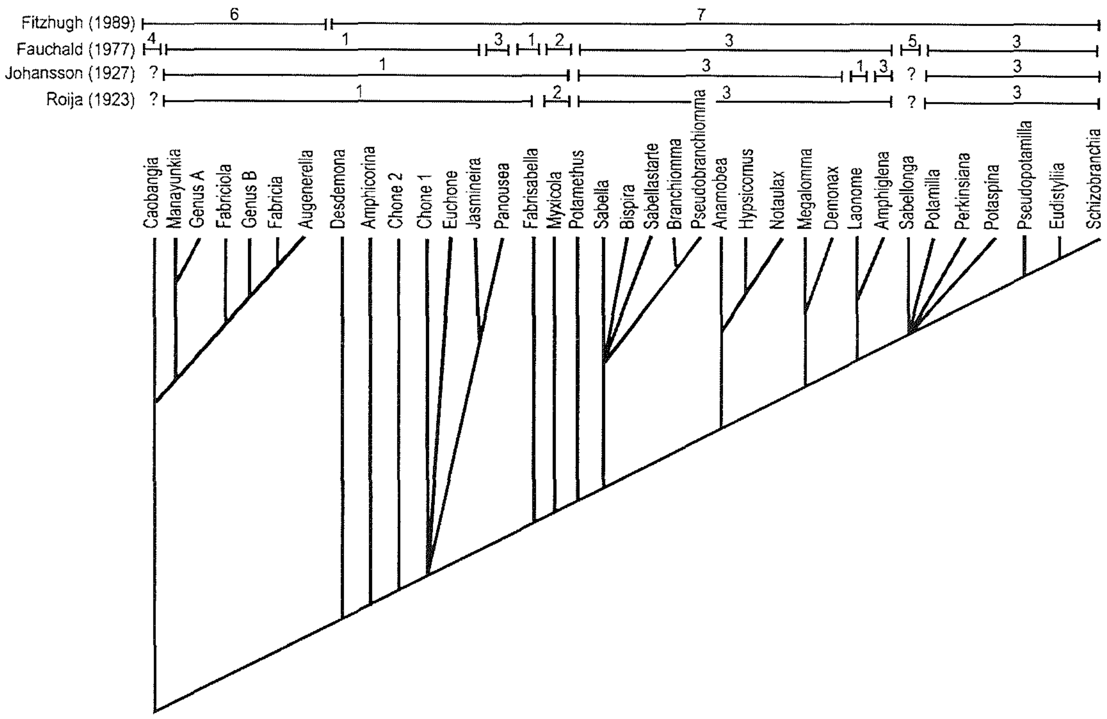

Figure 3.4.1. Adams consensus tree of the 16 minimum-length cladograms used as a basis for revision of the Sabellidae (after Fitzhugh 1989). The classification into families and sub-families according to Fitzhugh (1989), Fauchald (1977), Johansson (1927) and Rioja (1923) is indicated at the top of the figure. The numbers refer to the following taxa:
1 =Fabriciinae, 2 = Myxicolinae, 3 = Sabellinae, 4 = Caobangiidae,
5 = Sabellongidae, 6 = Fabriciinae, revised Fitzhugh (1989) and 7 = Sabellinae, revised Fitzhugh (1989).

It is clear that the clades recognised by Fitzhugh (1989) as sub-families are the only arrangement in which the higher taxa are monophyletic. All the previous systematic arrangements of the higher taxa do not include all descendants of the common ancestor. In recognising only two sub-families, the Sabellinae and Fabriciinae, both emended *sensu* Fitzhugh (1989), the following sub-families are rendered invalid: Myxicolinae, Caobangiidae and Sabellongidae. *Caobangia* appears within the Fabriciinae, while *Myxicola* and *Sabellonga* are included within the Sabellinae.

3.4.4 The family Sabellidae

In the above analyses, the sabellid clade formed a monophyletic group on the basis of at least five transformation states, although only three of these were synapomorphies.

The family Sabellidae was thus re-diagnosed as follows (Fitzhugh 1989). The three synapomorphies are indicated by italics:

Sabellidae Johnston, 1846, revised Fitzhugh (1989)

"Sabelliform polychaetes which produce a mucoid, gelatinous or horny tube; may be encrusted with sediment. Tentacular crown with or without skeletal supporting cells. Branchial lobes fused dorsally or completely separate. *Thoracic neuropodial uncini* (absent in *Caobangia*) *with main fang surmounted by a broad series of smaller teeth*; sub-distal breast present, either as narrow, inflated region or as large, distally directed projection; *proximal region of uncini with handle or shaft* (absent in *Laonome*). *Abdominal neurosetae hooded or appear to have a limbation along shaft.*"

The left-hand clade in the above figure (forming the emended Fabriciinae) was monophyletic on the basis of two synapomorphies, separating it unequivocally from the remaining taxa. The resulting diagnoses of the two emended sub-families within the Sabellidae were given in the 1989 paper. However, as these were shortly after emended (Fitzhugh 1991a), the 1989 diagnoses are not repeated here.

3.4.5 Emended diagnoses of the Fabriciinae and Sabellinae

Subsequent to the 1989 revision, further cladistic analyses were carried out using a slightly modified weighting technique (successive approximations weightings), resulting in an emendation of sabellid subfamilies (Fitzhugh 1991a). The major systematic difference between this and the previous work is that, whilst maintaining *Caobangia* within the Sabellidae, the taxon was moved from the Fabriciinae to the Sabellinae. This resolved certain ambiguities in the transformation series relating to dorsal fusion of the branchial lobes and presence of the branchial skeleton. The diagnosis of the Sabellidae *sensu* Fitzhugh (1989) remained unchanged. The removal of *Caobangia* to the Sabellinae allowed a stronger diagnosis of the sub-families. The emended diagnoses for the Fabriciinae and the Sabellinae are as follows, taken from the text of Fitzhugh (1991). Synapomorphies are indicated by italics. A discussion of the chaetal terminology used is given in Chapter 1.2.5.

Fabriciinae Rioja, 1923, emended Fitzhugh (1991a)

Diagnosis. Small-bodied sabellins with two or three pairs of radioles. Radiolar skeleton absent, branchial lobes separate. *Branchial hearts present.* Ventral lips absent. Anterior margin of anterior peristomial ring collar present as 1) thin, membranous collar, 2) wide, ventral, triangular or lip-like lobe or 3) low ridge. Posterior peristomial ring collar absent. Inferior thoracic notochaetae[3] elongate, narrowly hooded in all chaetae, or replaced in some chaetigers by pseudospatulate or broadly hooded, flagellate chaetae. Abdominal neurochaetae modified, elongate, narrowly hooded. Thoracic uncini acicular with narrow breast and long-handled; hood present. Abdominal notopodial uncini usually rasp-shaped plates; *breast an elongate manubrium*; handles absent. Abdominal chaetigers numbering three or four.

Sabellinae Johnston, 1846, emended Fitzhugh (1989)

Diagnosis. Small-bodied to large-bodied sabellids. *Radiolar skeleton present, branchial lobes fused mid-dorsally*. Radiolar flanges, and dorsal and ventral radiolar appendages common. Anterior margin of anterior peristomial ring as either 1) a wide, ventral triangular lobe, 2) a narrow, ventral triangular lobe or 3) a low, even surface. Posterior peristomial collar usually present. Post-chaetal glandular girdle sometimes present on chaetiger 2. Inferior thoracic notochaetae present as anterior or posterior groups, or both. Abdominal neurochaetal fascicles as anterior or posterior groups, or both. Thoracic uncini ranging from acicular to avicular. Abdominal uncini rasp-shaped plates with poorly-developed breasts or well-developed manubria, or avicular with expanded or narrow breasts and handles absent or present.

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[3] Publications by Fitzhugh use the term 'seta' and derivations thereof.

3.4.6 Further comments

It should be noted that many of the characters described in the above diagnoses show a certain amount of variation between the taxa. For example, some Fabriciinae do possess a radiolar skeleton, comprising a single row of cells, while the diagnosis at the sub-family level indicates that these structures are lacking. These small discoveries highlight the plasticity of certain characters, and they serve to emphasise the complex processes of reversalism, parallelism and convergence that may have played a role in the developmental history of the taxa concerned.

The emendments made by Fitzhugh (1991a) to the sub-family diagnoses established only two years previously also highlight the flexible nature of cladistic analyses, and the “endless task” of phylogenetic systematics as outlined by Hennig (1966). Fitzhugh’s (1989) cladistic analyses were the first to be carried out on the Sabellidae. As the techniques involved still are in a state of development, it is to be expected that results obtained at any given point in time will not remain absolute or static over the years. As more characters are revealed and opinions on coding strategies change with time, so too will the details of phylogenetic classification systems. While previously this may have led to frustration and nomenclatural instability, the aim of phylogenetic systematics is to consider the clades and how they relate to one another. It becomes of lesser importance if a terminal taxon moves from one clade to another, providing named clades always are monophyletic.

As seen in in Chapter 3.4, phylogenetic analyses, although based on very simple fundamental principles, are subject to much controversial and often heated debate. Perusal of the relevant journals in chronological order clearly shows the changing state of knowledge and opinions over time and, as such, the details of sabellid systematics is expected to change yet again, as new information and techniques become available. However, the main monophyletic groupings are expected to remain stable. These changes and developments should be seen as an exciting challenge, rather than reflecting systematic instability.

3.5 Phylogenetic analyses of *Euchone* and related taxa

3.5.1 Background

Systematic difficulties in *Chone* Krøyer, and related taxa such as *Jasmineira* Langerhans and *Amphicorina* Quatrefages, are evident in the literature as well as in specimens encountered in faunal samples (see Chapter 2). Both *Chone* and *Jasmineira* lack adequate synapomorphies, and *Euchone* Malmgren currently is differentiated from *Chone* solely on the basis of the presence of an anal funnel. Despite this apparently straightforward diagnosis for *Euchone*, the form of the anal funnel shows a certain amount of variability between *Euchone* taxa, and some transitional states are evident in taxa such as *Euchone limnicola* Reish, which lacks lateral wings bordering the depression (see Chapter 1.3.5).

The presence or absence of differentiated glandular ventral shields usually is noted in taxon descriptions. Banse (1972) noted the presence of differentiated ventral shields in *Chone paucibranchiata* (Krøyer) and used this as part of his argumentation that the taxon is discrete from *Chone infundibuliformis* Krøyer, but otherwise, the feature generally has been given little attention in a systematic context.

Another interesting phenomenon which merits further investigation in the Sabellidae is the number of abdominal segments present. Whereas some sabellids have a constant number of abdominal segments, in others, segments are continuously added immediately anterior to the pygidium as the animal grows. Thus, in these organisms, young individuals tend to have far fewer segments than mature animals. This appears to be the case amongst most, if not all members of *Chone*, whereas in *Euchone*, the segmental arrangement seems largely to be fixed. Interestingly, whereas there is little or no variation in numbers of abdominal segments between individuals of the 'small' *Euchone* taxa (*sensu* Banse 1970) such as *Euchone incolor* Hartman and *Euchone x* (Chapter 2.3), amongst 'larger' taxa such as *E. rubrocincta* (Sars), a certain degree of individual variation is evident. A similar situation exists within *Jasmineira*. Whereas *Jasmineira caudata* Langerhans and *Jasmineira shaudinni* Augener appear to add abdominal segments throughout growth, other taxa such as *Jasmineira candela*

Grube and *Jasmineira oculata* Langerhans (Chapter 2.4) have a constant number of abdominal segments. The growth strategy affects the overall morphology of the adult worms. The segment length:width ratio is generally far smaller in those taxa that grow by continually adding abdominal segments, than is the case in taxa that retain a constant number of segments throughout growth. In the latter organisms, growth appears to be by increasing the breadth and width of the extent segments.

Discussions of the phylogeny of *Euchone* are by no means new. In 1970, Banse noted the presence of pectinate uncini similar to those found in *Amphicorina* (formerly *Oriopsis* Caullery & Mesnil) in the 'small' taxa of *Euchone*, such as *E. incolor* Hartman and *E. hancocki* Banse. In *E. arenae* Hartman, a combination of these uncinal types was found - the ontogenetically first-formed uncini, located in the ventral part of the tori were of the pectinate form, whilst avicular uncini 'typical' of *Chone* and *Euchone* were present in the most dorsal part of the tori. Banse interpreted the presence of pectinate uncini as being a "primitive" feature. Therefore he regarded those *Euchone* taxa which possess this feature as primitive, in at least this respect.

Banse also noted other features shared between the 'small' *Euchone* taxa and *Amphicorina*, which he considered to be close to the "basis" of the Sabellidae. In these organisms, the radioles are bordered by a flange and the pinnules end at the same height distally ('snowflake-like', see Chapter 1.2). This radiolar arrangement previously was noted for certain members of the family Amphicorinidae (Benham 1896), which included small sabellins such as *Fabricia* Blainville and *Manayunkia* (Bourne). Banse (1970) also noted a common lack of an inter-radiolar membrane amongst the 'small' *Euchone* and *Amphicorina*, but it has later become apparent that at least some of these taxa do indeed possess this feature, albeit in a very low state. These taxa also appear to lack differentiated glandular shields.

The possibility was discussed that these morphological similarities, with the exception of the uncini, have arisen as a result of convergence. Banse (1970) also presented several hypotheses of evolutionary pathways amongst these sabellid taxa (as genera). Banse (*op. cit.*) used the term *Chone* group to refer to *Chone* and *Euchone* together. His concept of the Sabellinae used the now invalid diagnosis that excludes forms with acicular thoracic uncini. He suggested that "evolution might have proceeded from *Amphicorina* (as *Oriopsis*) through the *Chone* group, toward the Sabellinae, or *Amphicorina* might be on a side branch (starting from near *Chone-Euchone*) of the line leading to the Sabellinae".

The present work uses the phylogenetic analyses of Fitzhugh (1989) as a starting point for a narrower investigation of first and foremost *Euchone*, together with a restricted number of taxa within *Amphicorina, Chone* and *Jasmineira.* In doing so, the hypotheses of Banse (1970) as to the phylogeny of the taxa in question will be re-assessed. Because the present analyses are carried out at a lower level of inclusiveness than those of Fitzhugh (1989), a more detailed investigation of the concept of the *Chone* complex (*sensu* Fitzhugh 1989) or the *Chone* group (*sensu* Banse 1970) is made possible.

3.5.2 Aims

Using phylogenetic analyses, the following issues are addressed, using a data set focusing mainly on *Euchone* Malmgren and a restricted inclusion set of members of *Amphicorina* Quatrefages, *Chone* Krøyer and *Jasmineira* Langerhans.

1) are there distinct monophyletic groups within the taxa included in the analyses?
2) is the concept of the "*Chone* complex" supported?
3) is *Euchone* a monophyletic taxon?
4) is the presence of an anal depression a diagnostic character of *Euchone*?
5) do the present analyses support the hypothesis that *Amphicorina* is a more 'primitive' taxon than *Chone*/*Euchone*, which in turn are more 'primitive' than those sabellins possessing avicular thoracic uncini?
6) do *Jasmineira candela* and *Jasmineira oculata* group together with other taxa currently recognised within *Jasmineira*?

3.5.3 Ingroup taxa

The main study group is taxa currently recognised within *Euchone*. For practical reasons, it was not possible to include all *Euchone* taxa listed world-wide, as listed in Table 2.3.2. Taxa for which the description is inadequate, or there is potential controversy as to its identity, were excluded from the present study. For comparative purposes, selected members of *Chone*, *Amphicorina* and *Jasmineira* were included in the study group. The 'type species' of *Amphicorina* is not among the ingroup taxa because a full character list could not be obtained. Instead, three taxa for which there exists a detailed description were used. The *Chone* taxa chosen are among those encountered in northern Atlantic waters, and for which an adequate description exists (thereby excluding *Chone kroyeri* Sars, *Chone fauveli* McIntosh and *Chone suspecta* Krøyer). Amongst taxa currently recognised within *Jasmineira*, the 'type species' *Jasmineira caudata* Langerhans and *Jasmineira elegans* Saint-Joseph were selected. *Jasmineira candela* Grube and *Jasmineira oculata* Langerhans were chosen to investigate further the apparent anatomical discrepancies between those and other taxa within *Jasmineira* (see Chapter 2.5).

A total of 35 terminal taxa were included in the ingroup, listed in Table 3.5.1 according to their current designation to genus. The ingroup comprised 20 members of *Euchone*, including one new taxon (see Chapter 2.4), three members of *Amphicorina*, six members of *Chone*, including one taxon of uncertain identity (see Chapter 2.6) and four taxa currently included within *Jasmineira*.

To carry out a phylogenetic revision of the taxa, the ingroup must be monophyletic. Therefore, an analyses must be conducted that also include the other taxa appearing on the relevant area of the Fitzhugh (1989) tree shown in Figure 3.4.1. In addition to taxa within *Jasmineira, Euchone*, *Chone* (1 and 2) and *Amphicorina*, those within *Desdemona* and *Panousea* also should be included in the analyses. Further, the data set should be improved such that the characters are all supported by personal observations.

Table 3.5.1. Terminal taxa included in the ingroup.

Euchone	***Chone***	***Jasmineira***	***Amphicorina***
alicaudata Moore & Bush	*infundibuliformis* Krøyer	*candela* Grube	*androgynae* (Rouse)
analis Krøyer	*duneri* Malmgren	*caudata* Langerhans	*anneae* (Rouse)
arenae Hartman	*filicaudata* Southern	*elegans* Saint-Joseph	*paramobilis* (Rouse)
bansei Ruff & Brown	*longocirrata* Sars	*oculata* Langerhans	
capensis Day	*paucibranchiata* (Krøyer)		
elegans Verrill	*y* informal taxon		
hancocki Banse			
incolor Hartmann			
limnicola Reish			
pallida Ehlers			
papillosa (Sars)			
rosea Langerhans			
rubrocincta (Sars)			
scotiarum Hartmann-Schröder			
southerni southerni Banse			
trilobata (Banse)			
undulocincta Hartman			
velifera Banse			
variabilis Hutchings			
x new taxon			

3.5.4 Outgroup selection

The Fabriciinae (*sensu* Fitzhugh 1989) as a whole was used for outgroup comparison. This group is shown to be the sister-group to the Sabellinae (Fitzhugh 1989) and, as such, allows basal polarity of the characters under investigation (see Maddison *et al.* 1984). Thus, state 0 is always that of the outgroup, and is therefore pleisiomorphic to the study group, or ingroup taxa, while states 1, 2 etc. are derived conditions of the character. Because basal polarity allows for the possibility of reversal back to the ancestral state 0, the ancestral-derived transition series is not necessarily universal (see Maddison & Maddison 1992). For the present analyses, multiple derived character states were all unordered, i.e. no statements were made as to the order of character transformation from ancestral to derived states.

3.5.5 Coding strategies

Coding variable characters

As discussed in Chapter 3.5.8, character coding presents a number of logistic challenges, and the decision to use either multi-state or A/P coding is not free of debate. Character coding of sabellid taxa is particularly challenging, due to the way in which a single character (such as number of radioles or abdominal segments) may show considerable variation within one taxon but may be constant in another. Grouping of continuous-valued characters into a range of appropriate values coded as a single state was avoided as far as possible, because in many cases, the designation to one or another state would have been arbitrary. Several approaches were tried. First, all states were coded in multi-state form as discrete units. As a result, characters such as numbers of abdominal segments and numbers of radioles had more than 15 states, while others, such as presence or absence of differentiated ventral shields had only two. For comparison, the data also were coded in A/P form, resulting in over 100 characters.

Heuristic searches of the A/P coded data set gave very incongruent results (thousands of equally-parsimonious trees retained). The consensus tree showed only two main taxon groups within the ingroup; that of the five *Euchone* taxa with 'snowflake-like' radioles and all the remaining taxa. Both clades were represented as polytomies. The multi-state data set also gave similarly incongruent results as were obtained using the A/P approach, although a slightly lower number of trees were retained. It was concluded that coding variable characters was inappropriate for the present large-scale analysis. For example, some taxa possess a fixed number of abdominal segments and this number is constant between individuals and throughout the growth of each individual. Others add segments throughout their lifetime. In this case, the recorded number of segments for a particular taxon is dependent on the maturity of the specimens examined. Coding numbers of segments as discrete values means that the difference between 40 and 45 segments is treated as completely different character states, when in fact the difference may be of little consequence.

An alternative approach was adopted for the present analyses, whereby highly variable characters were coded with only two states. The numbers of radioles and numbers of abdominal segments were coded as the outgroup condition of three or otherwise, i.e. more than three. In compensation for the loss of information on segment numbers, a character for whether the animal has a fixed number of segments or grows by adding segments, was included. The anal depression was coded as being absent (0), comprising only three segments (1) or more than three (2). It is proposed that more detailed information on these characters is appropriate to analyses of a more restricted inclusion set.

Missing data and inapplicable states

Because the ingroup comprised a series of single taxa (or 'least inclusive taxonomic units'[1]), these were generally monomorphic; i.e. could be coded as having a single state for each character. However, the outgroup comprised a more inclusive monophyletic taxon, and therefore was polymorphic in some characters; i.e. more than one state was applicable. In these cases, the relevant characters were coded as polymorphisms (for example MacClade accepts a data entry of "1&2", where both states are applicable). Missing data were simply coded as "?".

Some characters were not applicable to all taxa. For example, the anal depression was coded as being absent, or any one of a series of states reflecting the number of posterior segments it encompasses. The next character referred to the presence of lateral wings. These are present in *Euchone* taxa, with the exception of *Euchone limnicola* Reish in which the feature is reduced. However, coding lateral wings as being absent in taxa that do not possess an anal depression at all may cause inadvertent weighting of that feature. Similarly, the presence of a scalloped anterior collar margin (derived from the posterior peristomial ring) is inapplicable to taxa in which the collar, when present, is derived from the anterior peristomial ring. Therefore, inapplicable states also were coded as "?".

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[1] term used in a broad sense

3.5.6 The characters

The term 'character' is here used to denote a single feature or component of a feature, which is entered into the data matrix. The term 'character states' refers to the different morphologies which that feature might assume throughout a transition series. Although some authors argue that the terms 'transformation series' and 'character', respectively, are more correct (Wiley *et al.* 1991), the chosen terms are compatible with much of the recent phylogenetic research (such as Rouse & Fauchald 1997).

In total, 35 characters were used in the analyses, a summary of which is given below. All characters were unordered, with an equal weight of 1. More detailed information and illustrations of the structure and morphology of the sabellid taxa in question are given in Chapter 1. Further information on the descriptive characters of the Sabellidae as a whole may be found in Fitzhugh (1989). Appendix I shows a complete list of characters and character states and the data matrix is presented in Appendix II.

Crown characters (Characters 1-11)

The three synapomorphies of the Fabriciinae (presence of branchial hearts, a single row of cartilaginous cells forming the radiolar skeleton and completely separate lobes of the branchial crown) were recorded for all taxa as two states, present or absent. The pinnules were recorded as two states, paired or alternating, and their relative length along the radiole was coded as three states. The numbers of radioles were coded with two states, three or more than three pairs. The height of the inter-radiolar (palmate) membrane was coded as five states and the presence or absence of a flange was coded with two states. The relative width of the flange was not taken into account due to problems of subjectivity. The shape of the tips of the radioles was coded as three states, and the extent to which the tips exceed the height of the distal-most pinnules was coded as two states. The presence of a 'breaking plane' at the base of the radioles, characteristic of certain *Jasmineira*, was assigned two states.

Peristomial characters (Characters 12-20)

Ventral cirri were recorded as being present or absent, without specification of their numbers. The modification (if any) of the anterior peristomial ring (APR) as a collar or lobe was coded as four states and the eventual modification of the posterior peristomial ring (PPR) as a collar where the dorsal margins are free or attached to the APR was given three states. Fusion of chaetiger 1 with the peristomium was coded as two states: in the Sabellinae, this is evident as the first bundle of thoracic notochaetae appearing to arise from the base of the collar. The extent to which the anterior peristomium protrudes beyond other structures was allotted three states. The presence of a ventral incision, or split, in the collar (here referring to that derived from the posterior peristomial ring) was given two states, as was the angle of that structure seen laterally. Oblique refers to collars that are markedly higher ventrally than dorsally. The width of the dorsal gap and eventual scalloping of the anterior collar margin was coded as two states.

General thoracic characters (Characters 21-24)

The eventual differentiation of ventral glandular shields was coded as two states, as was the presence or absence of a post-chaetal glandular girdle. Biannulation, at least in thoracic segments, was allotted two states, as was presence or absence of notopodial lips in the thorax. No attempt was made to distinguish between post-chaetal and pre-chaetal lobes.

General abdominal characters (Characters 25-31)

The number of abdominal segments was coded with two states, that of the outgroup and otherwise (see Chapter 3.6.5). The presence or absence of a glandular girdle in the abdomen was coded as two states. The anal depression was coded with three states; absent or comprising three, or more than three posterior segments (see Chapter 3.6.5). The presence of well-developed or reduced lateral wings bordering the anal depression was coded as three states. The growth strategy whereby segments are added immediately anterior to the pygidium, rather than by expansion of the extant segments was coded as two states. The presence or absence of pygidial eyespots or a pygidial filament each were coded as having two discrete states.

Chaetal characters (Characters 32-40)

The superior thoracic notochaetae were coded as two states. In the present analyses, this character was uninformative, being shared by ingroup and outgroup members alike. The anterior row of inferior thoracic notochaetae were given three states: pseudospatulate, bayonet-type or short, swollen. No attempt was made to distinguish between the relative widths of the short 'swollen' type of chaetae. The posterior row of inferior chaetae were coded as four states, either absent, short and swollen, pseudospatulate or spatulate. The thoracic uncini (neurochaetae) were coded as two states, according to the presence or absence of teeth of unequal sizes above the main fang. Coding abdominal uncini (notochaetae) as a single feature with a series of different character states resulted in incongruous trees. Thus, the uncini were coded according to their main components, a strategy adopted by Fitzhugh (1989). As noted in Chapter 1.2.5, the logic of this approach is not entirely consistent with the strategy for coding the elongate chaetae, but a better alternative for coding subtle variations in uncini was not achieved. Thus the presence of a main fang was given two states, the form of the breast was coded with five states and the eventual presence of a posterior handle was given two states. Figure 1.2.13 shows the main features of the types of uncini encountered.

The abdominal notochaetae were coded as being of the elongate, narrow form or otherwise and was uninformative. Marked variation in uncinal form within a torus was coded as two character states.

3.5.7 Characters and taxa not included in the analyses

In the present study, there are a number of characters that it would be advantageous to include in the analyses. Data availability for a large number of taxa prevented the use of dorsal and ventral lip morphology, segment length:width relationship and crown:body length relationship. The absolute numbers of abdominal segments and numbers of radioles were not analysed because the characters show great between-taxon variability, such that a reappraisal of coding strategy for continuously varying characters is required. These issues should be attended to in the continuation of the present work.

Ideally, the ingroup also would have included *Jasmineira bermudensis* Hartman and *Jasmineira filiformis* Hartman. These are interesting because they share the general abdominal chaetal characteristics with *Jasmineira caudata* and *Jasmineira elegans*, but differ in lacking a breaking-point at the base of the radioles. The description of *J. bermudensis* did not include details of the crown and the available study material lacked an intact crown, resulting in an incomplete character list for that taxon. *Jasmineira filiformis* shares certain characteristics with *Amphicorina*, such as having pinnules that are longest mid-radiole, but it was not possible to confirm or dispute the description of these as paired. Including those two taxa with missing data resulted in such a high degree of incongruity between trees that the relationships between the remaining ingroup taxa were partially obscured. *Jasmineira bermudensis* and *J. filiformis* were therefore excluded from the analyses, although they are included in the character list in Appendix I, to aid further research on *Jasmineira*.

3.5.8 Analyses

Hard and software

Phylogenetic analyses were carried out using an Apple Macintosh PowerBook 520. The data matrix and tree diagrams were created using MacClade version 3.04 (Maddison & Maddison 1992). Tree reconstruction and computation of consensus trees were carried out using PAUP version 4.0b2 (Swofford 1999).

Tree reconstruction

Reconstruction of trees was carried out by a heuristic search using the default settings of PAUP (tree-bisection-reconnection (TBR) branch-swapping, MULTREES and COLLAPSE options in effect). Branches with zero length were collapsed to yield polytomies and topological constraints were not enforced. A random stepwise addition sequence of ten replicates was used with a starting seed of 1.

Consistency and retention indices - background

The consistency index (ci) (Kluge & Farris 1969; Farris 1989) was calculated as the ratio of *m*, the minimum number of steps the same character can exhibit on any cladogram to *s*, the minimum number of steps the same character can exhibit on the cladogram in question. Therefore, the consistency index measures the amount of homoplasy in the data (reviewed in Kitching *et al.* 1998).

Consistency indices always have a value between 0 and 1, although a zero value cannot be attained. If a character has no homoplasy (i.e. only occurs on one clade) the ci would have a value of 1. If there were twice as many steps as needed (e.g. if one reversal of the character has occurred within a clade), then the ci value would be 0.5 and so on. Potential problems with the use of ci are that autapomorphies (characters unique to a single taxon) and invariant or uninformative characters will inflate its value. In general, the value of the ci tends to be inversely proportional to the number of taxa included in the analysis (see Kitching *et al.* 1998).

The retention index (ri) (Archie 1989; Farris 1989) deals with the degree of 'fit' of a character to a cladogram, as opposed to the amount of homoplasy displayed by a character. The ri was calculated as $(g - s)/(g - m)$, where g is the greatest number of steps a character can exhibit on any cladogram. The retention index measures the amount of similarity (as synapomorphies). In contrast to the ci, the ri may reach a value of zero (see Kitching *et al.* 1998). As with ci, a high ri value indicates a high degree of character fit to the cladogram.

Both indices ci and ri are therefore used to examine how individual characters 'behave' on the cladogram in question. For a combined assessment of all the characters on a particular cladogram, the ensemble CI and ensemble RI was used as follows: $\mathrm{CI} = M / S$ and $\mathrm{RI} = (G - S) / (G / M)$, where M, S and G are the sums of all the m, s and g values for the individual characters, respectively (Farris 1989). Therefore, the ensemble CI for all characters on a tree is the minimum possible treelength divided by the observed treelength.

If all the characters in the data matrix are perfectly congruent with each other and the tree, with no homoplasy (i.e. ocurring only once), then the observed number of steps will equal the minimum conceivable number of steps and the CI will be 1.00. The more discrepancies and incongruence in the data set, the greater the amount of homoplasy will be. The greater the amount of homoplasy, the greater the number of steps will be, and the smaller the CI value.

To avoid inflating the CI value with autapomorphies of terminal taxa, i.e. character states which are unique to these taxa, the 'exclude uninformative' command was used before calculating the consistency indices. Likewise, the ensemble RI will have a value of 1 if the characters in the data set are perfectly congruous with each other and the tree (i.e. maximum amount of synapomorphy). The greater the incongruence, the greater the RI value.

The consistency index can be used for *a posteriori* character weighting, i.e. assigning weights to characters after selection of the most parsimonious cladograms. However, because the value of the consistency index can never be zero, Farris (1989) advocated rescaling the ci using the retention index, producing the rescaled consistency index (rc). The rescaled consistency index was calculated as follows:

Character rc = (character ci) * (character ri)
where m_i is the minimum conceivable number of steps for character i on any tree, M_i is the maximum conceivable number of steps and s_i is the number of reconstructed steps for character i on the particular tree under consideration. The RC index for all characters on a tree was calculated as CI*RI. As with CI and RI, RC values range from 0 to 1, with higher values indicating higher character congruence.

In the present analyses, character weighting was not carried out. Therefore, the rescaled consistency index is not discussed further, but merely presented for background information.

Justifying the consensus tree

A consensus tree is a form of 'summary tree', which condenses the information in the minimum-length parsimonious trees retained by the analyses. Incongruities between trees are represented as polytomies, i.e. two or more branches radiating from a single point of origin. In this way, both incongruent and congruent taxa are highlighted.

However, there is a certain risk associated with consensus trees. Whereas polytomies also may occur in the parsimonious trees, these are not to be treated in the same manner as those in the consensus tree. In a single tree, all possible dichotomous resolutions of the polytomy, which arises from zero-length collapsing, are equally parsimonious. However, this principle cannot be applied to the consensus tree. Whereas the consensus tree is compatible with all the parsimonious trees from which it was derived, there may be other trees which are compatible with the consensus, but which are not among the most parsimonious. After the trees are condensed into the consensus, information on which dichotomous trees went into it is lost. As a result, tracing character evolution on a consensus tree may show a reconstruction sequence corresponding to a tree which was not one of the most parsimonious. This may give a result which is not in accordance with any of the parsimonious trees. Therefore, character tracing is not carried out on the consensus tree in the present study. Instead, one or several of the minimum-length parsimonious trees are used for this purpose.

There has been some debate as to the benefits of using consensus trees at all (e.g. Eibye-Jakobsen & Nielsen 1996). However, in the present study, a strict consensus tree is used for reference purposes only, bearing in mind the above restrictions.

3.5.9 Results

Using the full data matrix, a total of 68 equally parsimonious, minimum-length trees were obtained, each with a tree length of 95 steps. After exclusion of uninformative characters, the following descriptive indices were obtained for all trees: CI = 0.54, RI = 0.82 and RC = 0.44, indicating a certain amount of incongruence in the characters on the trees. The indices for the strict consensus tree (Figure 3.5.1) were: CI = 0.57, RI = 0.84 and RC = 0.48.

The three terminal taxa within *Amphicorina* Quatrefages are grouped together into a discrete clade, which forms the sister group to the remaining ingroup taxa. It is immediately evident that *Euchone* Malmgren is paraphyletic as terminals within that taxon form two discrete groups. Strikingly, the smallest group forms a sister group to the remaining taxa within *Chone, Euchone* and *Jasmineira*. There is some incongruence as to the position of *Jasmineira* relative to *Chone* and the remainder of *Euchone*. All six terminal taxa within *Chone* and 15 within *Euchone* form a monophyletic group. Hereafter, the larger clade comprising *Euchone* is named *Euchone* 1 and the clade comprising only five taxa is named *Euchone* 2.

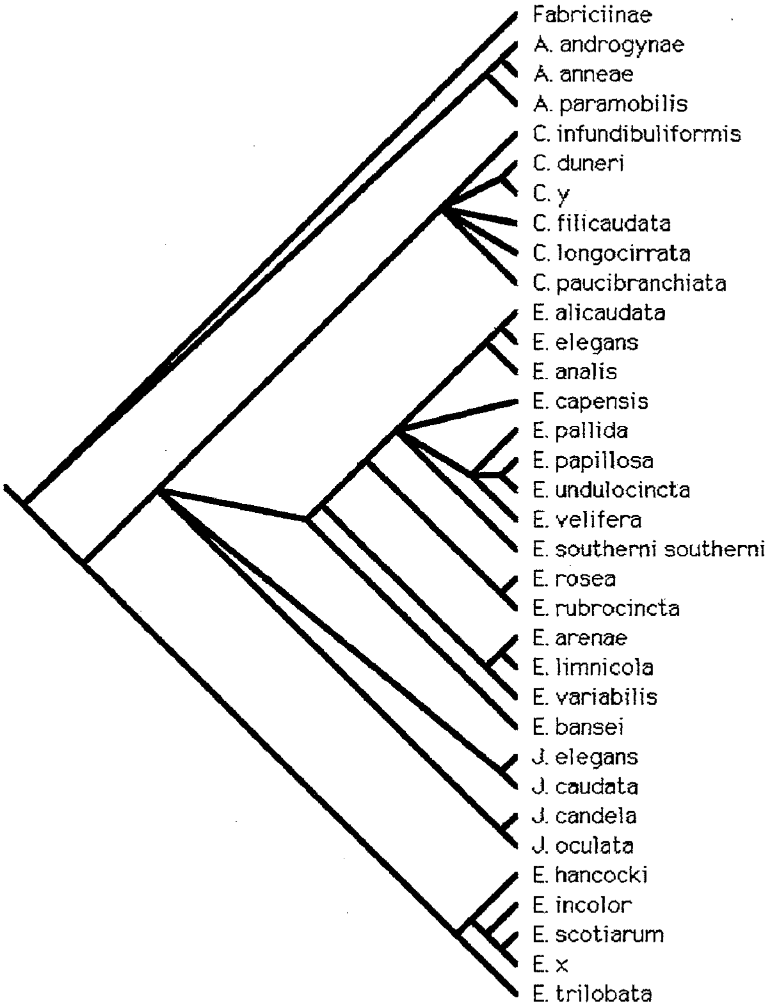

Figure 3.5.1. Strict consensus tree of 68 individual trees.

Because removal of absolute values for numbers of radioles, numbers of abdominal segments and number of segments comprising the anal depression obscured some of the differences between terminal taxa, there was a lack of resolution within parts of the *Euchone* 1 clade in particular. Therefore, the precise relationships between taxa within those clades will not be discussed further.

The most interesting incongruity observed was in the position of the *Jasmineira* taxa on the trees. Four equally plausible alternatives were obtained and trees PAUP 10, 40, 60 and 21 were chosen to illustrate these. On a broad scale, the four *Jasmineira* taxa either join the *Chone* clade (as in Figure 3.5.2a, b) or form part of a more inclusive clade comprising *Chone* and *Euchone* 1 (Figure 3.5.2c, d).

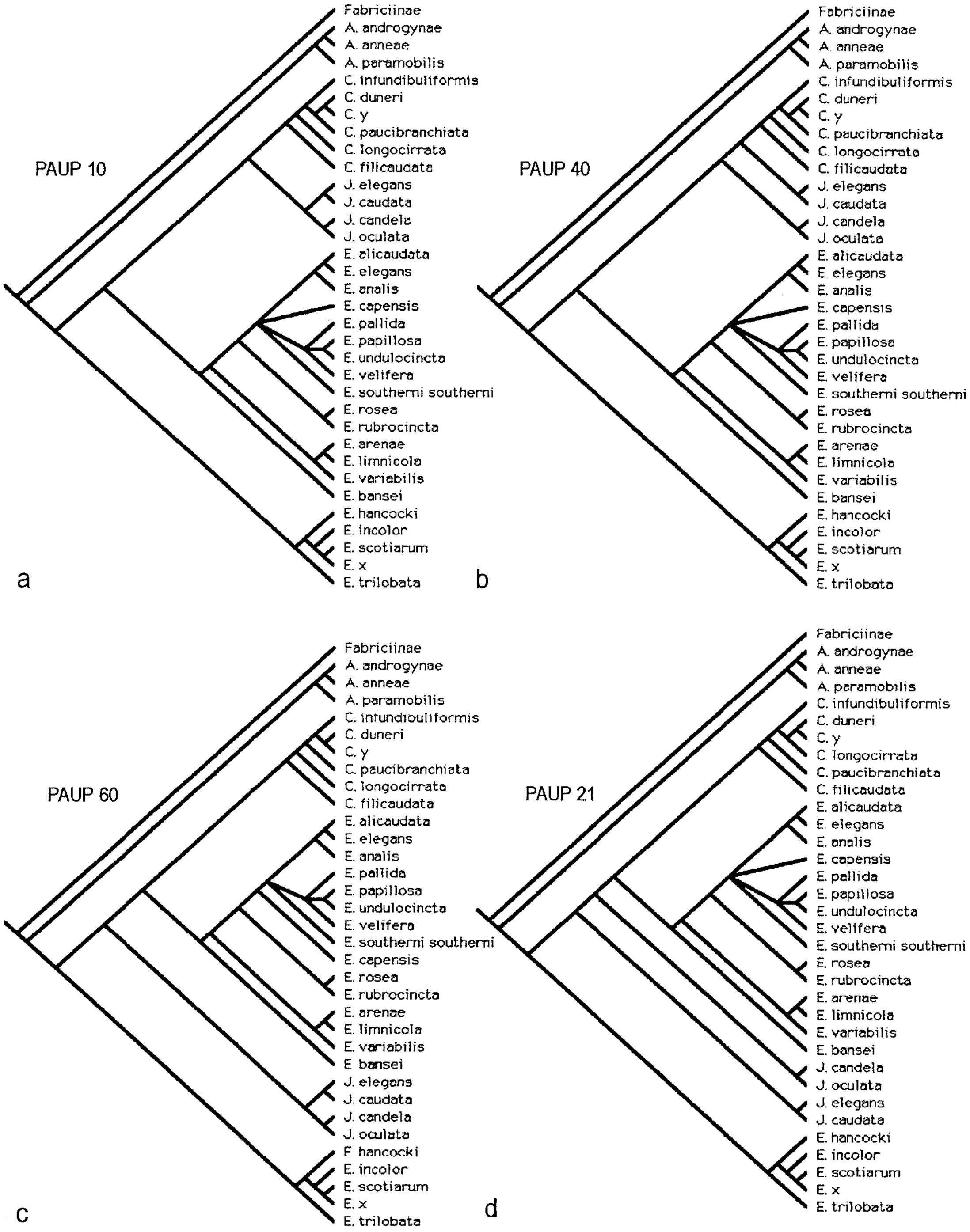

Figure 3.5.2. Four of the 68 minimum-length trees: a) PAUP 10, b) PAUP 40, c) PAUP 60 and d) PAUP 21. Note the incongruity in position of Jasmineira *terminal taxa, relative to* Chone *and* Euchone.

Figure 3.5.2a shows all four *Jasmineira* taxa to form a monophyletic sister group to the *Chone* clade. Within this group, *Jasmineira caudata* and *Jasmineira elegans* are sister taxa to *Jasmineira candela* and *Jasmineira oculata*. In Figure 3.5.2b, only the former pair of taxa form a sister group to *Chone*. *Jasmineira candela* and *J. oculata* form a sister group to *Chone* plus *J. caudata* and *J. elegans.* In Figure 3.5.2c, all four *Jasmineira* taxa form a similar clade to that seen in Figure 3.5.2a, only as a sister group to both *Euchone* 1 and *Chone*. In Figure 3.6.2d the two pairs of *Jasmineira* taxa form separate clades on the tree, prior to the splitting event of *Chone* and *Euchone* 1. This tree, PAUP 21, is considered subjectively to be the most conservative of the hypotheses and was chosen to investigate character changes.

Figure 3.5.3 shows the characters that change unambiguously on each branch of tree PAUP 21. Note that character changes are not shown on polytomous branches. Only character changes within the main clades will be discussed in detail. The *Amphicorina* clade is separated from the remaining ingroup taxa by four character changes (Characters 35, 34, 15 and 12). A further four changes occur on the branch between the *Euchone* 2 clade and that comprising *Chone, Euchone* 1 and *Jasmineira*.

Only one unambiguous change occurs on the branch between the *Jasmineira candela/ oculata* clade and its sister group. Similarly, only one change occurs between *Jasmineira caudata/ elegans* and its sister group, the *Chone* and *Euchone* 1 clades. Two changes occur on the branch leading to the *Chone* clade and four changes occur along the branch leading to *Euchone* 1.

Because these changes are not necessarily diagnostic of the taxa within the various clades (the features may reverse further up the tree), the characters are not discussed in detail here. Further details may be obtained in the full character list and the character matrix in Appendix I and II, respectively.

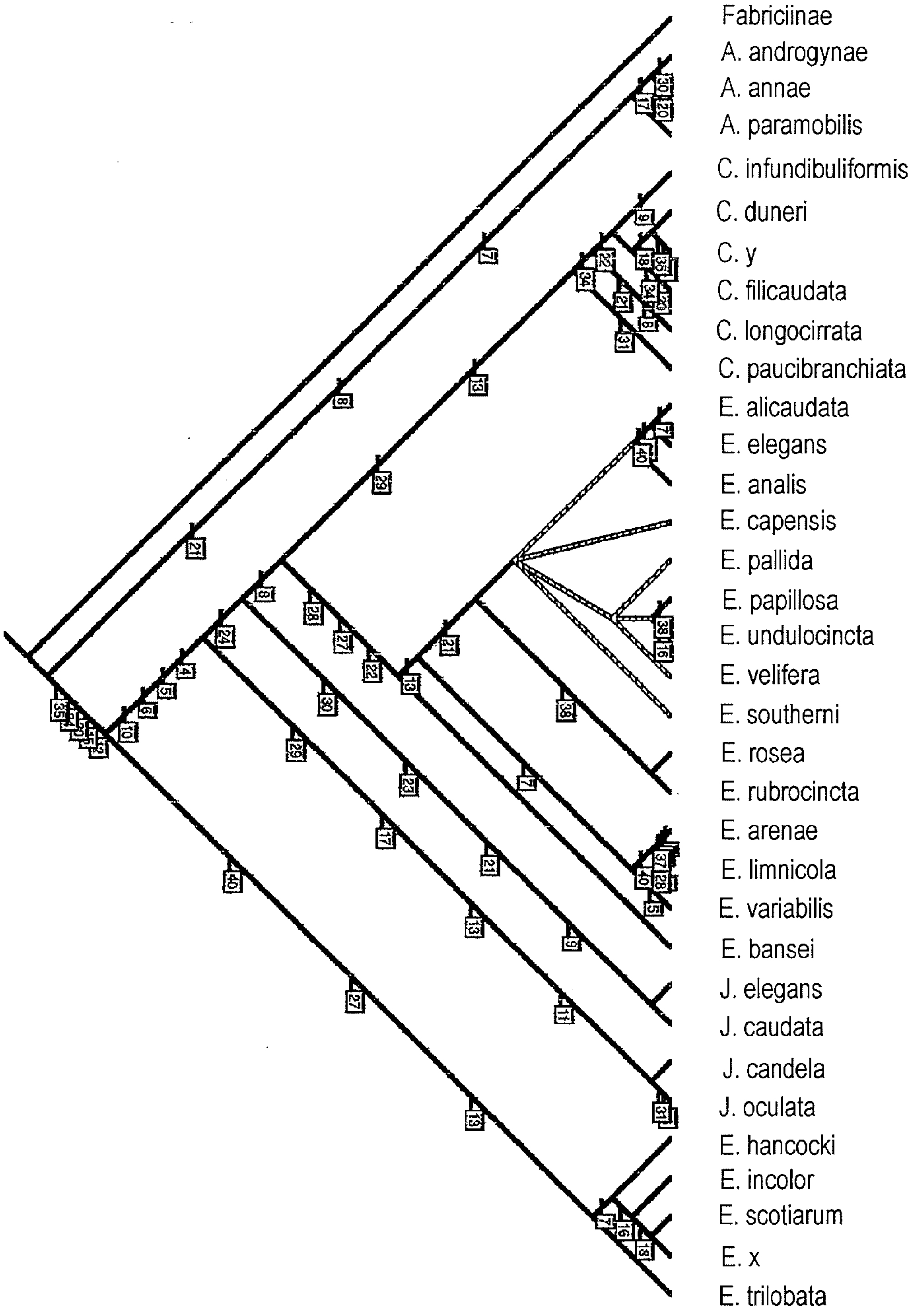

Figure 3.5.3. Unambiguous changes shown on tree PAUP 21. Note no changes are shown on polytomous branches.

Figures 3.5.4 and 3.5.5 show selected transformation series traced onto tree PAUP 21.

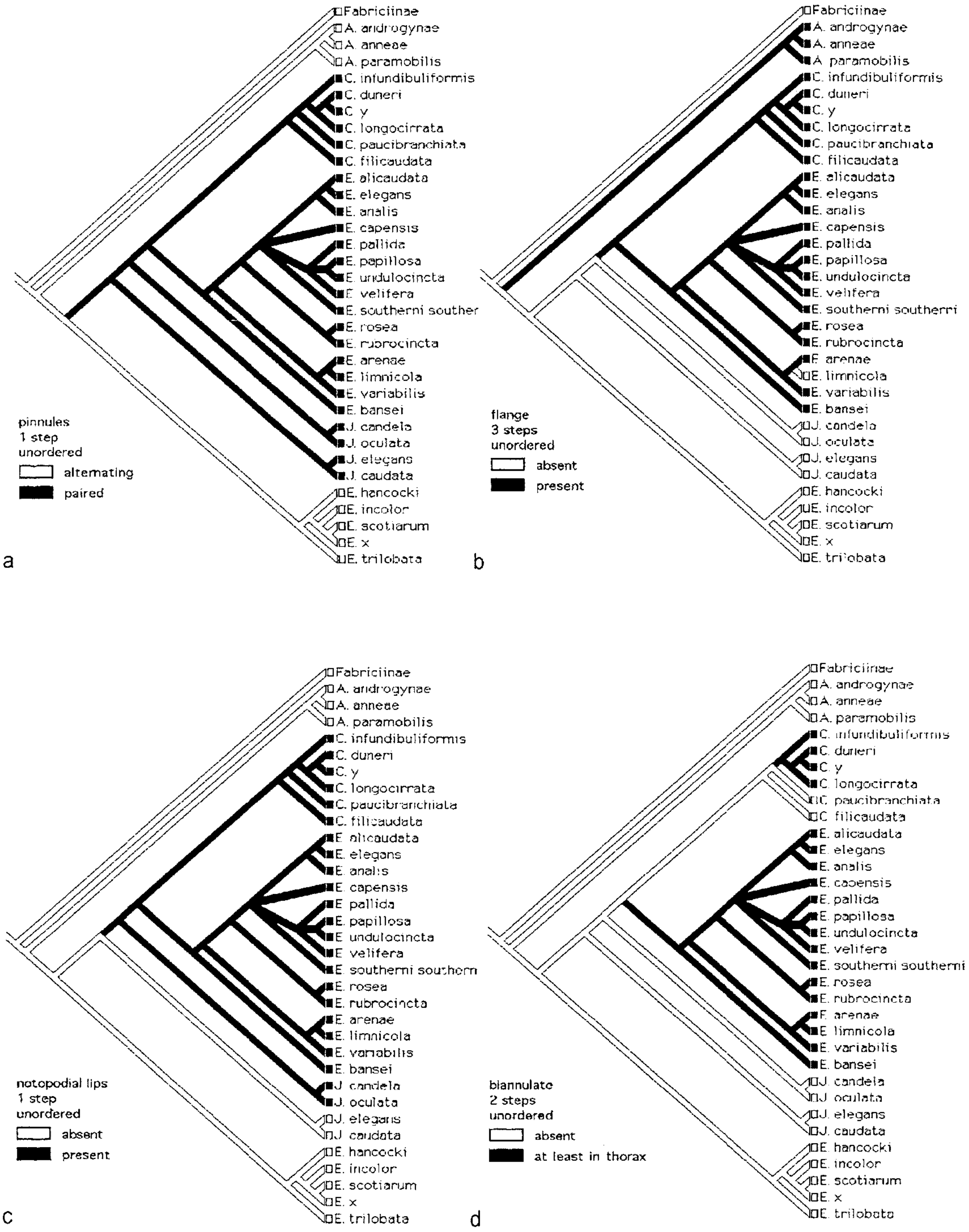

Figure 3.5.4. Selected character state transformations traced on tree PAUP 21: a) pinnules (arrangement of), b) flange (radiolar), c) notopodial lips and d) biannulate (segments). A full list of characters and character states is given in Appendix I.

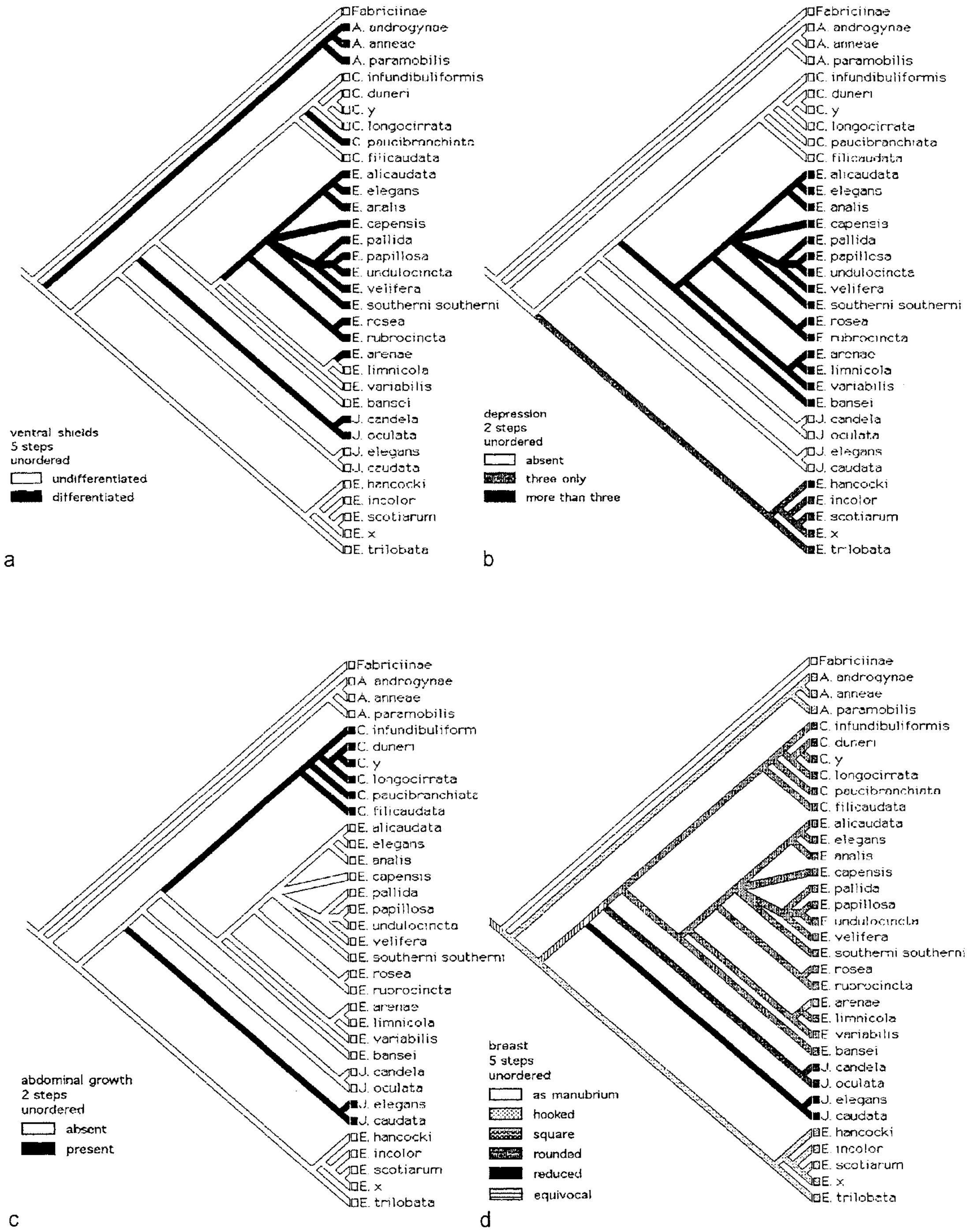

Figure 3.5.5. Selected character state transformations traced on tree PAUP 21: a) ventral shields, b) depression (anal depression), c) abdominal growth (growth by addition of posterior segments) and d) breast (of abdominal uncini). A full list of characters and character states is given in Appendix I.

Taxa within *Euchone* 2 and *Amphicorina* share the outgroup condition of having pinnules that alternate along the radioles, rather than being arranged in pairs, as in the remainder of the ingroup taxa (Figure 3.5.4a). Taxa within *Amphicorina*, *Chone* and *Euchone* 1 (with the exception of *Euchone limnicola*) all possess radiolar flanges (Figure 3.5.4b), whereas all *Jasmineira* and *Euchone* 2 taxa lack those structures. *Chone*, *Euchone* 2 and *Jasmineira candela* and *Jasmineira oculata* share the possession of notopodial lips, to the exclusion of the other taxa (Figure 3.5.4c). Biannulate segments are present in all *Euchone* 1 taxa and some of *Chone*, but absent in all other taxa (Figure 3.5.4d).

All *Euchone* 2 taxa possess an anal depression comprising only three posterior segments, whereas in *Euchone* 1 taxa, the anal depression comprises more than three segments (Figure 3.5.5a). All but two *Euchone* 1 taxa possess differentiated glandular ventral shields, as do all three *Amphicorina* taxa, the *Jasmineira candela/ oculata* clade and *Chone paucibranchiata*[2] (Figure 3.5.5b). The growth strategy whereby segments are added immediately anterior to the pygidium is evident only in the *Chone* clade and the *Jasmineira caudata/ elegans* group (Figure 3.5.5c). The form of the breast in the abdominal uncini is square in all *Chone* and *Euchone* 1, with the exception of *Euchone arenae*, which also possesses a hooked form in the first-formed uncini (Figure 3.5.5d). The hooked breast is shared between the *Euchone* 2 taxa and *Amphicorina*. Within the four *Jasmineira* taxa analysed, two discrete forms are evident. The uncini of *J. caudata* and *J. elegans* have a reduced breast, while that in *Jasmineira candela* and *Jasmineira oculata* is rounded.

Assessing homology of the anal depression

Homology of the anal depression was further investigated by coding the character in binary form, either present or absent. The results were not changed relative to those presented here, except that the shortest treelength was 94, rather than 95, steps. Therefore, however coded, no natural group of taxa was found, whose members all share the presence of an anal depression.

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[2] according to Banse 1972, not supported by study material from the Barents Sea (*pers. ob.*)

3.5.10 The initial questions answered

1) Are there distinct monophyletic groups within the taxa included in the analyses?

Yes, the following four distinct monophyletic groups were revealed by the analyses:

- all three *Amphicorina* taxa examined;
- *Euchone* 2, comprising five *Euchone* taxa with only three pairs of snowflake-like radioles and an anal depression comprising a constant three posterior segments;
- *Euchone* 1, comprising the remaining 15 *Euchone* taxa, all of which possess more than three pairs of feather-like radioles and an anal depression comprising more than three posterior segments;
- all five taxa within *Chone* formed a monophyletic group.

*2) Is the concept of the "*Chone *complex" supported?*

Based on the taxa included in the present analyses, the concept of the *Chone* complex is supported, but restricted to *Chone*, *Jasmineira* and *Euchone* 2, i.e. not including *Amphicorina.*

3) Is Euchone *a monophyletic taxon?*

No, *Euchone* is paraphyletic, comprising two discrete clades.

4) Is the presence of an anal depression a diagnostic character of Euchone*?*

No, a monophyletic group including all taxa that possess an anal depression (with or without lateral wings) does not exclude other taxa that lack an anal depression. The presence of an anal depression that either evolved twice, or evolved once and has subsequently been lost, is a homoplastic character.

5) Do the present analyses support the hypothesis that Amphicorina *is a more 'primitive' taxon than* Chone/ Euchone*?*

Yes, but the issue also includes *Jasmineira*. *Amphicorina* was revealed as a sister group to all included taxa within *Euchone*, *Chone* and *Jasmineira*. Taken one step further, *Euchone* 2 was revealed as a sister group to taxa within *Jasmineira, Euchone* 1 and *Chone*.

6) Do Jasmineira candela *Grube and* Jasmineira oculata *Langerhans group with other taxa currently recognised within* Jasmineira*?*

The inclusion set of taxa and/or characters is inadequate to resolve the status of *Jasmineira* as a whole, but *Jasmineira candela* and *Jasmineira oculata* are more related to each other than to any other taxa, as are *Jasmineira caudata* and *Jasmineira elegans.*

3.5.11 Discussion and conclusions

Accepting that higher taxa should comprise monophyletic groups, it is clear that the concept of the genus *Euchone*, as diagnosed by the presence of an anal depression, cannot be continued with any meaning. Both traditional and phylogenetic taxonomists would agree that *Euchone* 2 should be recognised as distinct from *Euchone* 1. Taxa within *Euchone* 2 have only relatively recently been discovered, whereas many of the forms within *Euchone* 1 have been recognised since the last century. Therefore, the taxon name *Euchone* should be maintained for the *Euchone* 1 group. The *Euchone* 2 group should be assigned a new name.

Whether a new traditional taxon, i.e. Linnean genus, or a phylogenetic taxon, i.e. an apomorphy-defined clade, should be erected to describe *Euchone* 2 is expected to be the subject of some debate. Because *Euchone* 2 was revealed as a discrete taxon using phylogenetic analyses, assigning either a genus name or a clade name to the taxon would describe a monophyletic group. The main difference would be seen after future research, if further taxa were discovered. In phylogenetic taxonomy, the clade comprising the taxa would simply become more inclusive while still retaining its original meaning. Eventual sub-groups arising within that clade could be given discrete taxon names without affecting the monophyly of the main group. In traditional taxonomy, dealing with such sub-groupings is more complex and requires more nomenclatural changes. For example, suppose after future research *Euchone* 2 comprised two discrete groups of taxa, one group showing character state A and the other showing state A'. All taxa still share the series of apomorphies that define the group *Euchone* 2. In phylogenetic terms, *Euchone* 2 would then comprise the new less-inclusive taxa *Euchone* 2A and *Euchone* 2B. The meaning and inclusion set of *Euchone* 2 is unchanged.

In traditional taxonomy, the issue is more complex. Removal of *Euchone* 2B from the main group *Euchone* 2 and assigning a new Linnean taxon name to it is straightforward. However, in doing so, the meaning of *Euchone* 2 is altered and that taxon must be rediagnosed. Therefore, although the name *Euchone* 2 is preserved, which might be thought of as nomenclatural stability, its meaning is changed. Thus, the traditional approach in this case would lead to conceptual instability.

The names chosen for new taxa would differ between phylogenetic and traditional taxonomy. Thinking traditionally, an appropriate taxon name would contain a reference to *Euchone*, the genus from which the taxa were removed. In this case, an appropriate name would be *Pareuchone* n.n.[3] or similar. However, using phylogenetic 'tree thinking', such a name would be confusing. Because the traditional concept of *Euchone* is a false taxon, then naming the more distantly related clade, *Euchone* 2, after it is illogical. In phylogenetic taxonomy, it would be more appropriate to give the clade a descriptive name, perhaps referring to the snowflake-like radioles or the presence of a very small anal depression.

Based on the present analyses, the taxa *Chone* and *Euchone* 1 do not require changes in nomenclature. However, when the absolute numbers of radioles and abdominal segments, including those comprising the anal depression, were used in the analyses, some *Chone* taxa appeared on a separate branch between the *Euchone* 1 and *Chone* clades. Other than this, the structure of the trees obtained was congruent with those shown in Chapter 3.5.9. Therefore, future research should reassess coding strategies for those highly variable characters. Having done so, the analyses should be rerun, using a more restricted inclusion set. The status of *Jasmineira* remains uncertain and also requires further investigation.

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[3] taxon name used informally as an example of possible nomenclature

3.5.12 Diagnosis of *Euchone* 2[4]

Euchone 2

Sabellins with a body length less than 5 mm, excluding crown, usually very thin trunk (depending on reproductive state). Invariably three pairs of radioles, with pinnules alternating along their length and longest mid-radiole. Free ends short and filiform. Low inter-radiolar (palmate) membrane, when present, not exceeding one quarter of the length of the radioles. Radiolar flanges absent. Bilobed extension of the anterior peristomial ring, protruding ventrally above the anterior collar margin. Chaetiger 1 at least partially fused with the collar (peristomial) segment. Dorsal collar margins attached to the peristomium. Glandular patches spread uniformly over body, differentiated glandular shields absent. Segments not biannulate. Post chaetal girdle of glands on the second thoracic chaetiger and sometimes also present in anterior abdomen, usually on abdominal segment 2 or 3. Notopodial lips absent. Anal depression comprising only three posterior segments, bordered by lateral wings, often difficult to see in small specimens using light microscopy. Fixed number of abdominal segments throughout the life of the individual, little, if any, individual variation in segment numbers. Superior thoracic notochaetae narrow, elongate. Anterior row of inferior thoracic notochaetae short and broadly swollen, not spatulate. Thoracic uncini avicular, with a main fang surmounted by a series of rows of equal sized smaller teeth. Abdominal neurochaetae elongate, narrow. Abdominal notochaetae (uncini) mainly of the quadrangular type typical of *Amphicorina*, with a mall main fang surmounted by a series of rows of equal sized smaller teeth. Breast of uncini mostly hooked, but some square forms seen in the ontogenetically younger parts of the torus.

Inclusion set

Currently five taxa (genus name not stated):

hancocki Banse, *incolor* Hartman, *trilobata* Banse, *scotiarum* Hartman, *x* new taxon

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[4] new taxon name withheld for reasons of formal nomenclature

Tube

The tube usually is made of a thin layer of fine silt particles adhering to a mucus lining and is relatively flexible.

Ecological notes

Members of *Euchone* 2 are often found in high densities, in presumed oxygen-minimal areas, suggesting a degree of opportunism. *Euchone x* is known to be capable of feeding from the sediment surface as well as suspension feeding (see Chapter 4). It is likely that taxa within *Euchone* 2 display some form of brood protection behaviour.

3.6 Could phylogenetic taxonomy resolve the "*Chone* complex"?

3.6.1 Disclaimer

Because it would be clumsy to discuss taxa in terms of "taxon A", "taxon B", a series of informal clade names are used in the present chapter. These are for demonstration purposes only and are not to be cited in any form beyond the context of the present thesis. The proposed scheme for systematisation is given merely as a demonstration of how phylogenetic taxonomy might function for the selected group of soft-bottom sabellins and is not to be treated as firm conclusions. The ideas presented here are to be considered merely as a step forward into future research on sabellid taxonomy and systematics.

3.6.2 A phylogenetic alternative to the "*Chone* complex"

Figure 3.6.1 shows the strict consensus tree obtained in Chapter 3.5. Suggested inclusion sets for taxa are indicated on the branches leading to each of the main clades. Hereafter, the concepts of 'species' and 'genus' are ignored and all taxon names are italicised. Least inclusive taxonomic units (LITUs) refer to the terminal taxa (i.e. *candela*, *oculata* and so on) and are indicated as such by a lower case first letter. More inclusive taxa are given a capitalised first letter. With some exceptions, the taxa revealed by the present tree are largely in agreement with the previous genera, but the two concepts should not be confused.

Amphicorina is not included in any of the other clades and therefore refers only to three taxa in the present example. The taxon is not contained within a more inclusive taxon. '*Chonea*' is a highly inclusive taxon and encompasses several less inclusive taxa. Whether the name '*Chonea*' should be fixed on the branch leading to all the included taxa or whether it should exclude the small clade here named '*Chiade*'[5] could be discussed. Within '*Chonea*' the meanings of the less inclusive taxa *Chone* and *Euchone* are clearly defined.

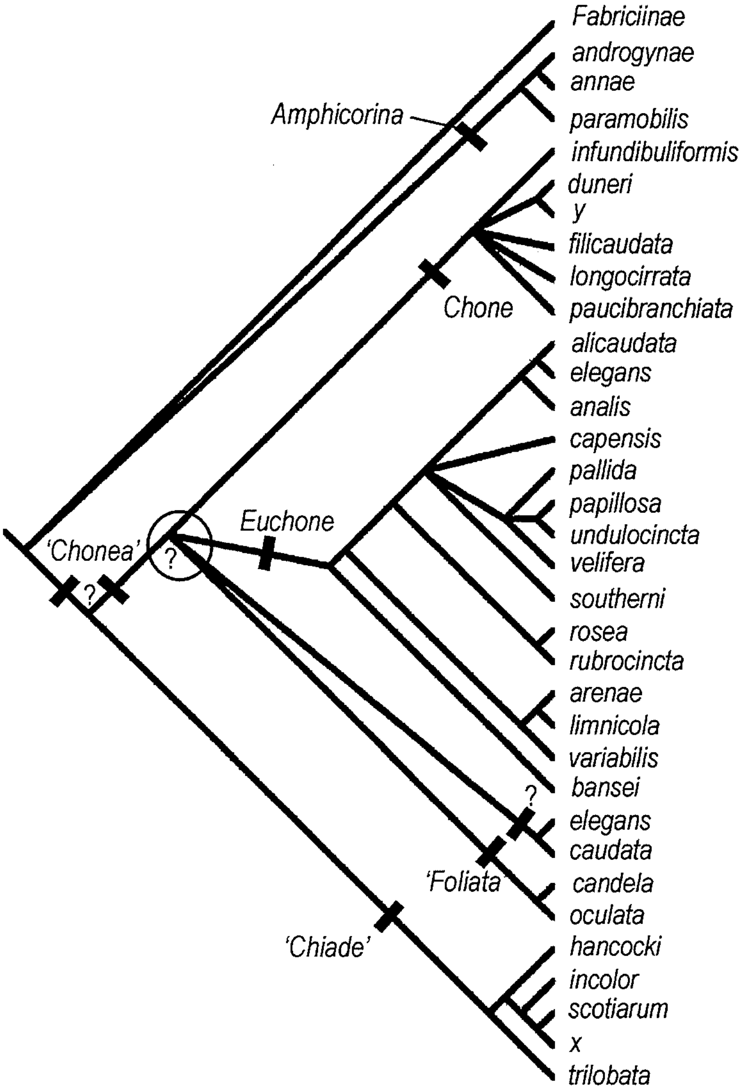

Figure 3.6.1. Consensus tree from Chapter 3.6, used to demonstrate how phylogenetic taxonomy could be applied to the study group. Note all taxon names italicised.

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[5] The name Chiade, daughter of Niobe in Greek mythology, is thought to be derived from the Greek 'chionos niphades', meaning 'snowflakes', and refers to the pinnular arrangement of the radiolar crown.

An alternative approach would be to use the name *Euchone* rather than *Chonea* to refer to the more basal taxon. This basal *Euchone* clade would then include all the taxa traditionally recognised within *Euchone* as well as those within *Chone* and at least some of those currently referred to as *Jasmineira*. The approach illustrated in Figure 3.6.1 was used because the name *Chone* is older than *Euchone* and previously was a more inclusive taxon than in its present-day sense (see Table 2.3.1). The issue will be given further attention should it be appropriate to carry out a phylogenetic revision of the taxonomy of this particular group of sabellin polychaetes.

It also remains for future research to clarify the position of the two LITU groups *candela* and *oculata* and *caudata* and *elegans*. If all these LITUs do group together as a single clade comprising two sub-groups (as shown in Figure 3.6.2a, c) then the whole clade would be named *Jasmineira*. The sub-groups would be given a descriptive name such as '*Foliata*' for the *candela/oculata* LITU group, referring to the sub-terminal radiolar appendages. The *caudata/elegans* LITU group would perhaps be named something like '*Stipata*', or '*Severata*', referring to the tendency for the radioles to break off near their bases, leaving a prominent stump. Alternatively, if the two groups remained separate (as in Figure 3.6.2b, d), it is proposed that the *caudata/ elegans* clade should bear the name *Jasmineira*, as distinct from '*Foliata*'. Each of the new phylogenetic taxa would then be defined by a series of apomorphies.

It is likely that future research will reveal further sub-divisions within *Euchone* and *Chone*, perhaps based on the presence or absence of differentiated ventral shields, the form of the abdominal uncini, or the form of the anal depression, where present. As discussed in 3.6.11 for *Chiade* (as *Euchone* 2), the meaning of *Euchone* will not change, only the sub-groups within *Euchone* will have a more restricted meaning. This would allow the relationships between the LITUs to be made more obvious by the sub-groups within which they are contained.

3.6.3 Conclusions - would it work?

Taxonomy

The traditional taxonomist is concerned with the discovery and description of discrete ‘species’, and the appropriate allocation to ‘genus’. The phylogenetic taxonomist thinks in terms of least inclusive units within a hierarchical series of more inclusive taxa. The main difference is that ‘species’ are allocated to ‘genus’ on the basis of assessment of morphology without reference to where in the phylogeny the characters might have appeared, whereas the position of LITUs within more inclusive taxa is revealed by the phylogenetic tree.

Because current ‘species’ names will remain unchanged should they become LITUs, a transition from traditional to phylogenetic taxonomy will cause little change in practical terms. The main change will be that the LITU, being a uninomial concept, is not automatically associated with a fixed higher taxon, as in binomial nomenclature.

Systematics

The main difference between phylogenetic and traditional taxonomy is the abolition of fixed, inflexible higher taxa. The traditional ranks of class, order, family and genus are implied by the endings of the taxon names. In phylogenetic taxonomy, the hierarchical position of the more inclusive taxa is not implied in the taxon names, and the number of ‘levels’ of the hierarchy is not fixed. Therefore, there will be no direct replacement for genus or the other traditional higher taxa. As a result, comparisons of the number of taxa included at each level cannot be made between different groups of organisms. To the traditional systematist, this is perceived as a loss of stability. However, as discussed in Chapter 2.5, comparing the inclusion set of different Linnean genera even within the same family also is misleading in terms of the relationships between organisms.

To accept a transition to phylogenetic taxonomy, systematists must accept the loss of a rigid hierarchical structure. Instead, conceptual stability is achieved, because the meanings of the taxon names do not change, only the inclusion sets. In the present opinion, the need for conceptual stability far outweighs the need for a rigid hierarchy.

Applied faunal identification work

Applied workers using 'species' determination for assessment of biological diversity may initially be confused by the introduction of a uninomial system. Based on personal experience, this is mainly because families and genera are familiar concepts and the operator initially feels 'lost' without them. This loss is most keenly felt for well-defined genera that contain taxa free from intermediate characters and 'overlap' with other taxa. However, this being the case, using only the 'species' name as a LITU is equally informative as automatically attaching a 'genus' name to a 'species' name.

In many cases, workers encounter 'species' whose placement within 'genus' is subject to change. For example, the commonly encountered oweniid *Myriochele oculata* (Zaks, 1922) recently was removed to *Galathowenia* Kirkegaard, 1959. Therefore, the meaning of *Myriochele* as a higher taxon was changed and because the name *oculata* is attached to *Myriochele*, the meaning of that binomial taxon as a whole was changed. This might have been avoided if phylogenetic taxonomy had been practised. Purely hypothetically and in the absence of the appropriate phylogenetic tree, *Galathowenia* might have appeared merely as a less inclusive subdivision of *Myriochele*. Therefore, the meaning of both *Myriochele* and *oculata* would have remained stable, only made more informative by its inclusion in the intermediate taxon *Galathowenia*. The present study has shown the need for further clarification of the traditional genus *Jasmineira*. It is expected that using phylogenetic taxonomy will result in less confusion to the routine identifier than eventual rearrangement of the 'species' into different 'genera'.

Cataloguing LITU records in terms of the various higher taxa may cause some minor changes in nomenclature. However, the changes in assignment to genus that occur in traditional taxonomy do not cause any less frustration. Therefore, the present opinion must be that having dispelled the mystique of phylogenetic taxonomy, the routine faunal worker will notice little difference between 'species' or LITU determination.

ECOLOGICAL PART

"There's not much you can say
When others Big and Tall,
With their great muscular
Strength and all,
Find they can't do what you <u>can</u> do,

And you stand there, not feeling small.
What if I had been bigger, and
What if I had been tall?
Think what I would have missed out on -
Not so small, after all."

A.A. Milne, *in* Hoff (1992), *The te of Piglet*

4 Ecological part: a study of *Euchone x*

4.1 Special thanks

This study was made possible by Hans-Petter Mannvik, Asle Gunneriussen, Tor Jensen and Sam Arne Nøland, who humoured me by transporting buckets of 'live' mud as hand luggage by plane from the petroleum fields in the North Sea to Tromsø. Histological work and photography was made possible by Randi Olsen, Helga Marie Bie and Reidar Myklebust. I am grateful to Matt Bentley for information on reproduction and Myles O'Reilly, Wim Vader and the late Professor Jan Stock for comments on parasites. Thanks also to Roy Lyså for creating Figure 4.4 and Tom Pearson for providing comparative observations of live *Euchone papillosa* from Spitsbergen. Finally, Saga Petroleum AS are acknowledged for use of specimens.

4.2 Introduction

Previous investigations of selected members of the Sabellinae have shown a general reliance upon suspension feeding, with well-developed particle sorting mechanisms, such as in *Sabella penicillus* L. (Nicol 1931), *Sabellastarte magnifica* Shaw (Fitzsimons 1965) and *Chone mollis* Moore (Bonar 1972). However, surface deposit feeding also has been demonstrated in some members of the Fabriciinae. The brackish *Manayunkia aestuarina* Bourne may capture particles by surface deposit feeding, secondary deposit feeding on re-suspended near-bottom particles, or by suspension feeding directly from the water column (Lewis 1968). *Fabricia sabella* (Ehrenberg) has been shown to use the radiolar crown to collect particles from the substratum for tube-building (Lewis 1968), and it is suggested that the Fabriciinae as a whole are capable of sweeping the substratum with the crown to obtain food particles (Day 1967).

In a recent study of the offshore Norwegian Sea faunal communities at the Snorre field, *Euchone x* (recorded as *Euchone* sp. A) was the most numerous taxon found across the field as a whole, comprising 11.2% of the total zoobenthic population (Pearson *et al.* 1996). At the Troll Vest field, *Euchone x* (recorded as *Euchone* sp.)

also numerically dominated the benthic fauna in both the 1994 and 1995 investigations (Mannvik *et al.* 1996). It is clear, therefore, that *Euchone x* plays an important ecological role within the communities it dominantes.

Not much is known about reproductive strategies in *Euchone* in general, but some of the larger taxa with 'feather' radioles (see Chapter 1.2 and 1.5) are known to be broadcast spawners (Rouse & Fitzhugh 1994). On the other hand, *Euchone incolor* Hartman, which morphologically resembles *E. x*, is reputed to brood its young (Levin *et al.* 1994). Brood protection behaviour in the Sabellidae in general has been shown to be correlated with a small body size (Rouse & Fitzhugh 1994), and it is therefore highly possible that all the small *Euchone* with only few pairs of 'snowflake-like' radioles may exhibit some kind of brood protection behaviour. Methods of brood protection have been proposed as a basis for reclassification of the Spirorbinae (Bailey 1969), and also are likely to be informative in sabellid systematics (Rouse 1992, 1994). Future studies should aim to address the issue of brood protection in *Euchone x*, incorporating observations of live material as well as ultrastructural examination of the spermatozoa, according to Rouse & Jamieson (1987).

4.3 Materials and methods

4.3.1 Live material

Sampling for live material was carried out at the Troll Vest field (Saga Petroleum a/s, $60^0$45'N, $3^0$25'E) in May 1995 and at the Snorre field (Saga Petroleum a/s, $61^0$30'N, $2^0$10'E) in May 1996, using supply vessels chartered by Møkster Shipping AS. At sampling stations where the sediment is known to contain high densities of *Euchone x*, surface sediment was taken from 0.1 m^2 van Veen grab samples, and carefully placed into plastic containers, which were then filled with bottom sea water and kept in a cool dark place on deck. The ratio of sediment to water was approximately 1:6. A period of five days elapsed between sampling and transfer to the laboratory. During one day of transport, it was not possible to keep the samples cool, but they were refrigerated at approximately 5°C immediately upon arrival at the laboratory and an airstone inserted into the sample containers.

Observations of the material were carried out through a Nikon SMZ-2B binocular dissecting microscope, using red-filtered fibre-optic lights to minimise disturbance to the animals. A 'settling period' of approximately 30 minutes was required after removal of the containers from the refrigerator to the laboratory bench. Specimens removed from the sediment were examined in a petri dish placed on a bed of ice. Observations were carried out at regular intervals over a period of one year, on approximately 50 individuals. Coloured markers were used to allow observations of the same animal on different days. The animals were fed a suspension of finely ground Nestlé powdered baby food in sea-water.

4.3.2 Preserved material

Specimens for histological work were taken from previously formalin-fixed material (Chapter 3.4). These were transferred through a rehydration series, post-fixed in 1% osmium tetroxide, and then transferred through a dehydration series. The specimens were placed in 95% ethanol, followed by two changes of clean, absolute alcohol. Dehydrated specimens were infiltrated and embedded in Epon araldite, and 1 μm thick sections cut using a Reichert-Jung FC4D Ultracut microtome, with glass knives. Sections were stained with 0.3% toluidine blue in 0.1M phosphate buffer and mounted in 'Histokit' mounting medium.

4.4 Results & Discussion

4.4.1 Tube-building and burrowing

Upon capture, specimens of *Euchone x* readily re-establish themselves in the sediment within one day of transfer to the aquarium. The tubes generally are vertically orientated in the sediment and generally are up to 3 cm in total length, usually with up to 0.5-1 cm projecting into the water column. The anterior part of the tube often is bent into various configurations (see Figure 4.4.1).

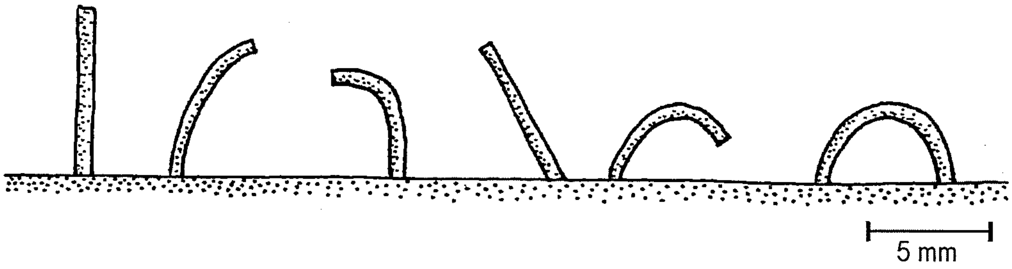

Figure 4.4.1. Euchone x. *Various configurations of occupied tubes.*

Individuals removed from the sediment and placed in a petri dish containing only seawater become very active, rhythmically bending the body and tube in a serpentine fashion. The worms do not leave their tubes unless forced to retreat by pinching the tubes with forceps, beginning at the head end and working downwards until the worm emerged. Animals thus removed from the tube and placed into a clean petri dish containing seawater generally remained on the bottom of the dish, actively probing with the pygidia. After some time, mucus sheaths are secreted, and the worms adhered to the bottom of the dish. Tubeless individuals placed upon the sediment surface quickly re-buried themselves, pygidium first. Animals in tubes placed on the sediment surface showed little activity at first, but after approximately 24 hours appeared to re-establish themselves in the sediment. It is not clear whether such animals remained in their original tubes, or whether these are discarded in favour of constructing new ones.

The elongate ventral cirri (*sensu* Krøyer 1856, see Chapter 1.2) are involved in particle sorting and tube construction and are of different lengths, with the ventral-most pair being the shortest. During tube construction, the appendages brush the mucous-producing glands on the ventral surface of the worm, and 'glue' the sediment particles in place at the tube opening, spiralling slowly as the tube is built. Within an hour, up to 1 mm of tube may be constructed.

Specimens of *Fabricia* kept in calm aquarium conditions have been shown to continue constructing their tubes until they project approximately 2.5 cm above the sediment surface. In the field, however, the length of the tubes is dependent on the degree of erosion by wave action (Lewis 1968), and the same might extend to *Euchone x*. Over a period of months in captivity, the live specimens examined in the present study were seen to continue building tubes until almost 2 cm projected above the sediment surface. The worm often dismantles the upper part of such long tubes by loosening the bound sediment particles with the ventral cirri, and then ejecting a 'ring' from the top of the tube, using the radioles for leverage (Figure 4.4.2).

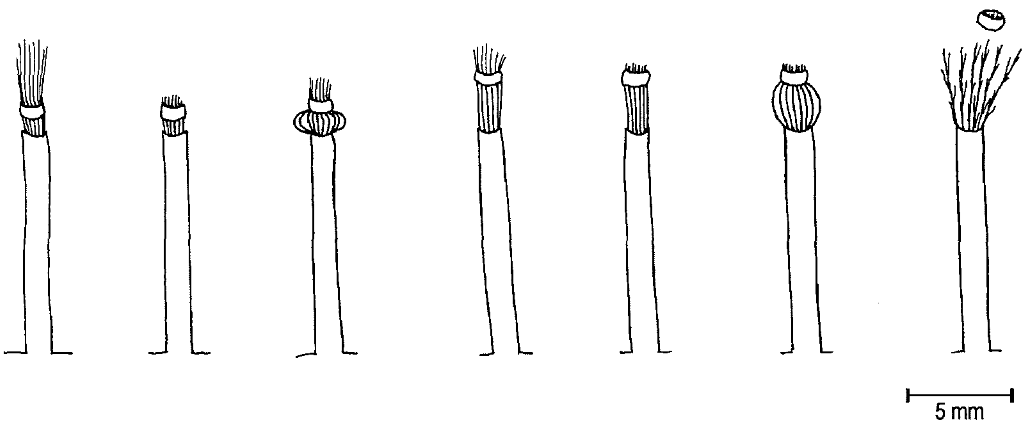

Figure 4.4.2. Euchone x. *Dismantling the upper part of the tube.*

The precise function of the anal depression in *Euchone* in general remains somewhat unclear, although Evenkamp (1931) suggested that in *Euchone papillosa* Sars it may function as an anchor or sucker used for locomotive purposes. Live specimens of *E. papillosa* removed from their tubes and placed on a mud substratum were seen to use the anal funnel as a scoop, shifting relatively large amounts of sediment (Pearson pers com. and pers. obs.). More detailed examination of the structure and ciliation of the depression, as well as higher-power observations of live material will provide more information on its possible function in *Euchone x*.

Preliminary cladistic analyses indicate that *Euchone* taxa with a 'snowflake-like' radiolar crown (see Chapter 3.5), such as *Euchone x*, are a discrete sister group to those with a 'feather-like' crown, such as the 'type species' *Euchone analis* and *Euchone papillosa*. It is likely that this fundamental difference in form is accompanied by some equally fundamental differences in function.

4.4.2 Suspension feeding and particle sorting.

On emerging from vertically or obliquely orientated tubes, the radiolar crown is stiffly extended (Figure 4.4.3) and the animal begins rotating in its tube; one or more complete revolutions may be made in each direction, often with the anterior 3-4 thoracic segments extending from the tube opening.

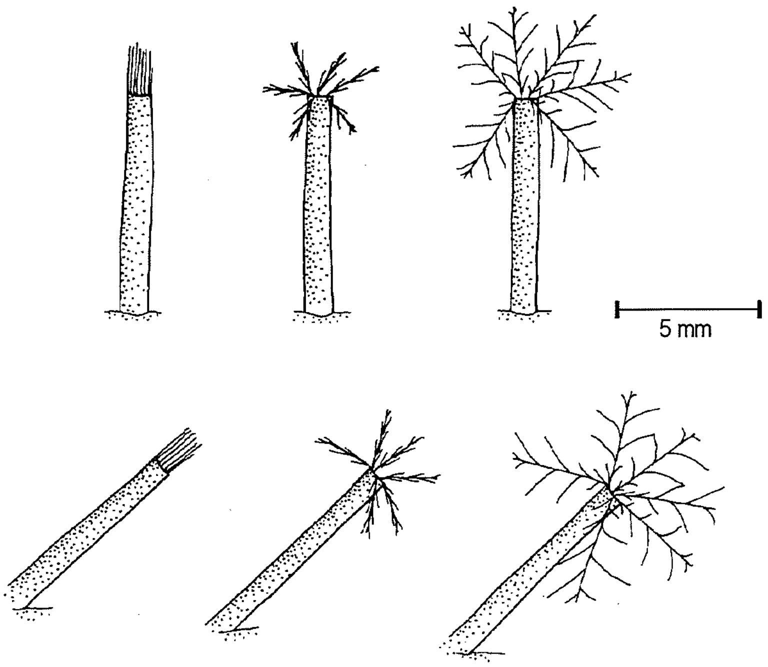

Figure 4.4.3. Euchone x. *Emergence from the tube and suspension feeding.*

After a few minutes of this rotating behaviour the animal generally settled, retreating such that only the crown itself was exposed, and it may begin suspension feeding for 15 minute periods or longer (Figure 4.4.4).

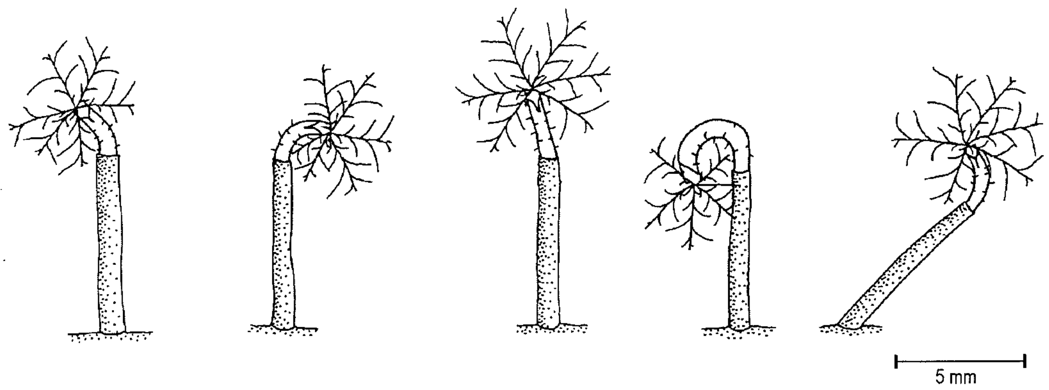

Figure 4.4.4. Euchone x. *Various attitudes adopted during suspension feeding.*

Very large particles brushing the radioles caused the animal to retract into its tube, for up to 10-20 minutes. Small particles 10-50 µm in diameter are transported by ciliary action along the radioles towards the mouth. Both the radioles and their pinnules seem to be able to move independently of each other. On encountering an intermediate-sized suspended particle (50-100 µm), the nearest radiole moved towards it, capturing the particle and passing it down within the crown towards the mouth. Such particles are often 'knocked' down within the crown by the pinnules. This suggests an olfactory ability, rather than mere passive filtering of the water column. On receiving a food particle into the lower part of the crown, the short lower pinnules moved in unison towards the centre of the crown, in a rapid clasping movement, pushing the particle to the mouth. On occasion, the animal attempted to push food particles of a larger diameter than the worm itself into the mouth. Several attempts were often made to insert over-sized particles into the mouth before these were finally rejected and allowed to fall through the crown. Rejected particles were expelled by simply letting them drop, or by an active 'coughing' movement of the crown, creating an expulsion current, which also dispels faecal pellets.

During suspension feeding the four pairs of ventral cirri are very active, often handling relatively large clumps of sediment particles at the tube opening. The ventral appendages may also extend stiffly and move up towards a radiole or pinnule and 'pick off' an adhering particle. These are either transported to the mouth or used in tube building. The appropriate filament is used, according to the position of the particle on the radiole. After 10-20 minutes of active suspensivorous behaviour most individuals ceased the movements of the crown, often 'hanging' motionless for some minutes before slowly retreating into the tube. After prolonged activity, the worm tended not to re-appear from the tube for more than 30 minutes.

4.4.3 Surface deposit activity.

Several behaviour patterns were observed for individuals with the upper part of their tubes orientated at an oblique angle or parallel to the sediment, as well as those lying horizontally or in an inverted 'u'-shape (Figure 4.4.5). In those animals where the anterior end of the tube was bent into a sickle-shape, with the opening parallel with the sediment surface, the emergent crown generally moved from side to side and with the radioles less spread than vertically-orientated animals. The worm often emerged from the tube, such that the anterior 4-5 thoracic (and on occasion also most of the abdominal) segments were exposed.

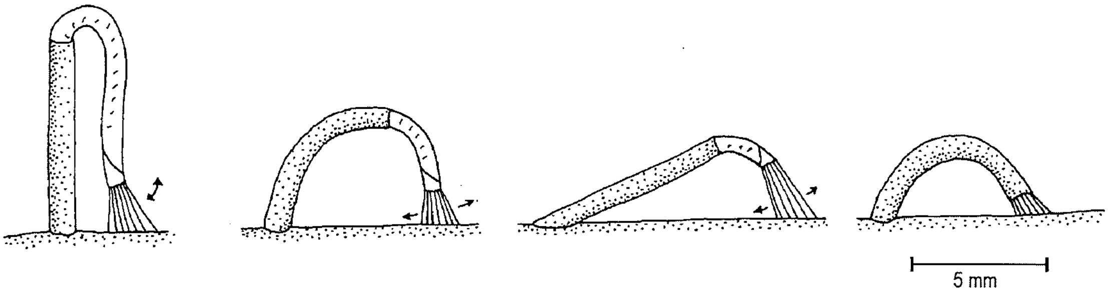

Figure 4.4.5. Euchone x. *Surface deposit feeding.*

Where the anterior end of the tube lies flat on the sediment surface, there often is activity at the anterior end of the tube, with the movements of the radiolar crown creating an obvious depression in the sediment around the tube opening. The ventral cirri were extremely active in particle sorting and handling at the mouth of the tube. Often, after approximately 10 minutes of this behaviour, the anterior of the tube rose to an oblique angle to the sediment surface, and the anterior end of the tube underwent slow lateral movements. During this time, the animal often emerged from the tube, actively taking particles into the crown and then retreating. This behaviour was often repeated over a 5-10 minute period. In some instances, the worm retreated, and the tube moved towards a vertical position. One individual was seen to emerge with the radiolar crown stiffly extended, but with the filaments close together and only the ventral cirri moving actively. The crown began to point towards the sediment surface and the anterior of the tube bent noticeably into an inverted 'u'-shape, such that the tube opening became buried in the sediment.

4.4.4 Response to conditions of food deprivation and zero current flow.

The possibility that some of the behaviour patterns described above may be influenced by the lack of flow or currents in the aquaria should not be ignored. In particular, it is possible that the occasional emergence of worms from their tubes, or the spiralling or side-to-side movements before the commencement of feeding may be a response to local hypoxic conditions, or an attempt to create small-scale local water movement. However, the survival of the animals despite these apparently sub-optimal conditions, and particularly the unstable conditions during transport, was itself of interest and inspired further attempts to investigate the environmental tolerance of *Euchone x*.

On two separate occasions, particulate food matter was not added to the aquaria for a period of three weeks. During this time, the animals appeared to cease most of their activity and, after the first days, were not observed to emerge from their tubes at all. Most of the tubes were bent into the inverted 'U' position described above, whereas only a few remained upright. After the three weeks, addition of food material to the aquarium caused more than 50 % of the individuals to begin suspension feeding within approximately 10 minutes.

Removal of the airstone from the aquarium for a period of up to one week, resulting in conditions of zero flow and no additional aeration of the bottom water, also produced a tendency for the the worms to retract into their tubes as described above, and to reduce activity. However, on occasion, some of the animals emerged almost fully out of their tubes and began vigorous swaying movements. After 10 to 15 minutes of such behaviour, the individuals tended to retract and were not seen to emerge for several days. It is probable that such behaviour is a response to local hypoxic conditions in the tube and in the near-bottom water. No notable mortality was observed as a result of these periods of deprivation of food or aeration.

4.4.5 An assessment of *in situ* conditions.

The sampling areas where *Euchone x* occurs in high densities are located on the slope between the Norwegian Continental Shelf and the Norwegian Deep. It is interesting to compare the faunal assemblages from there (see Pearson *et al.* 1996) with those described from the lower summit of Volcano 7 in the eastern Pacific Ocean. These areas were found to support a high density, low diversity faunal assemblage, within which *Euchone incolor*, which is morphologically similar to *E. x*, was among the numerically most abundant organisms (Levin 1991; Levin *et al.* 1991). Parallels were drawn with population responses to gradients of organic enrichment (Pearson & Rosenberg 1978) and assessments of the reproductive and feeding strategies of the dominant organisms were carried out (Levin *et al.* 1991, 1994). The areas dominated by *Euchone incolor* contained a high density, low diversity faunal assemblage, typical of areas just outwith the maximum impact of organic enrichment. The majority of the taxa present were classed as being mainly surface-deposit feeders and there was a general pattern of direct larval development and brooding behaviour.

Interestingly, striking similarites also were found in the structure of the faunal assemblages at Volcano 7 with those along an oxygen gradient off the southern coast of Africa (Sanders 1969). Similar types of macrofaunal assemblages also were found at the upper and lower edges of the central California oxygen minimum zone (OMZ). These 'edge effects' comprise a complex interaction of dissolved oxygen concentrations, bottom currents, food availability and bacterially-mediated nutrient recycling (Mullins *et al.* 1985). By analogy, it is not unlikely that *Euchone x* on the continental slope in the northern North Sea/Norwegian Sea exists in conditions where intermittent down-slope currents are a major source of food.
Maximum niche utilisation in the semi-oligotrophic environments from which the specimens were taken would be achieved if the animals adopted a flexible, suspensivorous and detrivorous feeding strategy. In this case, the observed flexibility in feeding strategy and the ability to survive periods of low food supply and intermittent stagnation of the bottom water and rapid exploitation of a food source when it becomes available indeed would allow *Euchone x* to survive in inherently variable environmental conditions. In view of the structure of the faunal assemblages where *Euchone x* is dominant numerically, and the apparent parallels with other

faunal assemblages dominated by similar *Euchone* taxa, it is proposed that the large populations of *Euchone x* found in the present study area are opportunistic in nature. This is supported by the high spatial (Mannvik *et al.* 1996) and temporal (Mannvik *et al.* 1998b) variation in the abundances of *Euchone x*. It also is interesting to note that *Euchone hancocki* Banse, another morphologically similar taxa, is recorded at high densities (Banse 1970). It is proposed that these 'small' *Euchone* with highly adaptable behaviour and feeding patterns are capable of opportunistic niche exploitation.

4.4.6 Reproduction

Euchone x appears to be gonochoric, with females collected in May containing oocytes/eggs in the coelomic cavity extending from thoracic setiger 5 through to abdominal setiger 4. There is sequential oocyte maturation, with pre-vitellogenic, as well as early, mid and late vitellogenic oocytes seen in the same female. Further histological work is required to ascertain whether the direction of development occurs from anterior to posterior segments, or vice versa. Late vitellogenic oocytes were relatively large (approx. 40-50 μm in diameter in a worm of 125 μm width), and reproductive segments each generally contained from 6-8 oocytes. Figure 4.4.6 shows part of a segment of a mature female containing oocytes.

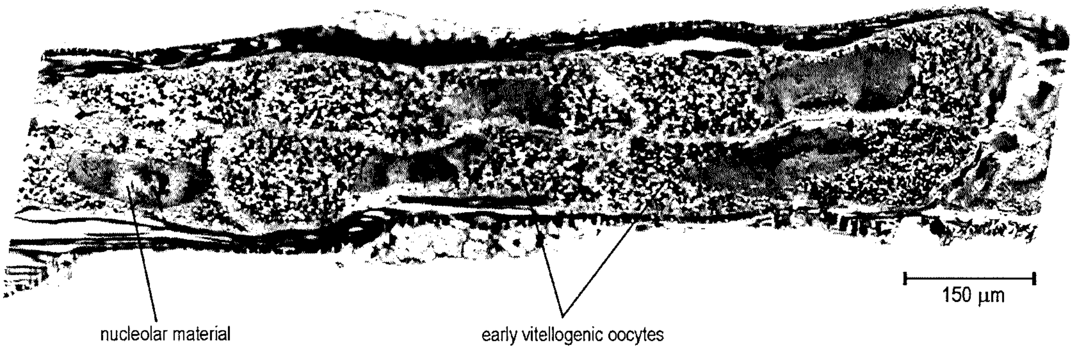

Figure 4.4.6. Euchone x. *Longitudinal section of anterior abdominal segment of a mature female.*

The precise method of oocyte release from the body cavity is still unclear, but it is possible that these are released through the parapodia, as is the case in *Fabricia* (Kahmann 1984). The large size and small number of eggs produced by the female suggests that *Euchone x* is not a broadcast spawner, because egg size is positively correlated with brooding behaviour (Rouse & Fitzhugh 1994). Larvae were not observed in the adult tubes in the present study, but some inhabited juvenile tubes were observed in July.

One individual was seen to emerge and bend its thorax over the tube opening, moving down until only a few abdominal segments remained in the tube. The worm began plucking at a lower part of the tube, loosening the particles. The following day, a juvenile tube was observed attached to the adult tube, and both occupants were engaged in suspension feeding (Figure 4.4.7). This is reminiscent of *Amphiglena mediterranea* (Leydig), in which the posterior part of an adult tube was observed to have a side branch, probably made by a juvenile (Knight-Jones & Bowden 1984). Other adult individuals of *Euchone x* were observed with juvenile tubes in close proximity. The juveniles were capable of bending the tubes into various configurations in a manner similar to the adults.

Because the developing juveniles were not removed from the sediment, the full developmental pattern of *Euchone x* was not observed. However, some interesting observations were made of the radiolar crown. Some juveniles possessed only one pair of fully formed radioles with pinnules, and two developing radioles, in addition to the ventral cirri. Others possessed two pairs of fully formed radioles and one pair of developing radioles (Figure 4.4.7). By late July/August, all the juveniles observed possessed a fully formed radiolar crown.

The study would have benefited from more detailed observation of developing juveniles, but from the limited observations made, it is likely that juvenile *Euchone x* are held in the maternal tube, until capable of constructing their own tubes. At least in some cases the radioles appeared to develop in pairs, rather than at all the same rate. This would allow the juvenile to feed while the crown is still under development.

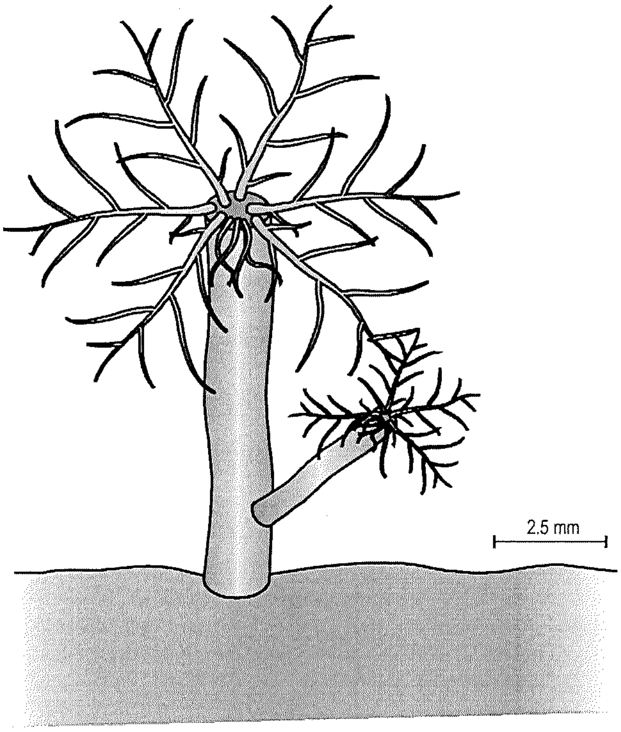

Figure 4.4.7. Euchone x. *Adult with attached juvenile tube, both occupants suspension feeding.*

4.4.7 Parasites

Some individuals in mid-May were found with stacks of up to 8-10 small, translucent yellowish flattened discs with a central hollow similar to that in erythrocytes, contained within a membranous sac. Up to five such stacks were found within a single individual, in thoracic setigers 2-4. At the present time, the identity of these discs is unclear, but it is thought that these are of parasitic origin.

Some females (both preserved and live) observed between late May-July had a brood mass attached to the dorsal-most radiole on the right branchial lobe (in dorsal view). This was composed of a proximal mass comprising irregularly shaped, unfertilised oocytes contained within a membrane (Figure 4.4.8). Distally, there was often a column of spherical fertilised eggs, each enclosed within a membrane. The proximal mass is developed first, followed by the fertilised eggs. The column of fertilised eggs appeared to grow in length while the worm underwent a series of pulsing movements. The identity of these 'sacs' has been the subject of much speculation. At first, it was thought that these were produced by the worms themselves, as a means of incubating the developing eggs in the crown, similar to certain members of the Spirorbinae

(Bailey 1969; Knight-Jones & Knight-Jones 1972, 1994; Knight-Jones & Thorp 1984). However, after detailed histological examination of the sacs, this is considered highly unlikely. If the sacs were for incubation of *Euchone* eggs, then the oocytes seen within the coelom of the females most likely would be at an earlier stage of maturation than those held within the crown. Since this was not the case, it is proposed that the structures belong to a parasitic organism.

The majority of sabellid parasites cited in the general literature appear to be Copepoda, but these generally produce paired egg-strings. As far as can be discerned, the only organisms that produce unpaired egg-strings similar to those observed attached to *Euchone x* belong to *Rhizellobiopsis* Hovasse, 1926 (Protista: Ellobiopsidae Coutière, 1911). *Rhizellobiopsis* is reported as being a parasite of polychaetes, and the sole inclusive taxon, *Rhizellobiopsis eupraxiae* Zaks, 1923, was described from the parapodia of *Nephtys ciliata* Müller in the White Sea.

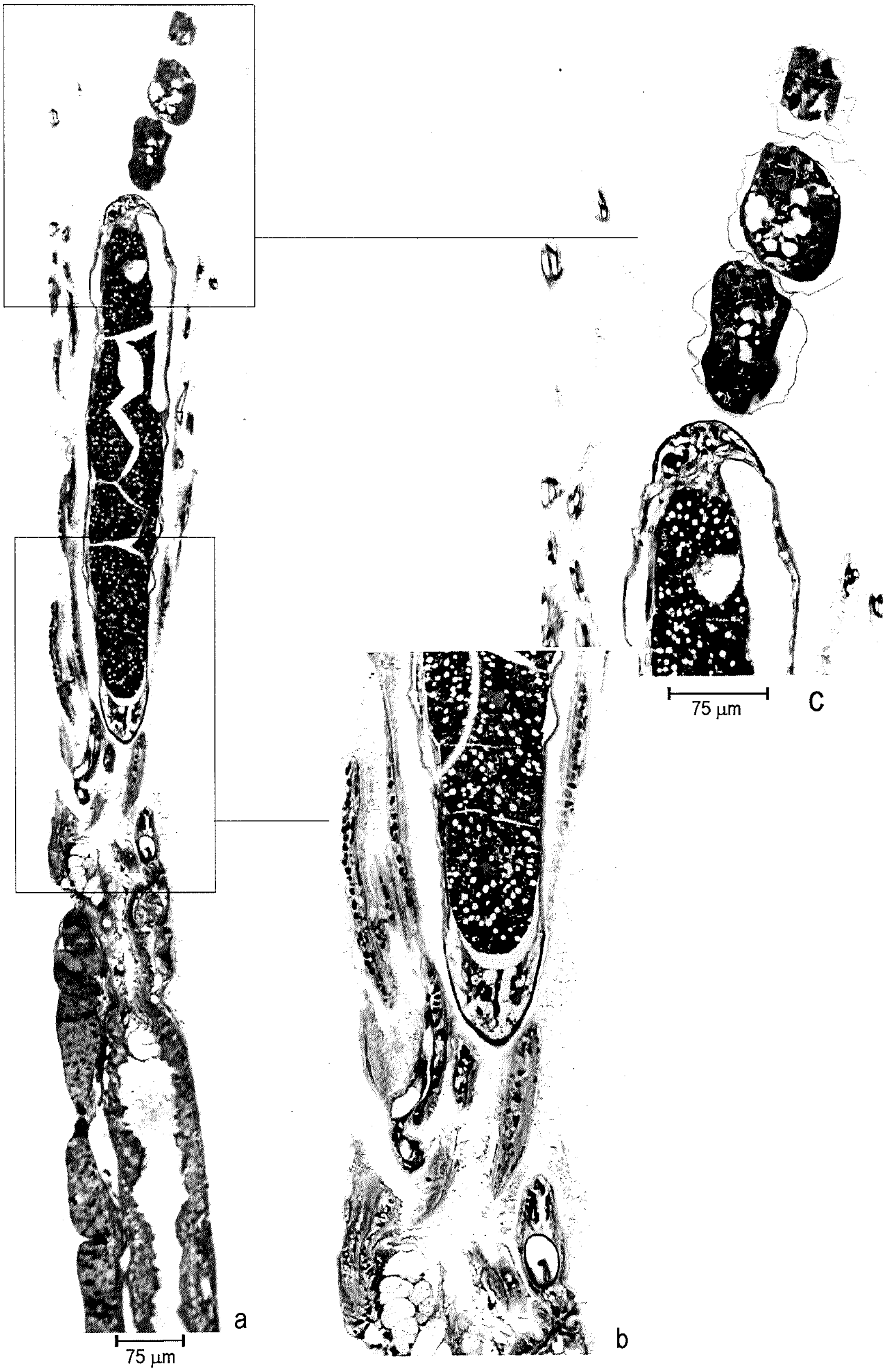

Figure 4.4.8. Euchone x. *a) longitudinal lateral section through the crown and anterior thoracic segments, b) and c) detail of basal and proximal parts of the brood mass, respectively.*

Grassé (1953), after Zaks (1923), depicted a 'gonomere' with a proximal ramified base and a series of attached globular structures, the distalmost undergoing sporulation. Although the drawing is not detailed, it is the only illustration found to date in the literature that approximates with the structures found in the present study.

A further point of interest is the indication that within the Ellobiopsidae, *Amallocystis* Fage, 1936 and *Ellobiopsis* Caullery, 1910 are thought to have two stages in their developmental cycle; passing through an internal stage within the host organism, before emerging and completing development externally (Grassé 1953). In the case of *Amallocystis*, this is thought to explain the constancy in point of attachment to the host organism (Fage 1938 *in* Grassé 1953). No such information is available for *Rhizellobiopsis*. However, the observation of the cyst-like structures in anterior segments of *Euchone x*, and the later appearance of the sac-structures, consistently attached to the same radiole in all the individuals examined, would appear to support a two-stage developmental process of the parasite.

More detailed histological work is required to determine conclusively if the enigmatic radiolar brood sacs seen in *Euchone x* belong to *Rhizellobiopsis*. The phylogeny of the Ellobiopsidae has been the subject of some speculation, and possible relationships with fungi or certain groups of zooflagellates have been proposed (Hovasse 1926; Grassé 1953). In any case, the Ellobiopsidae as a whole, and *Rhizellobiopsis* in particular, appear to be little known, so the inability to state for certain the identity of the structures found in the present study is not surprising. However, there are numerous records of Ellobiopsidae occurring on hosts in the North-East Atlantic, the northern North Sea (Vader 1973; Smith 1981) as well as in the Barents Sea (Timofeev & Timofeeva 1984). Ellobiopsid parasites might therefore be expected in material collected from the sampling locations of the specimens in the present study. In the absence of more plausible alternatives, it is proposed that the parasitic structures found in *Euchone x* might belong to *Rhizellobiopsis* or a related taxon. Comment and feedback is welcomed on the observations and interpretations presented here, in the hope of eventually achieving a conclusive identification.

4.5 Conclusions

The present study, although being of a qualitative nature, indicates that *Euchone x* is capable of adopting a wide range of behaviour patterns and a flexible feeding strategy. The animals appear to be able to survive relatively long periods of low food and oxygen availability by entering a quiescent state, but are quick to exploit a food source when it becomes available. Adults were seen to display at least some brooding behaviour and, in aquarium conditions, the young and adults co-exist. *Euchone x* appears to play host to a parasitic organism, which possibly belongs within *Rhizellobiopsis* (Protista: Ellobiopsidae) or a related taxon.

There is a striking similarity in the population densities of *Euchone x* found in the present study with those of *Euchone incolor* found on certain seamount slopes in the Pacific Ocean. It is suggested that complex and dynamic patterns of food and oxygen availability via down-slope currents play a major role in structuring the benthic assemblages dominated by *Euchone x* and related small *Euchone*.

DISCUSSION

"If, without modifying the structure of its logic, biological science is capable of annexing as its parish the entire survey of living matter, there remains no nicely defined boundary at which science ends and philosophy begins."

Lancelot Hogben (1930), *The nature of living matter*

5 Concluding discussion

5.1 Achievements and contributions

5.1.1 Descriptive characteristics

Identification of sabellid polychaetes is often regarded as being "difficult". This is mainly because the descriptive characters are not always clear in the general literature, or are misinterpreted. This is particularly true of the taxa found in soft-bottom sediments, which are not always well-described in the general literature. Although those few taxonomists specialised in sabellids have little difficulty understanding which features to look for (and where to look for them), general workers dealing with a broad range of taxa are often confused by the terminology in the literature. This confusion is confounded by the discrepancies between different literature sources or where identification guides have failed to keep abreast of taxonomic or systematic advances. In addition, some literature sources place emphasis on features that can vary markedly between individuals, or with state of preservation. Without knowledge of these pitfalls, understanding sabellid polychaetes can seem far more complex than necessary. The need for a simplified guide to the external anatomy of sabellid polychaetes became apparent.

Chapters 1.2 and 1.3 clarified the main features of sabellid polychaetes in a clear and logical manner, such as to help non-specialists become familiar with this group of animals. In doing so, several features were highlighted that have not received much attention in the literature, or have been misinterpreted. These may be summarised as follows:

- emphasis on the fundamental differences between the Fabriciinae and the Sabellinae, as revised by Fitzhugh (1989); these issues have not been incorporated in the most commonly-used identification literature;
- schematic illustration of the two main types of radiolar crown found in sabellid polychaetes ('snowflake-like' and 'feather-like' forms);
- a schematic illustration was given of the fundamental difference in collar origin between the Fabriciinae and the Sabellinae; the concept of the anterior and

posterior peristomial rings, which is often misunderstood by non-specialists, is made clear; difficulties in distinguishing between fabriciin specimens with a well-developed collar and small sabellins that to the untrained eye may resemble fabriciins are thereby resolved;

- a schematic illustration was given of the modification of the anterior peristomial ring in some sabellins to form a triangular or bilobed structure; this feature is homologous to the fabriciin collar;
- the subtle variations in sabellid chaetae that make it difficult to assign them to the discrete categories found in the literature were discussed; instead a more flexible approach to identification and recognition of chaetal forms is proposed;
- attention was drawn to the difference between the *Chone*-like collar, where the dorsal margins are curled inward and attach to the peristomium (anterior peristomial ring); this contrasts with the form found in *Amphicorina*, where the dorsal margins are not attached and stand upright;
- despite its common use in the literature, the presence or absence of lateral notches is shown to be an unreliable feature that may be confused with preservation artefacts.

In addition to clarifying the morphology of sabellid polychaetes, attention was drawn to the importance of scale, and the diversity of reproductive strategies even within a group of closely related taxa. The above aspects are not new to science. What is unique to the present work is the presentation of information from a large body of literature, together with a wide range of study specimens, in a compiled form suitable for the non-specialist. This part is targeted for future publication as an informative guide for students of sabellid polychaetes.

5.1.2 Taxonomic part

Chapter 2.3 provided a list of the taxa currently assigned to *Euchone* Malmgren in chronological order, together with the relevant synonymies and redesignations of taxa that have occurred with the advancement of knowledge. As far as possible, the location of type material was given and taxa of uncertain status, or where the reference material is lost, were indicated. Such an updated overview has not previously been available in the literature. In Chapter 2.4, *Euchone x* new taxon was described from the North Sea and northern Norwegian Sea, together with comparative comments on related taxa.

In Chapter 2.5 a redescription of *Jasmineira candela* Grube was given, and *Jasmineira oculata* Langerhans, which previously was regarded as a junior synonym of *J. candela*, was reinstated. Existing information of *J. oculata* was compiled from little-known literature sources, and new records and a description of that taxon from Atlantic waters were given. The likelihood that records of *Jasmineira candela* from around the British Isles, the North Sea and Norwegian Sea should be referred to *Jasmineira oculata* was discussed.

Existing information on various *Chone* taxa recorded from Atlantic waters was compiled in Chapter 2.6, mainly from little-known literature, unpublished information and study specimens. The status of the various taxa were discussed and gaps in knowledge were outlined. Although far from comprehensive, this review represents a first step towards a much-needed compilation of detailed information from the older literature, together with recent observations. In so doing, the foundation for a comprehensive review of *Chone* in Atlantic waters is prepared.

Further, a description of *Chone duneri* Malmgren from Arctic waters was given and compared with the original, rather brief, description. The status of *Chone filicaudata* Southern was outlined and specimens from the North Sea and Norwegian Sea were compare with previous records. In addition, the possibility for misidentification of material from other areas was discussed.

5.1.3 Systematic part

In Chapter 3, the systematics of the Sabellidae was placed in a historical context. It was emphasised that the system of binomial taxonomic nomenclature (*Genus species*) still in use today was devised well over a century before the concept of evolution was recognised. Although by no means new to the present study, highlighting this observation puts the inconsistencies and 'overlap' in characters seen in the taxonomic part of the present thesis into a logical context. The need for a shift in emphasis from looking at differences between taxa to looking for similarities and relationships was made apparent. Instead of placing taxa into systematic categories based on morphological similarity, the concept of phylogenetic systematics was outlined. As in Chapter 1, little prior specialist knowledge was assumed and a background review of the subject was given. In addition, a number of current issues, some of which still are controversial, were discussed.

The possibility that apparently similar features may have arisen independently through evolution, or been lost in certain groups of organisms, was highlighted in the context of the Sabellidae. The relevance of this concept to taxa diagnosed by the shared presence of a certain morphological feature was illustrated using the example of *Euchone* Malmgren. *Euchone* is diagnosed by the presence of an anal depression, but there has never been any attempt in the literature to determine whether the feature is homologous between all members of the taxon, or whether the feature has arisen more than once in the evolutionary history of the organisms.

Phylogenetic analyses were carried out of those *Euchone* taxa for which it was possible to obtain a full morphological description. For comparison, a restricted number of taxa within *Amphicorina, Chone* and *Jasmineira* were included in the analyses. The results indicated that *Amphicorina* (at least the three taxa included in the present study) represents a discrete sister group to taxa within *Chone, Euchone* and *Jasmineira. Euchone* Malmgren was shown as being an artificial taxon, i.e. it does not comprise all the descendants of its common ancestor. The anal depression was shown either to have evolved on two separate occasions, or to have occurred on an evolutionary branch between *Amphicorina* and what has been referred to as the *Chone* complex.

The results obtained therefore disagree with previous research, such as Banse (1970), where *Euchone* is considered to be a natural group and adequately diagnosed by the presence of an anal depression. Further, the assumption is refuted that the anal depression is a specialised feature and, as such, *Euchone* cannot be ancestral to taxa such as *Chone*, as Banse (1970) suggested. Instead, the present results suggest that the anal depression is a plesiomorphic feature, that subsequently was lost in more apomorphic taxa.

On the basis of the phylogenetic analyses, five taxa currently assigned to *Euchone* were recognised as belonging to a discrete group. In traditional terms, these would be assigned to a new genus, diagnosed by the presence of only three pairs of 'snowflake-like' radioles, only three segments comprising the anal depression and the presence of abdominal uncini reminiscent of those in *Amphicorina*. However, alternative avenues for systematising these taxa were explored. Using phylogenetic taxonomy, the clade comprising five taxa would be given an appropriate name. The current 'species' names would merely be considered as the least inclusive taxonomic units (LITUs), accepting that these might in the future be 'split' into further sub-groups. The LITUs bear the name of the author that described the taxon, but are not automatically appended to the name of a higher taxon.

In phylogenetic taxonomy, taxon names are uninomial, and the rigid hierarchy of class, order, family and genus is abandoned. Instead, higher taxon names are defined by the attributes that characterise a natural group, or clade, of organisms. The discovery of further sub-groups within the original clade will never change the meaning of that taxon, only the organisms included in it may be further assigned into smaller, less inclusive, groups. Opponents of phylogenetic taxonomy claim this to be a lack of taxonomic stability and wish to maintain the traditional hierarchies. The viewpoint taken here is that rearranging and rediagnosing existing Linnean higher taxa into monophyletic groups is not a satisfactory compromise. Although the familiar structure and names may be retained, their meanings will change repeatedly as knowledge increases. Therefore, using the pre-evolutionary Linnean system to classify groups of organisms that are phylogenetically inter-related to various degrees is here regarded as being conceptually unstable.

Like most taxonomic studies, the present work aims to maintain a sense of tradition and respect for the historical roots of taxonomy and systematics. In the present opinion, continually changing the meanings of certain Linnean taxa is confusing and does not consistently maintain tradition. Linnean taxa were never intended to provide a system for naming groups of related organisms, but were intended to place discrete and invariant products of creation into a logical order. If evolution theory had been proposed at the time Linnaeus was alive, it is by no means certain that the *Systema Naturæ* would have taken the form it did. Eventual removal of Linnean taxa from modern usage is here not regarded as a disrespect of tradition. On the contrary, attempts to change the meaning of Linnean taxa to make allowances for new discovery is seen as an impossible or even an undesirable task. Eventually, the taxa will be changed so much in meaning that the historical roots are obscured anyway, a situation that could be regarded as equally disrespectful. Because the LITUs and higher taxa retain the author names, a historical perspective is maintained. However, the original Linnean higher taxa (family, genus etc.) are put to one side, as valuable and fascinating historical reference works, and not further changed.

The present work regards phylogenetic systematics to be compatible with Linnean classification if, and only if, the taxa are monophyletic in the Hennigian sense. Because phylogenetic taxonomy is not currently recognised by the International Code for Zoological Nomenclature, the results and ideas expressed here on the subject are not used formally, but are offered as a contribution towards future research. In the meantime, until the matter is resolved, the group of taxa removed from *Euchone* will be described in the traditional manner to put a stop to the use of the artificial taxon name *Euchone*. However, because the new taxon was revealed using phylogenetic methods, an eventual transition to phylogenetic taxonomy will not change its meaning.

5.1.4 Ecological part

Chapter 4 drew attention to the flexibility in feeding strategy in *Euchone x*, which was observed to be capable of both suspension and deposit feeding. In this respect, the results support previous findings where some small members, mainly of the Fabriciinae, were seen to be multi-trophic. The likelihood that the animals display brood protection behaviour was discussed in the light of the previously-held notion that broadcast spawning represents the 'primitive' reproductive strategy. Attention also was drawn to an enigmatic parasite, possibly belonging to *Rhizellobiopsis* Hovasse (Protista: Ellobiopsidae). In this way, the complexity and ecological diversity of sabellids is further illustrated.

5.2 Future directions and challenges

5.2.1 Taxonomy

A full taxonomic revision of *Euchone* Malmgren demands availability of type material of all taxa currently recognised within it. Because the type material of a number of taxa is lost, and records in the literature are either very scant or confused, such a complete revision was not possible in the present study. However, the continuation of the present research will address this issue. A concerted effort will be made to acquire material from close to the type localities of the 'missing' reference specimens. If the material agrees with the descriptions, a new reference collection, or neotype series, will be made. If searches for material prove unsuccessful, those taxa that are incompletely described and for which appropriate specimens are not available, will be assigned as taxa of uncertain status. If at any time in the future the status of such a taxon is clarified, it can easily be included once more within the valid taxa. A similar strategy will be adopted for a revision of North Atlantic *Chone* and *Jasmineira*.

5.2.2 Systematics

Continuation of the present systematic work offers a number of challenging possibilities. Because of the inherent difficulties in coding continuous characters, such as numbers of segments and radioles, the first step would be to carry out the analyses on more restricted groups of taxa. The less inter-taxon variability in features, the higher the level of detail that can be used.

First, detailed analyses will be carried out of all taxa within *Amphicorina* Quatrefages, together with the five taxa removed from *Euchone* (referred to as *Euchone* 2) and using the Fabriciinae as an outgroup. If the taxa within *Amphicorina* still form a monophyletic group, then it may correctly be interpreted as a sister group to *Euchone* 2, *Jasmineira* and *Euchone* 1. This being the case, *Amphicorina* may be used as the outgroup for analyses of taxa within, for example, *Euchone* 2 and *Jasmineira*. Using *Amphicorina* as an outgroup has the advantage of reducing the problem of inapplicable states. Because the collar in that outgroup would be homologous to that of the ingroup, all the characters relating to the feature could be coded in a similar manner.

Using a suitable outgroup, focus will be given to resolving the relationships between taxa within *Jasmineira, Chone* and *Euchone* 2. Excluding the *Euchone* 1 group reduces the range of character states found within the ingroup. It is anticipated that, once an appropriate strategy for coding variable characters is devised, the relationships between these taxa will become clear.

5.2.3 Applied benthic faunal analyses

A further area that will be addressed during the continuation of the present work is how changing taxonomic and systematic strategies will affect workers using 'species' determination for applied faunal community analyses. Most faunal workers must deal with a wide range of taxa and it is difficult to keep abreast of taxonomic advances in all groups. Each time a new taxon is described from the relevant area, or the meaning of a higher taxon is changed, such as to exclude some of its previous members, faunal workers must update their databases. In addition, all comparative taxon lists must be altered accordingly, where spatial or temporal trends are to be investigated.

Most faunal workers accept the need for taxon names that describe natural groups. However, frequent changes in names complicate the tasks in hand. Because adjusting

Linnean taxa to conform with phylogenetic advances involves both changes in taxon names and often their meanings, the scepticism some faunal workers express towards phylogenetic systematics might be expected. Similarly, because opponents of phylogenetic taxonomy have claimed that the method represents "taxonomic instability", the instinctive horror with which the concept often is met is understandable. The following discussion aims to examine the fundamental requirements of faunal analyses as regards taxon names, and the ways in which traditional and phylogenetic taxonomy and systematics can fulfil them.

Just as taxonomy and systematics were presented as means of communicating information (Chapter 3.5), so also faunal statistics are merely a means of communicating information about a particular environment. For this to function, it is essential that the taxon names themselves, as the basic units of the analyses, also function as effective communication tools. It is clear that faunal analyses function best if there is a minimum of changes in taxon names. However, also the meanings of those taxa must be stable.

As discussed in Chapter 3.5, altering Linnean taxa such that they support phylogenetic knowledge leads to changes in both the taxon names and their meanings. The traditional hierarchy of higher taxa is maintained. Faunal statistics, like phylogenetic methods, operate at the lowest identified taxonomic level. Each 'species' name and its attached affiliation to 'genus' is treated as a single unit. The computer treats 'species' identifications in the same manner as records left at the 'genus' level. Therefore, higher taxa are not necessary for the statistical analyses themselves. The higher taxa that are listed in the taxon list help the operator to interpret the faunal distributions found. However, the operator is little helped if the meanings or the use of those names are subject to repeated change.

It could be claimed that faunal statistics could equally well be run using the least inclusive taxonomic units (LITUs) of phylogenetic taxonomy as with binomial 'species' names. In contrast to traditional names, once assigned, a phylogenetic name will never change its meaning. Therefore, the task of standardising the names of taxon lists compiled at different times or by different operators is simplified. The statistics can be run using uninomial taxa without any difference in results. Taxa in taxon lists are listed with the informative names of the clades that contain them, to show their relationships with other organisms.

The present opinion therefore must be to share the concern expressed by many faunal workers when faced with ever-changing Linnean taxa. Although the cause and aims of these changes are supported, the methods used to obtain natural 'genera' are believed to carry a high risk of confusion. The conservative approach of retaining taxon names to refer to changed concepts is here challenged. Continuation of the present research will investigate whether a satisfactory reform in taxonomy and systematics, and the applied uses thereof, would not better be achieved by turning towards a new system that from its beginning was designed to cater for evolved, rather than created, organisms. In doing so, the focus moves towards 'tree-thinking', rather than the ordered systems devised by natural theologists.

5.2.4 Afterthought

Lively discussions of the recent and proposed changes in taxonomy and systematics are expected to continue for the foreseeable future. The viewpoint taken here is that before subscribing to one or other strategy, the fundamental issues should be carefully considered without prejudice. In time, when the logic of the traditional and more radical approaches are examined and compared, the situation will become resolved. However, for the present, the subject matter remains an interesting challenge.

> "The difficulty lies, not in the new ideas, but in escaping the old ones, which ramify, for those brought up as most of us have been, into every corner of our minds."
>
> *John Maynard Keynes*, date unknown.

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"Roots and leaves themselves alone are these"

Walt Whitman (c1900), *Leaves of grass*

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Note:

Where these are subject to confusion, Russian journal or serial titles are given in both transliterated and translated forms. Transliteration, although clumsy to read, is useful for library searches for Russian publications because the translated titles are not always accurate in the literature.

APPENDICES

Appendix I. List of characters and states

Crown characters

1. Branchial hearts
0: present
1: absent

2. Branchial lobes
0: separate
1: fused dorsally

3. Radiolar skeleton
0: absent or single row
1: double row

4. Pinnules
0: alternating
1: paired

5. Pinnule length
0: longest mid-radiole
1: uneven
2: even

6. Radioles
0: three pairs only
1: more than three pairs

7. Inter-radiolar membrane
(relative to radiole length)
0: absent
1: less than quarter
2: quarter to third
3: half
4: two thirds to three quarters

8. Radiolar flange
0: absent
1: present

9. Free ends of radioles
0: filiform
1: broad or tapering
2: with appendages

10. Free ends
0: short
1: long

11. Breaking plane
0: absent
1: present

12. Ventral cirri
0: absent
1: present

Peristomial characters

13. APR projection
0: collar or flap
1: triangular
2: bilobed
3. absent
3: rounded
4: square

14. PPR projection
0: absent
1: attached collar
2: free collar

15. Fusion chaetiger 1
0: absent
1: at least partial

16. APR
0: fully exposed
1: partially exposed
2: covered

17. Ventral incision
0: absent
1: present

18. Angle collar
0: level
1: oblique

19. Dorsal gap
0: narrow
1: wide

20. Scalloped collar
0: absent
1: present

Thoracic characters

21. Ventral shields
0: undifferentiated
1: differentiated

22. Biannulation
0: absent
1: at least in thorax

23. Thoracic girdle
0: absent
1: present

24. Notopodial lips
0: absent
1: present

Abdominal characters

25. Abdominal segments
0: three only
1: more than three

26. Abdominal girdle
0: absent
1: present

27: Anal depression
0: absent
1: three segments
2: more than three segments

28. Lateral wings
0: absent
1: reduced
2: well-developed

29. Abdominal growth
0: absent
1: present

30. Pygidial eyes
0: present
1: absent

31. Pygidial filament
0: absent
1: present

Chaetal characters: thorax

32. Superior notochaetae
0: elongate, narrow
1: other

33. Anterior inferior notochaetae
0: pseudospatulate
1: bayonet
2: short, swollen

34. Posterior inferior notochaetae
0: absent
1: short, swollen
2: pseudospatulate
3: spatulate

35. Thoracic uncini
0: acicular unequal teeth
1: acicular, equal teeth

Chaetal characters: abdomen

36. Main fang on uncini
0: absent
1: present

38. Handle
0: absent
1: present

39: Abdominal notochaetae
0: elongate, narrow
1: other

40. Variation within torus
0: absent
1: present

Appendix II. Character matrix for the analyses presented in Chapter 3.6. Italics denote the outgroup and parentheses indicate taxa excluded from the analyses.

Character	**0**									**1**										**2**										**3**										**4**
Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**8**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**
Fabriciinae	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*?*	*?*	*?*	*?*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*?*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*
A. androgynae	1	1	1	0	0	0	1	1	0	0	0	0	1	2	0	1	1	0	1	0	1	0	1	0	1	0	0	?	0	1	0	0	2	0	0	1	1	0	0	0
A. anneae	1	1	1	0	0	0	1	1	0	0	0	0	1	2	0	1	1	0	1	1	1	0	1	0	1	0	0	?	0	0	0	0	1&2	0	0	1	1	0	0	0
A. paramobilis	1	1	1	0	0	0	1	1	0	0	0	0	1	2	0	1	0	0	1	0	1	0	1	0	1	0	0	?	0	0	0	0	2	0	0	1	1	0	0	0
C. infundibuliformis	1	1	1	1	2	1	4	1	1	1	0	1	2	1	1	2	0	0	0	0	0	1	1	1	1	0	0	?	1	1	0	0	1	3	1	1	2	0	0	0
C. duneri	1	1	1	1	2	1	4	1	0	1	0	1	2	1	1	1	0	1	0	0	0	1	1	1	1	0	0	?	1	1	0	0	1	3	1	1	2	0	0	0
C. filicaudata	1	1	1	1	2	1	4	1	0	1	0	1	2	1	1	2	0	0	0	0	0	0	1	1	1	0	0	?	1	1	1	0	1	1	1	1	2	0	0	0
C. longocirrata	1	1	1	1	2	1	4	1	0	1	0	1	2	1	1	1	0	0	0	1	0	1	1	1	1	0	0	?	1	1	0	0	1	1	1	1	2	0	0	0
C. paucibranchiata	1	1	1	1	2	0	4	1	0	1	0	1	2	1	1	1	0	0	0	0	1	0	1	1	1	0	0	?	1	1	0	0	1	3	1	1	2	0	0	0
C. y	1	1	1	1	2	1	4	1	0	1	0	1	2	1	1	1	0	1	0	0	0	1	1	1	1	0	0	0	1	1	0	0	1	2	0	1	2	0	0	0
E. alicaudata	1	1	1	1	2	1	2	1	1	1	0	1	3	1	1	2	1	0	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	2	1	0	1
E. analis	1	1	1	1	2	1	3	1	1	1	0	1	3	1	1	2	1	0	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	2	0	0	0
E. arenae	1	1	1	1	0	1	2	1	0	1	0	1	3	1	1	2	0	0	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	1	0	0	1
E. bansei	1	1	1	1	2	1	3	1	0	1	0	1	1	1	1	2	0	0	0	0	0	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	2	0	0	0
E. capensis	1	1	1	1	2	1	4	1	0	1	0	1	3	1	1	2	1	0	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	2	0	0	0
E. elegans	1	1	1	1	2	1	3	1	1	1	0	1	3	1	1	2	1	0	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	2	1	0	1
E. hancocki	1	1	1	0	0	0	1	0	0	0	0	1	2	1	1	2	0	0	0	0	0	0	1	0	1	1	1	2	0	1	0	0	1	1	1	1	1	0	0	1
E. incolor	1	1	1	0	0	0	1	0	0	0	0	1	2	1	1	1	0	0	0	0	0	0	1	0	1	1	1	2	0	1	0	0	1	1	1	1	1	0	0	1
E. limnicola	1	1	1	1	2	1	2	0	0	1	0	1	3	1	1	2	0	0	0	0	0	1	1	1	1	0	2	1	0	1	0	0	1	1	1	1	2	0	0	1
E. pallida	1	1	1	1	2	1	3	1	0	1	0	1	3	1	1	2	1	1	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	2	0	0	0
E. papillosa	1	1	1	1	2	1	3	1	0	1	0	1	3	1	1	2	1	1	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	3	1	1	2	1	0	0
E. rosea	1	1	1	1	2	1	4	1	0	1	0	1	3	1	1	2	0	0	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	2	1	0	0
E. rubrocincta	1	1	1	1	2	1	3	1	0	1	0	1	3	1	1	2	0	0	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	2	1	0	0
E. scotiarum	1	1	1	0	0	0	1	0	0	0	0	1	2	1	1	1	?	1	0	0	0	0	1	0	1	?	1	2	0	1	0	0	1	1	1	1	1	0	0	1
E. southerni southerni	1	1	1	1	2	1	3	1	0	1	0	1	3	1	1	2	1	0	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	2	0	0	0
E. trilobata	1	1	1	0	0	0	0	0	0	0	0	1	2	1	1	2	0	0	0	0	0	0	1	0	1	?	1	2	0	1	0	0	1	1	1	1	1	0	0	1
E. undulocincta	1	1	1	1	2	1	3	1	0	1	0	1	3	1	1	1	1	1	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	3	1	1	2	0	0	0
E. variabilis	1	1	1	1	1	1	2	1	0	1	0	1	3	1	1	2	0	0	0	0	0	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	2	0	0	0
E. velifera	1	1	1	1	2	1	3	1	0	1	0	1	3	1	1	2	1	1	0	0	1	1	1	1	1	0	2	2	0	1	0	0	1	1	1	1	2	0	0	0
E. x	1	1	1	0	0	0	1	0	0	0	0	1	2	1	1	1	0	1	0	0	0	0	1	0	1	1	1	2	0	1	0	0	1	1	1	1	1	0	0	1
(J. bermudensis)	1	1	1	?	?	?	0	0	?	?	0	1	3	1	1	1	1	1	0	0	0	?	1	0	1	0	0	0	1	1	0	0	1	2	1	1	4	1	0	0
J. elegans	1	1	1	1	2	1	0	0	0	1	1	1	3	1	1	2	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1	3	1	1	4	1	0	0
J. candela	1	1	1	1	2	1	0	0	2	1	0	1	1	1	1	2	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	3	1	0	0
J. caudata	1	1	1	1	2	1	0	0	0	1	1	1	3	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	1	2	1	1	4	1	0	0
J. oculata	1	1	1	1	2	1	0	0	2	1	0	1	1	1	1	2	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	3	1	0	0
(J. filiformis)	1	1	1	1	0	0	0	0	0	0	0	1	3	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1	1	1	1	4	0	0	0