

GÖTEBORG UNIVERSITY  
FACULTY OF NATURAL SCIENCES

**FROM INDIVIDUALS TO DEEP METAZOAN BRANCHES:  
RELATIONSHIPS AND DELINEATION OF RECENT AND  
FOSSIL CHRYSOPETALIDAE (ANNELIDA)**

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Dissertation

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Avhandling för filosofie doktorsexamen i zoologi som enligt beslut av tjänsteförslagsnämnden i biologi kommer att offentligens försvaras fredagen den 5:e maj 2000 kl. 10.00 i föreläsningssalen, Zoologiska Institutionen, Medicinargatan 18, Göteborg. Examinator: Professor Bengt Silverin. Fakultetsopponent: Danny Eibye-Jacobsen Zoologisk Museum, Köpenhamn.

FROM INDIVIDUALS TO DEEP METAZOAN BRANCHES: RELATIONSHIPS AND  
DELINEATION OF RECENT AND FOSSIL CHRYSOPETALIDAE (ANNELIDA)

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**Abstract:** The chrysopetalid polychaetes are a small group of marine worms that have a global distribution but are most common on tropical coral reefs. Most of the ca. 50 described forms are distinguished by flattened notochaetae which are arranged as roofing tiles on the dorsum. Recent attention to the group has focused on a possible close relationship between chrysopetalids and the Cambrian fossil worms *Wiwaxia* and *Canadia*, known mainly from the Burgess Shale, British Columbia. Despite several descriptive studies on the group, one part of the Chrysopetalidae, the “dysponetid” taxa, has been largely neglected. In papers I, II and III, two new (*Dysponetus bipapillatus* and *D. macroculatus*) and two poorly known taxa (*D. caecus* and *D. paleophorus*) are described from newly collected specimens.

Apart from the aim to increase our knowledge on the organismal diversity among the dysponetids, this thesis is the first attempt to resolve problems concerning the phylogeny of chrysopetalids and its allies. Traditionally the group is treated as a family group taxon within the order Phyllodocida, but there is no agreement on the closer position of chrysopetalids within this large assemblage of errant worms. Papers IV and V explore, among other issues, the delineation and position of Chrysopetalidae. They include three different analyses, applying both morphological and DNA sequence data. While the resulting trees indicate a well-delineated Chrysopetalidae, the topologies are not conclusive on identifying the sister group to the chrysopetalids. It is suggested, however, that either Hesionidae or Nereididae may represent the most likely candidate.

The last paper of the thesis (VI) discusses and analyses some of the disparate views that have been presented on the position of the Cambrian fossil *Wiwaxia*. The hypothesis that *Wiwaxia* is an annelid, close to the Phyllodocida, is further examined and related to recent advances in polychaete phylogeny. One implication is that, if *Wiwaxia* and *Canadia* indeed hold a basal position in the annelid tree, then the Phyllodocida (including *Wiwaxia* and *Canadia*) constitutes a grade in which the sister to all other annelids should be found. Alternatively, if the Phyllodocida represent a clade within the polychaetes, then *Wiwaxia* and *Canadia* are derived annelids.

**Keywords:** Annelida, Polychaeta, Phyllodocida, Chrysopetalidae, *Dysponetus*, *Wiwaxia*, phylogeny, systematics, cladistics, Cambrian, Burgess Shale

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## LIST OF ORIGINAL PUBLICATIONS AND MANUSCRIPTS<sup>1</sup>

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This thesis is based on the following studies, referred to in the text by their Roman numerals:

- I DAHLGREN, T. G. & PLEIJEL, F. (1995). On the generic allocation of *Chrysopetalum caecum* (Polychaeta: Chrysopetalidae). *Mitt. hamb. zool. Mus. Inst.* **92**, 159-173
- II DAHLGREN, T. G. (1996). Two new species of *Dysponetus* (Polychaeta: Chrysopetalidae) from Italy and Papua New Guinea. *Proc. Biol. Soc. Wash.* **109**, 575-585
- III DAHLGREN, T. G. (manuscript). Redescription of *Dysponetus paleophorus* Hartmann-Schröder, 1974 (Chrysopetalidae, Annelida) with reference to the spines of *Wiwaxia corrugata* (Matthew, 1899).
- IV PLEIJEL, F. & DAHLGREN, T. (1998). Position and delineation of Chrysopetalidae and Hesionidae (Annelida, Polychaeta, Phyllodocida). *Cladistics* **14**, 129-150
- V DAHLGREN, T. G., LUNDBERG, J., PLEIJEL, F. & SUNDBERG, P. (2000). Morphological and molecular evidence of the phylogeny of nereidiform polychaetes (Annelida). *J. Zool. Syst. Evol. Res.* **00**, 00-00. (In press.)
- VI DAHLGREN, T. G., PLEIJEL, F., & ROUSE, G. W. (manuscript). Annelid evolution and *Wiwaxia corrugata*; a synthesis

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<sup>1</sup> A doctoral thesis at a Swedish university is often presented as a collection of papers with a summarizing introductory part.

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## INTRODUCTION

This thesis is about worms. For most people in most situations the word “worm” is adequate to describe small, longer-than-wide crawling forms of life. Practising biologists, however, often need to be a bit more precise regarding just what kind of worm they refer to. One of the more obvious examples may be the medical doctor looking for a treatment against the worm he just found in a patient. For practical reasons or not, naming things and organisms in our surroundings has been an essential part of exploring the earth. Not until the 18<sup>th</sup> century, however, was there a generally accepted system for how organisms should be named and classified in the western world. Instead of simply calling a newly discovered clam “The Icelandic Clam” (or “Islandsmussla” in Swedish), the naturalist Carl von Linné suggested that species names should be in latin and be composed of two parts. In our example above the name would be *Venus islandica*, where the first part indicates to which more inclusive group the clam belonged, and the two names together denote the species. From this we understand that Linné was also interested in naming more inclusive groups of organisms. The name Vermes was erected for crawling critters of various sorts. A century later, the idea that organisms evolve into new forms and disappear by extinction became widely accepted as Darwin and Wallace presented the theory of evolution by natural selection. This, in turn, opened the field for research in biological systematics with organisms being grouped according to common descent. The depiction of the evolutionary relationships of organisms in a historical context is referred to as phylogeny; a “tree” diagram is often used to illustrate these relationships.

Among animal representatives of other groups, such as molluscs, seastars, sea urchins and nematodes, Linné’s Vermes included a group of organisms later called annelids (as Annélides Lamarck, 1802), composed of segmented worms. Although, for obvious reasons, the most commonly known annelids are those found on land and in fresh water (earthworms and leaches), most of them dwell in the sea. Annelids lack a shell and often loose colouration when preserved, which, together with their relative inaccessibility, make them less interesting for collectors and other groups of laymen. The diversity, as judged by number of described species, is also relatively low compared to invertebrate groups such as butterflies and beetles or various sea-shells.

Chrysopetalids are annelids. The scope of this thesis is to increase and summarize the knowledge of the group, and to place them into a wider context of annelid and metazoan evolution and phylogeny.

## THE CHRYSOPETALIDS

Chrysopetalids are polychaete annelids which, with some exceptions (i.e., “dysponetid” forms), carries flattened dorsal chaetae (paleae) arranged in a roof tile pattern on the dorsum. Chrysopetalids are small to medium sized worms (1-50 mm), live in sediment and rubble, and are distributed world-wide. Most are poor swimmers and move sluggishly. Many, however, have shiny golden colour which also contributed to their name (from the combination of the Greek words *chrysos* =gold and *petalon* =leaf).

### *Brief History of Research*

The first described chrysopetalids were *Chrysopetalum debile* (as *Palmyra debilis* Grube, 1855) from material collected in the Mediterranean, and *Chrysopetalum elongatum* as (*Palmyra elongata* Grube, 1856) from the Virgin Islands. Kinberg (1858) erected Palmyridae for *Palmyra aurifera* (Savigny in Lamarck, 1818), a paleae-bearing worm that was later recognized as closer related to Aphroditidae than to Chrysopetalidae (e.g., Racovitza 1896; Augener 1913; Horst 1917; Watson Russell 1989). Schmarda (1861),

working, among other places, in the Indian Ocean, added *Paleanotus chrysolepis* (Schmarda, 1861) and *Bhawania godei* (Schmarda, 1861), and referred them in Kinberg's family group name Palmyridae. The name Chrysopetalidae originates from Ehlers (1864) who, in describing the new *Chrysopetalum fragile* (synonymized with *C. debile* by Racovitza 1896), established the family based on the two genera *Palmyra* and *Chrysopetalum*. A list of more recent taxonomic revisions of the taxon include Hartman (1959), treating Chrysopetalidae and Palmyridae as separate families; Day (1967), who followed Schmarda (1861) and treated *Palmyra aurifera* as part of the chrysopetalids and labeled it Palmyridae; Mileikovsky (1977) recognizing two distinct families Palmyridae and Chrysopetalidae within the order Phyllodoceomorpha; Fauchald (1977a), agreeing with Mileikovsky (1977), but erecting the superfamily Chrysopetalacea to accommodate both Palmyridae and Chrysopetalidae; Pettibone (1982) treating Chrysopetalidae as an aberrant family within the order Phyllodocida; Perkins (1985) emphasizing the relationships between Chrysopetalidae, Hesionidae and Nereididae within the Phyllodocida; and Watson Russell (1989), removing *Palmyra* from Chrysopetalacea and placing the former in Aphoditidae. A list of type species of currently recognized genera is given in Table 1.

With the exception of a report from off northern Norway (Mileikovski 1962), paleate forms are known from tropical or temperate seas. They are typically found in association with corals or calcified algae, but also inhabits rubble and sand. A wide variety of habitats was recently reported by Watson Russell (1998) for *Arichlidon* Watson Russell, 1998 (e.g., among sponges, hydroids, rotting wood and deep sea sediments). A few reports exist of adult chrysopetalids from plankton, sometimes associated with occurrence of elongated compound neurochaetae and suggested to be epitokous (Watson Russell 1987, 1998). On the contrary, dysponetid taxa occur in all climate regimes and at all depths in a variety of habitat types (see below).

### ***General Morphology***

The anterior end of chrysopetalids is represented by a prostomium, a peristomium and the first two (and in some taxa three) segments. Such specialization ("cephalization") of the anterior segments is common in all forms of polychaetes. The cephalized segments differ from the following ones in presence, orientation, and shape of chaetae and cirri. Chrysopetalids have an achaetous first segment provided with one, or more commonly, two pairs of tentacular cirri. The second segment exhibits more variation among taxa, but all known forms of chrysopetalids have dorsal cirri and dorsal chaetae. The ventral rami of this segment can, apart from being normal (i.e. with cirri and chaetae), however, be completely reduced, or have either cirri or chaetae. Some dysponetids lack ventral cirri on the third segment (*Dysponetus bidentatus*, *D. bipapillatus*, and *D. macroculatus*; see e.g., Paper II). Cirri of cephalized segments are usually called tentacular cirri and are modified in most polychaete taxa where they occur. In chrysopetalids, however, they are similar in shape to the following ones (i.e. body segment cirri). Most chrysopetalids have two pairs of eyes. Exceptions are found mainly in interstitial and deep-sea dysponetid forms (Paper II) and adults of the deep-sea paleate taxon *Strepternos didymopyton* (Watson Russell in Baud and Cassaux 1987), that lack eyes (Watson Russell 1997). The prostomium carries two lateral antennae and a single median antenna. The antennae are elongated digiti- or fusiform, or spherical. *Vigtorniella zaikai* (Kiseleva, 1992) lacks a median antenna. The shape of the palps varies and can be globular-elongated, rectangular or fusiform. The pharynx is an eversible proboscis, although less muscular than in related groups such as nereidids and hesionids. The occurrence of terminal proboscis papillae has generally not been recorded for chrysopetalids, but Dahlgren and Pleijel (Paper I) reported a ring of 12-14 papillae for *Dysponetus*. Described chrysopetalids have a pair of stylet-shaped jaws, which may be smooth or ornamented with denticles and serrations. Again, *V. zaikai* is an exception with two pairs of platelike jaws in juveniles of which one pair is retained in adults. Pleijel and

Dahlgren (Paper IV) tentatively suggested that the mouthflap, which is present in most chrysopetalids, constitute an apomorphy for the taxon. A bulbous caruncle (nuchal fold) occurs in some, paleate taxa and *Acanthopale* San Martin, 1986. Nothing is known about the chrysopetalid brain structure or the innervation of palps and antennae.

The adult length in chrysopetalids ranges from 1 mm (*Dysponetus*) to 50 mm (*Bhawania*), with the number of segments in the latter group exceeding 300. The segments usually carry well-developed noto- and neuropodia with dorsal and ventral cirri. The dorsal cirrophores in some forms are pronounced and may have retractable cirri. Notochaetae are generally flattened paleae, or, as in most dysponetids, simple spines. Some dysponetids, however, have slightly expanded notochaetae (D-shaped in cross-section, e.g., *Acanthopale* San Martin, 1986). Moreover, flat notochaetae, similar to paleae, are reported in *D. gracilis* Hartman, 1965 (see also, Aguirrezabalaga *et al.* 1999) as well as in an undescribed deep-sea dysponetid from the North Atlantic (unpubl. obs.). Paleate chrysopetalids have flattened notochaetae (paleae) of various shape. These are inserted in distinct areas of the notopodium

**Table 1.** Summary of selected characters for described chrysopetalid type species. Data for these species are obtained from the literature and, in part, from own observations of type specimen (*Vigtormiella zaikai*).

Taxon	Cephalization <sup>1</sup>	No. eyes	Median antenna	Shape of palps	Caruncle	Retractile DC <sup>2</sup>	Pygidial projection	Pygidial cirri
<i>Acanthopale perkinsi</i>	$\frac{0-1}{0-1} + \frac{S-1}{S-1}$	4	anterior	elongated	present	absent	present	present
<i>Arichlidon hanneloreae</i>	$\frac{0-1}{0-1} + \frac{S-1}{S-0}$	4	anterior	elongated	present	absent	absent	present
<i>Bhawania myrialepis</i>	$\frac{0-1}{0-1} + \frac{S-1}{S-0}$	4	anterior	oval	absent	present	present	present
<i>Chrysopetalum debile</i>	$\frac{0-1}{0-1} + \frac{S-1}{S-1}$	4	dorsal	elongated	present	absent	absent	present
<i>Dysponetus pygmaeus</i>	$\frac{0-1}{0-0} + \frac{S-1}{S-0}$	0	dorsal	sphaerical	absent	absent	present	absent
<i>Hyalopale bispinosa</i>	$\frac{0-1}{0-1} + \frac{S-1}{S-0}$	4	anterior	oval	absent	absent	absent	present
<i>Paleaequor setula</i>	$\frac{0-1}{0-1} + \frac{S-1}{S-0}$	4	dorsal	elongated	present	present	absent	present
<i>Paleanotus chrysolepis</i>	$\frac{0-1}{0-1} + \frac{S-1}{S-0}$	4	anterior	oval	absent	absent	absent	present
<i>Strepternis didymopyton</i>	$\frac{0-1}{0-1} + \frac{S-1}{S-0}$	0 <sup>3</sup>	dorsal	oval	absent	presen	present	present <sup>4</sup>
<i>Treptopale rudolphi</i>	$\frac{0-1}{0-1} + \frac{S-1}{S-0}$	4	anterior	sphaerical	absent	absent	?	?
<i>Vigtormiella zaikai</i>	$\frac{S-1}{0-1} + \frac{S-1}{S-1}$	0	absent	sphaerical	absent	absent	absent	present

1) Segments separated with "+". S = chaetae present, 1 = tentacular cirrus, and 0 = absence.

2) DC = dorsal cirri.

3) 4 eyes present in juveniles.

4) Small papillae, often not visible.

and have been classified as lateral paleae, main fan paleae, and median paleae (Watson Russell 1986). In addition, subunits 1 and 2, which are a few paleae delimiting the main fan from the lateral (subunit 1) and median groups (subunit 2), have been recognized in some forms (Watson Russell 1986). With respect to the main fan the chrysopetalids can be divided into three groups, with slightly irregular (laterally in fan) and symmetrical (centrally in fan) paleae, (e.g., *Chrysopetalum*), with strongly irregular paleae with concave margins towards midline (e.g., *Paleanotus*), and with symmetrical paleae (e.g., *Bhawania*). Largely untested in a cladistical context (but see below), such subdivision is only used as a guide for identification and not intended as a statement of relationships. Ornamentation of the paleae is common, and includes raised knobs and ribs as well as serrated margins. Neurochaetae are

generally compound and includes heterogomph falcigers and spinigers. Additionally, there are 1-2 protruding simple chaetae occurring in some taxa, inserted close to the tip of the neuropodium (e.g., Paper I). The presence of such chaetae is easily overlooked and the character may have a more general distribution among chrysopetalid taxa than hitherto known (Paper I; II; Watson Russell 1997, 1998). The pygidium is rounded or triangular and may possess a single pygidial projection and paired pygidial cirri. The anus is situated dorsally in dysponetids (e.g., Paper I; unpublished obs.), but illustrations of pygidia by e.g., San Martin (1986: fig. 7a) and Watson Russell (1986: figs. 12, 21) suggest a ventral position in some other groups. A summary of the variation in some characters is provided for the type species of chrysopetalid genera in Table 1.

### *Ultrastructure*

Some unpublished information on chrysopetalid ultrastructure is available. Representatives of *Chrysopetalum* have sperm of the “aqua-sperm” type with spherical nuclei (see Jamieson and Rouse 1989 for a review of polychaete sperm types). *Dysponetus pygmaeus* from the White Sea, Russia have sperm with long nuclei, which, along with other new structural data, suggests internal fertilization (Alexander Tzetlin in litt.). In the same study (Alexander Tzetlin in litt.), chrysopetalids are reported to possess metanephridia (but see Fage 1906; Goodrich 1945). Also some small paleate chrysopetalid may be provided with sperm with long and curved nuclei (Greg Rouse pers. com.). Westheide and Watson Russell (1992) described the ultrastructure of chrysopetalid paleae in detail. The camerate (chambered) nature of chrysopetalid chaetae, also occurring in nereidid, hesionid, and nephtyid taxa (Paper IV), is confirmed and further described. Westheide and Watson Russell (1992) infer a structurally strengthening function of the septa in agreement with a hypothesis that cameration evolved as a pleisiomorphic feature in annelids to support large chaetae for protection in Cambrian forms such as *Canadia* and *Wiwaxia* (e.g., Butterfield 1990, 1994).

### *Diversity and Current Taxonomy*

Only limited efforts have been made to critically assess the evolutionary history of chrysopetalid taxa (Paper I) or the Chrysopetalidae in relation to other polychaete taxa (Glasby 1993; Paper IV; VI). A short review of the current taxonomy of the dysponetid forms (including *Acanthopale* and *Vigtorniella*) is presented to serve as an introduction to the group's morphological diversity. The reader is referred to Table 1 for a summary of characters for type species of other chrysopetalid genera.

#### *Acanthopale* San Martin, 1986

*Acanthopale perkinsi* San Martin, 1986 is known from two specimens collected off Cuba and Port Everglades, Florida, respectively. With 14 mm for 56 segments it is the largest described dysponetid. The erect notochaetae are not flattened but more sturdy than in *Dysponetus*, and have a pronounced “D”-shaped crosssection or a “rose-stalk” appearance. This form also possesses a large caruncle, partly extending over the prostomium, and a large pyriform mouthflap. Further, the presence of paired pygidial cirri only occurs in paleate chrysopetalids. San Martin (1986) suggested that *A. perkinsi* occupies an intermediate position between *Chrysopetalum* and *Dysponetus caecus*. A cladistic analysis based on morphological characters, confirmed a close relationship between *Acanthopale* and *Chrysopetalum*, but failed to unambiguously resolve deeper chrysopetalid branches (Paper I).

*Dysponetus* Levinsen, 1879

Levinsen (1879) described the polychaete *Dysponetus pygmaeus* from specimens collected in *Laminaria*-holdfasts off the western Greenland. Levinsen was not sure about the assignment of his new taxon and tentatively treated it as belonging to a monotypic family. This uncertainty was also expressed in the name “*Dysponetus*”, meaning “trouble causing”. In a later paper, however, Levinsen (1883) referred *Dysponetus* to Chrysopetalidae (as Palmyridae). In agreement with Levinsen, Augener (1913) placed *Dysponetus* within Chrysopetalidae and also assigned *Dysponetus caecus* (Langerhans, 1880) (see below) to this taxon.

Most dysponetids are small and will be overlooked in any studies which apply standard (i.e., bulk) treatment of samples and employ screens with larger mesh sizes than 250 µm. Furthermore, the specimens are fragile and, if not carefully relaxed, will easily break up into pieces when exposed to formaldehyde. For these reasons, preliminary results suggest that a large number of forms remains undescribed from deep-sea sediments (e.g., North Atlantic Ocean; J. Blake in litt.; pers. obs.), as well as from more shallow habitats (e.g., California, Wales, Hongkong, and the Kara Sea). The group currently includes nine described taxa (e.g., Paper II: App. 1) which are treated further below.

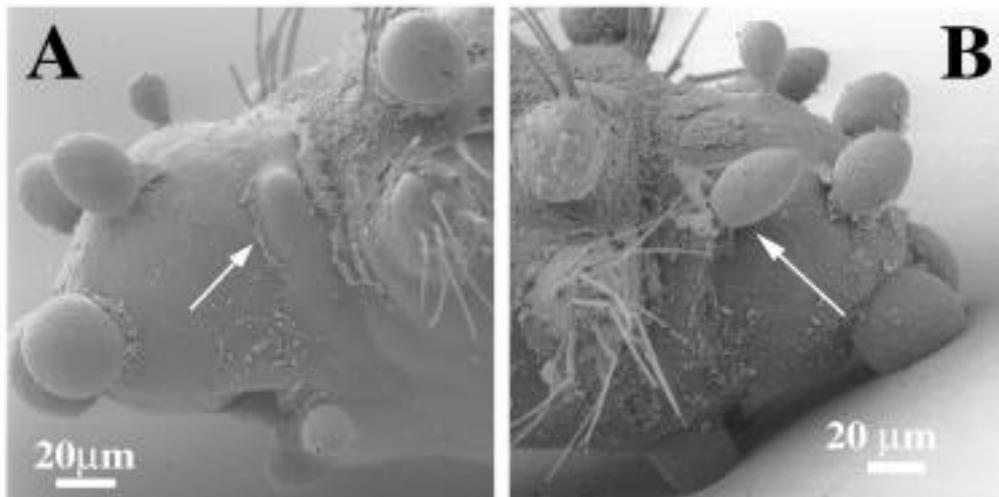
*Dysponetus bidentatus* Day, 1954 was described from specimens collected during a Norwegian expedition to the remote islands of Tristan da Cunha in the South Atlantic in 1937-1938. The specimens were found from the intertidal to about 60 m of depth. The name “bidentatus” refers to the bidentate blades of the compound neurochaetae. The animal has since been reported from off south-western Africa (Hartmann-Schröder 1974a). It is similar to *D. bipapillatus* Dahlgren, 1996, *D. caecus* and *D. macroculatus* Dahlgren, 1996 in the presence of two pairs of tentacular cirri on the first segment, uniramous second segment, and a single mouth papilla (see below). Further, *D. bidentatus*, *D. bulbosus* Hartmann-Schröder, 1982, *D. bipapillatus* and *D. macroculatus*, all have 4 eyes as well as share similarities in size and colouration of the eyes (red in live specimens). Information on characters associated with the pygidium and the putative presence of accessory, simple neurochaetae, is not given in the original description of *D. bidentatus* and is wanting. The syntype deposited in the British Museum of Natural History is lost (A. Muir in litt.).

*Dysponetus bipapillatus* is, with the length at maturity of about 1 mm, the smallest described dysponetid (with the possible exception in *Vigtorniella zaika*). It is known only from a few specimens collected at 10 m depth in sediment close to the main harbor at Ischia, Italy. Interestingly, some of the specimens found have paired ventral papillae on segment 8. These structures were interpreted as penal in the original description (Paper II). While no ultrastructural evidence is available, the discovery of sperm with elongated and curved nuclei, usually associated with internal fertilization (Greg Rouse pers. com.) are consistent with this conclusion. Other characters, e.g., the cephalization of the first segments and the presence of four eyes, suggest that *D. bipapillatus* is closely related to *D. macroculatus*. Further, availability of juvenile specimens allowed for a preliminary ontogenetic study with reference to cephalization of the tentacular segments (Paper II). In this paper (II) it is suggested that chaetae are lost from segments 1 and 2 during the development, and that the ventral cirri of segment 2 do not develop until at a late stage, and that ventral cirri of segment 3 are never present. A similar development is reported for some hesionids (e.g., Haaland and Schram 1982, 1983; Schram and Haaland 1984).

*Dysponetus bulbosus* Hartmann-Schröder, 1982 was described from material collected intertidally in western Australia. Hartmann-Schröder has since reported this taxon from South Australia (Hartmann-Schröder 1986) and the Antarctic (Hartmann-Schröder 1993). *Dysponetus bulbosus* is similar to e.g., *Dysponetus macroculatus* and *D. bipapillatus* in

lacking ventral cirri on segment three (see also *D. bidentatus*). It is probably most closely related to *D. bipapillatus* from which it differs e.g., in shape of notopodia and dorsal cirri, presence of notochaetae in segment 1, and presence of neurochaetae in segment 2. The type material, however, is in poor condition and occurrence of antennae, palps, tentacular cirri, mouth appendage and pygidial characters, could not be determined. The anterior fragment from South Australia (Zoologisches Museum der Universität Hamburg, P-18720, Hartmann-Schröder 1986) is, in the characters discussed above, similar to *D. macroculatus*. The identity of the taxon is uncertain and new specimens from the type locale should be examined.

*Dysponetus caecus* (Langerhans, 1880) was described from Madeira in the North Atlantic. Although possessing dorsal chaetae of spinuose type it was originally referred to the paleate genus *Chrysopetalidae* (Langerhans 1880). The taxonomic history of *D. caecus* is, however, confusing and the type material is presumed lost (Paper I). Intrigued by the recent discovery of *Dysponetus caecus* (then *Chrysopetalum caecum*) along the coasts of Denmark and Sweden (Kirkegaard 1992), a study was undertaken (Paper I) with a redescription of the taxon, from new material collected from the Mediterranean, the British Isles and western Sweden. These areas cover most of the known range of *D. caecus*. In addition, preliminary data suggest that it occurs also around Iceland and in the Kara Sea (pers. obs.). Since specimens from the type locality in Madeira were not available, a neotype (Swedish Museum of Natural History 4607) was designated from Banyuls-sur-Mer, Mediterranean coast of France. In a morphology-based cladistic analysis with a selection of terminal taxa that included *D. caecus* and all type species of recognized chrysopetalid genera, *D. caecus* appeared as sister to *D. pygmaeus*, and was accordingly re-allocated from *Chrysopetalum* to *Dysponetus* (Paper I). Should the results have indicated that *D. caecus* did not group with any single type species, then a new, more inclusive taxon name may instead have been erected (suggested but not carried through by Laubier 1964, 1968 and Perkins 1985). With *D. caecus* as sister group to *D. pygmaeus*, the tree topology information was better conveyed with a single taxon name than with an erection of a new, monotypic genus.



**Figure 1.** Anterior end of *Dysponetus paleophorus* from Barents Sea. A) 7 segment specimen. B) Adult specimen. Arrows indicate tentacular cirri.

*Dysponetus gracilis* Hartman, 1965 was described from sediment samples collected at 400-1.500 m off New England, USA. Reports of additional specimens from the same area (although deeper; Hartman and Fauchald 1971), extends the known maximum depth to 2.800 m. The species was also recently reported from 1.000 m of depth in the Bay of Biscay, North East Atlantic (Aguirrezabalaga et al. 1999). Among dysponetid chrysopetalids, *D. gracilis* is most similar to *D. paleophorus* and *D. pygmaeus* in the absence of eyes, and in the presence of rounded (as opposed to elongated) palps, antennae and the tentacular cirri, but unique in possessing flattened notochaetae approaching the shape of paleae. A closer relationship to *D. paleophorus* is evidenced by the presence of very long spinigerous neurochaetae in posterior segments.

*Dysponetus hebes* (Webster and Benedict, 1887) was originally described as *Taphus hebes* and referred to Hesionidae (Webster and Benedict 1887). Augener (1928), Annenkova (1935) and Wesenberg-Lund (1950, 1953), however, synonymized *T. hebes* with *D. pygmaeus* and thus, firmly assigning *T. hebes* to the chrysopetalids. In a redescription of *T. hebes* type specimens (mounted on slides) Pettibone (1963) suggested that ventral cirri and neurochaetae were absent from segments 2 and 3 but nevertheless agreed in the synonymy of *T. hebes* with *D. pygmaeus*. Laubier (1964) pointed out that *D. pygmaeus* is different and regarded *D. hebes* as a valid taxon. Dahlgren (Paper II) studied the slides and detected presence of neurochaetae in segment 2 and 3 as well as the presence of eyes (absent in *D. pygmaeus*). The presence (or absence) of ventral cirri of segment 2 and 3, however, could not be determined.

*Dysponetus macroculatus* Dahlgren, 1996 was collected in Madang, northern Papua New Guinea. This form was found in a few exemplars in sand with *Halimeda* (a type of calcified green algae) remains in shallow water near coral reefs. It is similar to *D. bidentatus* in e.g., the presence of the four very large, red eyes, and to *D. bidentatus* and *D. bipapillatus* in the absence of ventral cirri on segment 3. The only character distinguishing *D. macroculatus* from *D. bidentatus*, is the presence of ventral cirri on segment 2.

*Dysponetus paleophorus* Hartmann-Schröder, 1974b possesses a type of rounded chaetae not found in any other Recent chrysopetalid (or annelid). The significance of these aberrant chaetae was previously overlooked. In describing *D. paleophorus* from material collected from 255 m depth off south western Norway, Hartmann-Schröder (1974b) failed to report the rounded shape of these chaetae. In the figures (Hartmann-Schröder 1974b: figs. 1-4) the chaetae appears flat and paleae-like. *Dysponetus paleophorus* was previously known from only one specimen in poor condition, necessitating a redescription based on new material (collected at a similar depth to the type locale but in the Trondheimsfjord, western Norway; Paper III). Besides being rounded in cross-section, the chaetae are elongated fusiform, they are subdivided into a root and a blade section, and they lack external ornamentation such as ribs, knobs and serrations (Paper III). A few of these aberrant chaetae are found in *D. paleophorus* together with notochaetae of normal dysponetid shape, and are carried backwards over the dorsum, slightly erected. They have internal transverse and fine longitudinal striation as in other chrysopetalids (Paper I). Similar spines co-occurring with flattened paleae-like sclerites, were described from the Middle Cambrian *Wiwaxia corrugata* (Matthew, 1899). Conway Morris (1985) provided a detailed description of this fossil form. However, Conway Morris (1982, 1985) rejected the earlier proposed relationship between *Wiwaxia* and Recent annelids by Walcott (1911). Butterfield (1990, 1994), in analysing the fine structure and ornamental details of wiwaxiid sclerites, concluded that they (as well as sclerites of the unquestioned Burgess Shale polychaete, *Canadia spinosa* Walcott, 1911) are broadly comparable to chrysopetalid (and maybe palmyrid) paleae. The detailed structure of the wiwaxiid spines has, however, not been described. A comparison between wiwaxiid spines and the aberrant chaetae of *D. paleophorus* is given in paper III, and possible

implications of a close relationship between *Wiwaxia* and Recent chrysopetalids are discussed in paper VI.

*Dysponetus pygmaeus* Levinsen, 1879 have stout, often black, spinous chaetae that emerge in distinct fascicles from each notopodium. Live specimens from the Barents Sea (pers. obs.) had yellow colour, which, together with the black spines, made the animals look like small tigers. Kirkegaard (pers. com.) referred to species as “the little shaving brush”. *Dysponetys pygmaeus* occur along the coasts of the Arctic Ocean and off northern Japan (Annenkova 1935, Imajima and Hartman 1964). As in *D. paleophorus* and *D. gracilis*, this form has an achaetous segment 1 with one pair of cirri only (Fig. 1; see also discussion under “Phylogeny”). A pair of rounded papillae, also observed in *D. hebes*, surrounds the mouth. The latter taxon has been synonymized with *D. pygmaeus* but have a pair of eyes whereas *D. pygmaeus* lacks eyes.

#### *Vigtorniella* Kiseleva, 1996

*Vigtorniella zaikai* (Kiseleva, 1992) was described from pelagic polychaete larvae from the Black Sea and raised to maturity in the laboratory. The original name *Victoriella* Kiseleva, 1992 was pre-occupied and subsequently replaced with *Vigtorniella* Kiseleva, 1996. Larvae of this form were first reported by Kiseleva (1959), and have been known to occur in large numbers throughout the year. The larvae were also described in detail by Murina (1986) who misidentified them as *Pelagobia serrata* Southern, 1909 (Phyllodocidae). In 1994, live adults were collected for the first time, in sediments at 117-151 m depth at the oxic-anoxic boundary of the Black Sea (Sergeeva et al. 1997). This report is an abstract only and the full paper is not published, nor are adult specimens available for loan (V. Zaikai in litt.). Interestingly, a new polychaete taxon, similar to *Vigtorniella*, has been found attached to a whale-carcass in deep water off California (L. Harris in litt.). The characters that were emphasized by Kiseleva (1992) as justifying the erection of a new chrysopetalid genus are chiefly related to the anterior end. However, within Chrysopetalidae the lack of median antenna, the presence of (noto-) chaetae in segment 1, the presence of simple, whip-like neurochaetae in segment 2, and the plate-like jaws, are all autapomorphic characters (notochaetae of segment 1, however, also stated as present in *Dysponetus bulbosus*). Additionally, *Vigtorniella* possesses paired pygidial appendages, present in paleate chrysopetalids (and *Acanthopale*) but absent in *Dysponetus*. Due to the problems associated with the description from laboratory-reared larvae only, *V. zaikai* was not included in the cladistic analysis by Dahlgren and Pleijel (Paper I) and information on the preliminary position within Chrysopetalidae is therefore not available. The result from the cladistic analysis on dysponetid taxa presented below is not conclusive on the position of *V. zaikai*.

Dealing with characters which could link *Wiwaxia corrugata* to the Chrysopetalidae and other phyllodocid taxa, Butterfield (1990) noted the uniform presence of stylet-shaped jaws in chrysopetalids, as opposed to the two, or possibly three, denticulated plates associated with *Wiwaxia corrugata* (Conway Morris 1985). In discussing the position of *Wiwaxia* and contrasting old views with new information from annelid phylogeny and chrysopetalid diversity, Dahlgren et al. (Paper VI) draw attention to the aberrant shape of the jaws in *Vigtorniella*.

## METHODS

Phylogeny estimates, including those in this thesis, are based on the premise that organisms share characters due to common descent. Characters that are similar are initially considered to be homologous. Characters, however, can have the same properties and share similarities without being connected through common descent. Similar characters may appear several

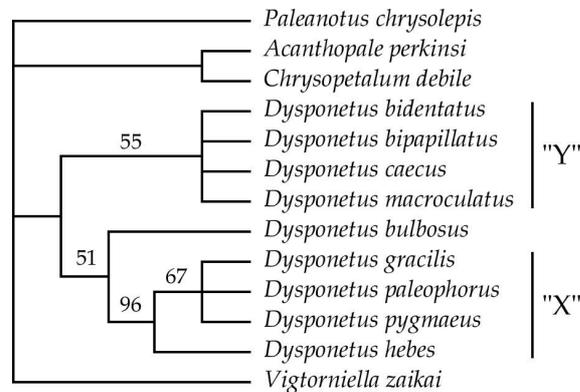
times independently in different groups, for example wings. Such non-homologous characters are called homoplasies. We have no *a priori* means to tell the nature of a character, but a theoretical framework for analyses was introduced by Hennig (1950, 1966) and further developed by e.g., Farris (1970) and Patterson (1982), where maximum congruence between all observed characters represented the criterion to determine homology. Consider, for example, the relationships between five taxa. These relationships can be illustrated by 15 rooted, fully bifurcating, trees. The most parsimonious explanation, given a set of characters, is depicted by the tree that requires the smallest number of homoplasies. With the development of more efficient search algorithms and faster desktop computers, it has now become possible to analyze large data sets with hundreds of terminal taxa (e.g., Farris et al. 1996). When dealing with morphological characters, the main problem with this approach relates to character coding, or, in other words, how homology statements actually should be formulated. A recent discussion can be found in Pleijel (1995), and an example of a consistent application of one coding approach (absent/present) is provided in paper IV.

Other disagreements appear in analyses of DNA sequence data. Sequence data are arguably not always independent from each other, and may thus make a parsimony analysis biased (e.g., paired positions in the RNA stem region). Common practise is to incorporate mutation models into the analyses (e.g., third positions in protein coding genes evolving at a higher rate than the first and second positions; Swofford et al. 1996). These type of considerations are accommodated for in e.g., maximum likelihood analyses (e.g., Felsenstein 1973) that calculate likelihood scores for possible trees given a specific set of characters. The tree with the highest likelihood is the best explanation for the data and incorporated assumptions. Because appropriate models for morphological character evolution have not been developed, this thesis uses parsimony, rather than likelihood analyses, throughout.

**Table 2.** Summary of characters and character states used in the dysponetid analysis below. Numerals correspond to characters, and numerals within parentheses to character states in Table 3.

- 
1. Shape of median antenna: sphaerical (0); elongated (1).
  2. Position of median antenna: anterior (0); dorsal (1).
  3. Shape of lateral antennae: sphaerical (0); elongated (1).
  4. Shape of palps: sphaerical (0); elongated (1).
  5. Shape of prostomium: round (0); rectangular (1).
  6. Eyes: absent (0); one pair (1); two pairs (2)
  7. Mouth appendage: absent (0); single papilla (1); double papillae (2); puriform projection (3).
  8. Caruncle: absent (0); present (1).
  9. Ventral cirri segment 1: absent (0); present (1).
  10. Ventral cirri segment 2: absent (0); present (1).
  11. Ventral cirri segment 3: absent (0); present (1).
  12. Notochaetae on segment 1: absent (0); present (1).
  13. Neurochaetae on segment 2: absent (0); present (1).
  14. Notopodia: reduced (0); pronounced (1).
  15. Shape of mainfan notochaetae: spines (0); paleae (1).
  16. Long spinigerous neurochaetae: absent (0); present (1).
  17. Paired pygidial cirri: absent (0); present (1).
  18. Single pygidial projection: absent (0); present (1).
-

Topological robustness (i.e., support of nodes) was assessed using bootstrap methods (Felsenstein 1985), jackknife trees (e.g., Farris et al. 1996), and Bremer support (e.g., Bremer 1988). Although the former two methods, by resampling characters within the original data set, are an attempt to statistically measure congruence between characters, Bremer support (or decay index) is a “non-statistical” method conveying only the number of extra steps it takes for a clade to collapse.



**Figure 2.** Unrooted strict consensus tree computed from three original trees (36 steps, CI= 0.58). Numbers correspond to bootstrap values (100 replicates, PAUP factory settings).

## PHYLOGENY

### Dysponetus

The term “dysponetid chrysopetalids”, including *Acanthopale*, *Dysponetus*, and *Vigtorniella*, but not e.g., *Chrysopetalum*, does not represent a monophyletic taxon (Paper I). Problems regarding the monophyly of the taxon *Dysponetus* based on presence of spinous notochaetae only (e.g., Augener 1913), are also evident from the summary given above (e.g., spinouse notochaetae absent for *Dysponetus gracilis*). In paper II, five characters was recognized as delineating the taxon *Dysponetus*; 1) circular notochaetae, 2) mouth appendage, 3) single pygidial projection, and 5) accessory simple neurochaetae. In addition to the problems with the shape of the notochaeta (1), dealt with above, the mouth appendage (2) is absent in *Dysponetus gracilis* but present as a flap also in many paleate chrysopetalids. Accessory neurochaeta (5) have later been found occurring also in paleate chrysopetalids (e.g., *Chrysopetalum debile* -pers. obs., and *Arichlidon* -Watson Russell 1998). Character 3 refers to the presence of a single pygidial projection only, as opposed to the presence of paired pygidial appendages with or without a single projection. It appears that this is the only synapomorphy (although weak in being based on a presumed reversal) remaining for *Dysponetus*. The character was in paper I erroneously scored as absent also for the paleate taxon *Strepternos didymopyton*.

A few observations indicate a subdivision of *Dysponetus* in two clades. A taxon X (containing *D. gracilis*, *D. hebes*, *D. paleophorus* and *D. pygmaeus*) could tentatively be recognized by the characters short and rounded palps, antennae and tentacular cirri, as opposed to elongated and fusiform or digitiform for Y (containing *D. bidentatus*, *D. bipapillata*, *D. caecus*, *D. macroculatus*); single mouth appendage in Y as opposed to absent or double ones in X (stated as unknown for *D. gracilis* in paper II but is absent;

Aguirrezabalaga et al. 1999). X contains taxa with a round prostomium whereas taxa in Y have a rectangular prostomium. The single pair of tentacular cirri in segment 1 (Fig. 1) appears to be peristomial in X (see Imajima and Hartman 1964) but of segmental origin in Y, where a ventral pair of tentacular cirri is also present (but see discussion on peristomial/segmental anterior segments in paper IV). The questionable taxon *D. bulbosus* is aberrant in that it possesses notochaetae (lacking in chrysopetalids except for *Vigtorniella*) and lacks ventral cirri on segment 1, and has short (but fusiform) antennae, elongated palps, and a rounded prostomium.

A preliminary cladistic analysis of dysponetids, based on the characters discussed above and additional characters also used in paper I, is presented herein. One paleate taxon (*Paleanotus chrysolepis*) other than *Chrysopetalum debile* was included to allow for the possibility of a close relationship between the latter and *Acanthopale perkisi* as indicated in the analysis by Dahlgren and Pleijel (Paper I). The 18 characters are summarized in Table 2, and the character states for included taxa are provided in Table 3. The three most parsimonious trees (not shown) are unrooted since no information on pleisiomorphic states for Chrysopetalidae is available. The analysis supports a clade X but evidence for a clade Y is weaker as indicated by the low bootstrap values (Fig. 2). Moreover, the monophyly of the taxon *Dysponetus* is corroborated by two unambiguous changes, both associated with the pygidium and discussed above.

**Table 3.** Character matrix. Question mark denotes missing value, a dash that the character is missing. Numbers correspond to characters in Table 2.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Chrysopetalum debile</i>	1	1	1	1	1	2	3	1	1	1	1	0	0	1	1	0	1	0
<i>Acanthopale perkisi</i>	1	0	1	1	1	2	3	1	1	1	1	0	1	1	0	0	1	1
<i>Dysponetus bidentatus</i>	1	1	1	1	1	2	1	0	1	0	0	0	0	1	0	0	0	1
<i>Dysponetus bipapillatus</i>	1	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	1
<i>Dysponetus bulbosus</i>	0	0	1	1	0	2	?	0	0	?	1	1	1	1	0	0	0	1
<i>Dysponetus caecus</i>	1	0	1	1	1	0	1	0	1	1	1	0	0	1	0	0	0	1
<i>Dysponetus gracilis</i>	0	1	0	0	0	0	2	0	0	1	1	0	1	0	1	1	0	1
<i>Dysponetus hebes</i>	0	0	0	0	0	1	2	0	0	?	?	0	1	0	0	0	0	1
<i>Dysponetus macroculatus</i>	1	0	1	1	1	2	1	?	1	1	0	0	0	1	0	0	0	1
<i>Dysponetus paleophorus</i>	0	1	0	0	0	0	2	0	0	0	1	0	1	0	0	1	0	1
<i>Dysponetus pygmaeus</i>	0	1	0	0	0	0	2	0	0	0	1	0	1	0	0	0	0	1
<i>Paleanotus chrysolepis</i>	1	0	1	1	1	2	0	0	1	0	1	0	1	1	1	0	1	0
<i>Vigtorniella zaikai</i>	-	-	1	1	0	0	0	0	1	1	1	1	1	0	0	0	1	0

### *Chrysopetalidae and Allies*

As noted above, not much is known about relationships within the chrysopetalids or their relationship to other annelid taxa. Watson Russell (1998), however, stated that *Dysponetus* probably constitutes neotenous forms retaining larval characters of other chrysopetalid genera. The only analysis spanning a variety of chrysopetalid taxa (Paper I) was based on morphological data and included the type species for chrysopetalid genera, *Dysponetus caecus*, and the outgroup taxa Aphroditidae, Polynoidae and Hesionidae. That study was not designed to analyze global relationship within Chrysopetalidae (see above) but, nevertheless, provided preliminary hypotheses and hinted towards some areas of interest; 1) the monophyly of paleate taxa was not supported, and 2) the monophyly of Chrysopetalidae was questioned. 1) This statement was indicated by that the clade containing *Chrysopetalum debile* fell outside the rest of the paleate chrysopetalids in some of the original trees (Paper I; fig. 1a). It may be argued, however, that this result is depending on uncertain rooting issues of the

analysis. Interestingly, *Dysponetus gracilis* have paleae instead of spines but appear within the dysponetids and well delineated from paleate chrysopetalids in the new analyses of dysponetids presented above. 2) A paraphyletic Chrysopetalidae (without inclusion of one or more hesionid taxa) is suggested by the analysis in paper I. This problem (see below) was, among other issues, targeted in later analyses (see below) based on morphology (Paper IV) and DNA sequence data (Paper V). Hypotheses including progenesis (“neoteny”) as an evolutionary process (Watson Russell 1998) can probably not be tested with morphological data without facing the risk of circularity. An analysis of chrysopetalid taxa, similar to the one in paper I but based on DNA sequence data, may, however, prove useful in resolving this issue.

It is generally agreed that chrysopetalids are parts of the Phyllodocida in the more inclusive taxon Aciculata (e.g., Rouse and Fauchald 1997). Two analyses were carried out in paper IV in order to address the problems of the delineation between Hesionidae and Chrysopetalidae, among other issues regarding inclusiveness of the Hesionidae. The first analysis (Phyllodocida) was designed to elucidate relationships within Phyllodocida, the result of which served as the basis for choice of terminal taxa in a study on the less inclusive Nereidiformia. The later analysis (Nereidiformia) was based on morphological characters from representatives of Pisionidae (treated as outgroup), Chrysopetalidae, Hesionidae, Nereididae, Pilargidae, and Syllidae. Data was collected in an exemplar approach in which individuals of each terminal taxon were chosen from one population only. The exemplar approach limited problems with assuming monophyletic terminal taxa in this analysis as well as in successive ones based on DNA sequence data from the same terminals (i.e., Paper V). The resulting trees indicated that the two chrysopetalid taxa included (*Chrysopetalum debile* and *Dysponetus caecus*) comprised a well delineated clade (Paper IV: Fig. 2), indicated by a Bremer support of 6. A sister relationship between the chrysopetalids and the hesionids (*sensu stricto*, e.g., Paper IV) was suggested by both of the two most parsimonious trees, but the Bremer support value for that clade was low (1) and it was collapsed in jackknife trees with a threshold of 50% support. No evidence, however, was found indicating that the hesionids and the chrysopetalids are nested relative to each other.

In an attempt to further examine the Nereidiformia topologies (Paper V), DNA sequence data from part of the mitochondrial protein coding CO1 gene were collected from the same populations as was used in paper IV. These data were analyzed alone and by combining them to Dahlgren and Pleijel’s (Paper IV) morphological dataset. The syllid and two of the hesionids were not sequenced due to lack of tissue or repeated negative PCR. A fragment of the CO1 gene was chosen because it has been proven useful in phylogenetic analyses of other annelid groups (Black *et al.* 1997; Kojima *et al.* 1997; Siddall and Burresson 1998; Christensen and Theisen 1998; Nylander *et al.* 1999). The aligned sequences resulted in 271 parsimony informative characters. A parsimony analysis of the partitioned dataset (sequences only) gave a single most parsimonious tree. A low retention index (RI=0.278) and low bootstrap support for all but the clade comprising the two hesionids, however, indicated a high level of homoplasy in this dataset. In the combined analyses (Paper V), which gave one tree (RI=0.333), the bootstrap support was generally higher. Of particular interest, the two chrysopetalids are sister to the nereidid. This alternative, previously suggested by Perkins (1985) and Glasby (1993), contrasts with the sister-group relation between hesionids and chrysopetalids found in paper IV. However, more characters and a less restricted taxon choice are needed to place a high level of confidence on this finding. In conclusion, the sister to the chrysopetalids is most likely a clade including the hesionids or the nereidids.

### *Annelida and Fossils*

The apparent burst of evolution in the Cambrian has been a major issue for debate during the last two decades (e.g., Brasier 1979; Whittington 1981; Briggs and Fortey 1989; Conway Morris 1989; Gould 1989; Gould 1991; Wills et al. 1994; Fortey et al. 1996; Abouheif et al. 1998; Balavoine & Adoutte 1998; Cooper & Fortey 1998; Lynch 1999; Valentine et al. 1999; Conway Morris 2000). The idea of an evolutionary leap originated in the lack of fossils older than Cambrian (noted by e.g., Darwin 1859) and was later emphasized by the extraordinary diversity found in Cambrian *lagerstetten* such as Burgess Shale, Canada and Shengjiang, China. The view of a major evolutionary event of some sort, however, is based on lack of evidence: no metazoan fossils have been found older than Vendian (excepting a few and sometimes disputable trace fossils; see e.g., Seilacher et al. 1998). Furthermore, recent efforts in molecular systematics point to a metazoan origin that is considerable earlier (reviewed in Cooper and Fortey 1998; Knoll and Carroll 1999; Smith 1999). Four explanations for this discrepancy could be considered (reviewed in part by Smith 1999): 1) molecular clock estimates are wrong, 2) there are major gaps in the fossil record, 3) both the fossil record and the molecular clock estimates are accurate, and 4) both the fossil record and the molecular clock estimates are wrong. Number 3 (e.g., Cohen and Massay 1983; Boaden 1989; Davidson et al. 1995; Fortey et al. 1996; Cooper and Fortey 1998; Parker 1998; but see Balavoine and Adoutte 1998) holds that Precambrian metazoans were small forms unlikely to leave a fossil record, and that some environmental or ecological event simultaneously in all diverged lineages triggered further development into larger forms (see also e.g., Fortey et al. 1996 for a cladistic analysis suggesting Precambrian radiation of arthropods). For more references on cladogenes in small-sized Precambrian animals, see Runnegar (1983) and Valentine and Erwin (1987).

The recognition of the possibility that Recent crown groups such as the annelids were old and diversified already in the Cambrian, opens a new field of possible explanations to some observed patterns. The enigmatic Cambrian fossil *Wiwaxia corrugata* (Matthew, 1899) was first believed to belong to the annelids (Walcott 1911). Conway Morris and co-workers have in a series of papers, however, proposed a position basal to molluscs (e.g., Conway Morris 1985), or at a branch leading to the annelids and possibly close to the chrysopetalids (e.g., Conway Morris & Peel 1995). Butterfield (1990, 1994) challenged the former hypothesis by detailed studies of isolated wiwaxiid sclerites, indicating a close relationship between *Wiwaxia* and Recent Phyllodocida (Polychaeta) such as the chrysopetalids. Further evidence for the latter hypothesis, e.g., regarding new information on some chrysopetalid features, including variation in jaw morphology from the common stylet-shape (Kiseleva 1992), and presence of a previously unknown chaetal type similar to the wiwaxiid spines (Paper III), are discussed in paper VI. The hypothesis that *Wiwaxia* is an annelid close to the Phyllodocida is further examined (Paper VI) and related to recent advances in the phylogeny of that group (e.g., McHugh 1997; Rouse & Fauchald 1997; Westheide 1997; Westheide et al. 1999). If the Phyllodocida is basal among the annelids, the conclusion may be that *Wiwaxia*, *Canadia* and Phyllodocida, form a grade. Within that grade, the sister to all other annelids should be found. Alternatively, if the Phyllodocida represent a clade within the polychaetes, then *Wiwaxia* and *Canadia* are derived annelids. Both hypotheses are intriguing, but the incomplete fossil record and preliminary nature of our current knowledge in annelid phylogeny prevent further development of more concise conclusions at this time. Rouse and Fauchald (1997) noted problems with homology statements in morphological analyses of annelids at that (global) level of inclusiveness, and additional efforts, preferably using molecular markers, may be important to the understanding of wiwaxiid relationships. Further, it may be suggested that a detailed examination of wiwaxiid spines, similar to the ones conducted by Butterfield (1990,1994) on sclerites, are of need for a possible rejection of the homology hypothesis concerning similar structures in chrysopetalids made in paper III.

## SUMMARY

Chrysopetalidae is a small group of worms, which the world possibly would do just as well without. Interesting, however, is what these organisms convey about evolutionary history. To help in the extraction of such information, I have presented new knowledge on the diversity within the group. This was achieved by describing new taxa and reconsidering previously described but poorly known forms. Included is also a summary of the literature of the chrysopetalids with emphasis on the dysponetid forms. The thesis presents five phylogenetic analyses of various inclusiveness of the group Chrysopetalidae and related polychaete taxa. They include the first analysis of major groups recognized within the taxon Chrysopetalidae, the first analysis of the dysponetid forms, and the first study focusing on phyllodocid taxa employing DNA sequence data.

The results provide means to further elucidate problems in the relationships within the Chrysopetalidae as well as between that taxon and other annelids. Although a few answers were found, many additional and exciting questions were raised. Almost by accident, I happened to pick a group that apparently had close relatives in Cambrian seas. Good fossil data of that age are rare and detailed information of the morphology and phylogeny on Recent relatives is important for further understanding of early metazoan radiation. Moreover, if *Wiwaxia* is indeed a close relative to the chrysopetalids, as some of the presented data suggests, it may have far reaching implications on future considerations of annelid phylogeny.

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The list of names I am looking at in this moment is long and I don't know what would be the best way to order them. One way, however, is chronological, by which I also avoid the problem of ranking. My late mother, **Mona Dahlgren**, and my father, **Gunnar Dahlgren**, are gratefully thanked for bringing me up in a “do easy” atmosphere, probably inherited from Kinnared in Västergötland, where things like slaughtering a cow, build a house or a piece of furniture, were made looking easy. Among a number of photographers and Fältbiologer in Ulricehamn, such as **Göran Fiås** and **Jan Töve**, **Jens Rydell**, also working as a biology teacher at my school, was also responsible for my interest in biology. **Per Westman** was early very influential in sharing with me his stories during months at isolated islands. Later he also proved that it is possible to juggle family life and thesis writing. I am sure he made a better job than I did. Thanks **Elke** and **Linnéa**, my family, for bearing with me all the times when I was physically, or mentally, in other places.

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## REFERENCES

- Abouheif, E., Zardoya, R. & Meyer, A. (1998). Limitations of metazoan 18S rRNA sequence data: Implications for reconstructing a phylogeny of the animal kingdom and inferring the reality of the Cambrian explosion. *J Mol Evol* **47**, 394-405.
- Aguirrezabalaga, F., San Martin, G., Petersen, M. E. & Ceberio, A. (1999). Presence of *Dysponetus gracilis* Hartman, 1965 (Polychaeta, Chrysopetalidae) in European coasts, Bay of Biscay. *Bol R Soc Esp Hist Nat (Sec Biol)* **95**, 21-25.
- Annenkova, N P. (1935). Über *Dysponetus pygmeus* Levinsen und *Euzonus arcticus* Grube. *Comptes Rendus Acad Sci USSR* **3**, 233-236.
- Augener, H. (1912). Beitrag zur Kenntnis verschiedener Anneliden un Bemerkungen über die nordischen *Nephtys*-Arten und deren epitoken Formen. *Archiv für Naturgeschichte, Berlin* **78**, 162-212.
- Augener, H. (1913). Polychaeta I. Errantia. In W. Michaelsen & P. Hartmeyer (eds.). *Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905*, **4**, 65-304. Gustav Fischer, Jena.
- Augener, H. (1925). Über westindische und einige andere Polychaeten-Typen von Grube (Oersted), Krøyer, Mörch und Schmarda. *Publ Univ zool Mus., København* **39**, 1-47.
- Augener, H. (1928). Ergänzung zu den Polychaeten von Spitzbergen. *Fauna Arctica, Jena*, **5**, 647-834.
- Balavoine, G. & Adoutte, A. (1998). One or three Cambrian radiations? *Science* **280**, 397-398.
- Black, M. B., Halanych, K. M., Maas, P. A. Y., Hoeh, W. R., Hashimoto, J., Desbruyeres, D., Lutz, R. A. & Vrijenhoek, R. C. (1997). Molecular systematics of vestimentiferan tubeworms from hydrothermal vents and cold-water seeps. *Mar Biol* **130**, 141-149.
- Boaden, P. J. S. (1989). Meiofauna and the origin of the Metazoa. *Zool J Linn Soc* **96**: 217-227.
- Brasier, M. D. (1979). The Cambrian radiation event. In M.R. House (ed). *The origin of major invertebrate groups*. Pp. 103-160. The Systematics Association, Special Volume 12. The Systematics Association.
- Bremer, K. (1988). The limits of amino acid sequence data in angiosperm phylogenetic reconstructions. *Evolution* **42**, 795-803.
- Briggs, D. E. G. & Fortey, R. A. (1989). The early radiation and relationships of the major Arthropod groups. *Science* **246**, 241-243.
- Butterfield, N. J. (1990). A reassessment of the enigmatic Burgess Shale (British Columbia, Canada) fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa* Walcott. *Paleobiology* **16**, 287-303.
- Butterfield, N. J. (1994). Burgess Shale-type fossils from Lower Cambrian shallow-shelf sequence in northwestern Canada. *Nature* **369**, 477-479.
- Christensen, B. & Theisen, B. F. (1998). Phylogenetic status of the family Naididae (Oligochaeta, Annelida) as inferred from DNA analysis. *J Zool Syst Evol Res* **36**, 169-172.
- Claparède, E. (1864). Glanures zootomiques parmi les Annélides de Port-Vendres (Pyrenées Orientales). *Mém Soc Phys Hist nat Genève* **17**, 463-600.
- Cohen, J. & Massey, B. D. (1983). Larvae and the origins of major phyla. *Zool J Linn Soc* **19**, 321-328.
- Conway Morris, S. (1982). *Wiwaxia corrugata* (Matthew), a problematic Middle Cambrian animal from the Burgess Shale of British Columbia. *Proc 3rd North Am Paleont Conv Montreal 1982* **1**, 93-98.
- Conway Morris, S. (1985). The Middle Cambrian metazoan *Wiwaxia corrugata* (Mathew) from the Burgess Shale and *Ogygopsis* Shale, British Columbia, Canada. *Phil Trans Roy Soc Lond, (Ser B)* **307**, 507-586.

- Conway Morris, S. (1989). Burgess Shale faunas and the Cambrian explosion. *Science* **240**, 339-346.
- Conway Morris, S. (2000). Evolution: Bringing molecules into the fold. *Cell* **100**, 1-11.
- Conway Morris, S. & Peel, J. S. (1995). Articulated halkieriids from the Lower Cambrian of North Greenland and their role in early protostome evolution. *Phil Trans Roy Soc Lond, (Ser B)* **347**, 305-358.
- Cooper, A. & Fortey, R. (1998). Evolutionary explosions and the phylogenetic fuse. *TREE* **13**, 151-156.
- Dahlgren, T. G. (1996). Two new species of *Dysponetus* (Polychaeta: Chrysopetalidae) from Italy and Papua New Guinea. *Proc Biol Soc Wash* **109**, 575-585.
- Dahlgren, T. G. & Pleijel, F. (1995). On the generic allocation of *Chrysopetalum caecum* (Polychaeta: Chrysopetalidae). *Mitt Hamb zool Mus Inst* **92**, 159-173.
- Darwin, C. (1859). On the origin of species by means of natural selection. Murray, London.
- Davidson, E.H., Peterson, K.J., & Cameron, R.A. (1995). Origin of bilaterian bodyplans: Evolution of developmental regulatory mechanisms. *Science* **270**, 1319-1325.
- Day, J. H. (1954). The Polychaeta of Tristan da Cunha. *Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937-1938*. **29**, 1-35. Det Norske Videnskaps-Akademi i Oslo.
- Day, J. H. (1967). *A monograph on the Polychaeta of southern Africa. Part 1. Errantia*. British Museum (Natural History), London.
- Ehlers, E. (1864). *Die Borstenwürmer, nach systematischen und anatomischen Untersuchungen dargestellt*. Wilhelm Engelmann, Leipzig.
- Ehlers, E. (1913). Die Polychaeten-Sammlungen der deutschen Südpolar- Expedition 1901-1903. *Deutsche Südpolarexp* **13**, 397-598.
- Fage, L. (1906). Recherches sur les organes segmentaires des Annélides Polychètes. *Ann Sci nat (Ser 9)*. **3**, 261-410.
- Farris, J. S. (1970). Methods for computing Wagner trees. *Syst Zool* **34**, 21-34.
- Farris, J. S., Albert, V. A., Källersjö, M., Lipscomb, D. & Kluge, A. G. (1996). Parsimony jackknifing outperforms neighbor-joining. *Cladistics* **12**, 99-124.
- Fauchald, K. (1977a). The polychaete worms. Definitions and keys to the orders, families and genera. *Nat Hist Mus Los Angeles County Sci Ser* **28**, 1-188.
- Fauchald, K. (1977b). Polychaetes from intertidal areas in Panama, with a review of previous shallow-water records. *Smithsonian Contr Zool* **221**, 1-81.
- Fauvel, P. (1923). *Polychètes errantes*. Faune de France, 5, Librairie de la Faculte des Sciences, Paris.
- Fauvel, P. (1932). Annelida Polychaeta of the Indian Museum, Calcutta. *Mem Indian Mus* **12**, 1-262.
- Felsenstein, J. (1973). Maximum likelihood and minimum steps methods for estimating evolutionary trees from data on discrete characters. *Syst Zool* **22**, 240-249.
- Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783-791.
- Fortey, R. A., Briggs, D. E. G. & Wills, M. A. (1996). The Cambrian evolutionary 'explosion': decoupling cladogenesis from morphological disparity. *Biol J Linn Soc* **57**, 13-33.
- Gallardo, V. A. (1967). Polychaeta from the Bay of Nha Trang, South Viet Nam. *Naga Rep* **4**, 35-276.
- Gathof, J. M. (1984). Family Chrysopetalidae Ehlers, 1864. In J.M. Uebelacker & P.G. Johnson (eds.). *Taxonomic guide to the polychaetes of the northern Gulf of Mexico. Prepared for U.S. Department of the Interior Minerals Management Service.*, Vol. 3, Chapter 26, pp. 26-1 to 26-10. Barry A. Vittor & Associates, Mobile, Alabama.
- Gibbs, P. E. (1971). The polychaete fauna of the Solomon Islands. *Bull Br Mus nat Hist (Zool)* **21**, 101-211.

- Glasby, C. J. (1993). Family revision and cladistic analysis of the Nereidoidea (Polychaeta: Phyllodoceida). *Invertebr Taxon* **7**, 1551-1573.
- Goodrich, E. S. (1945). The study of nephridia and genital ducts since 1895. *Q J microsc Sci* **86**, 113-393.
- Gould, S. J. (1989). *Wonderful Life*. W. W. Norton, New York.
- Gould, S.J. (1991). The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analyses: why we must strive to quantify morphospace. *Paleobiol* **17**, 411-423.
- Gravier, C. (1902). Contribution à l'étude des annélides polychètes de la Mer Rouge. *Nouv Arch Mus Paris, (ser. 4)* **3**, 147-268.
- Gravier, C. (1909). Annélides polychètes recueillis a Payta (Pérou) par M. le Dr. Rivet, membre de la Mission géodésique de l'Équateur. *Archs Zool Exp Gén, Paris, ser.4.* **10**, 617-659.
- Grube, A. E. (1855). Beschreibung neuer oder wenig bekannter Anneliden. *Arch Naturgesch* **21**, 81-136.
- Grube, A. E. (1856). Annulata Örstediana. Enumeratio Annulorum, quae in itinere per Indiam occidentalem et Americam centralem annis 1845-1848 suscepto legit cl. A. S. Örsted, adjectis speciebus nonnullis a cl. H. Kröyero in itinere ad American meridionalem collectis. Pt. 1. *Vidensk Meddr naturh Foren København.* **Vol for 1856**, 44-62.
- Grube, A. E. (1868). Über neue Anneliden. *Schles Gesells Breslau, Jahresber* **45**, 50-51.
- Haaland, B. & Schram, T. A. (1982). Larval development and metamorphosis of *Gyptis rosea* (Malm) (Hesionidae, Polychaeta). *Sarsia* **67**, 107-118.
- Haaland, B. & Schram, T. A. (1983). Larval development and metamorphosis of *Ophiodromus flexuosus* (Delle Chiaje) (Hesionidae, Polychaeta). *Sarsia* **68**, 85-96.
- Hartman, O. (1942). A review of the types of polychaetous annelids at the Peabody Museum of Natural History, Yale University. *Bulletin Bingham Ocean Coll, Yale University* **8**, 1-98.
- Hartman, O. (1945). The marine annelids of North Carolina. *Bull Duke Univ mar Stn* **2**, 1-51 + Index.
- Hartman, O. (1959). Catalogue of the polychaetous Annelids of the world. Part 1. *Occ Pap Allan Hancock Fdn* **23**, 1-353.
- Hartman, O. (1961). Polychaetous annelids from California. *Allan Hancock Pacific Exped* **25**, 1-226.
- Hartman, O. (1965). Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Occ Pap Allan Hancock Fdn* **28**, 1-378.
- Hartman, O. (1968). *Atlas of the errantiate polychaetous annelids from California*, Allan Hancock Foundation, University of Southern California, Los Angeles.
- Hartman, O. & Fauchald, K. (1971). Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic Areas. Part II. *Allan Hancock Monogr Mar Biol* **6**, 1-327.
- Hartmann-Schröder, G. (1959). Zur Ökologie der Polychaeten des Mangrove-Estero-Gebietes von El Salvador. *Beitr neotrop Fauna* **1**, 69-183.
- Hartmann-Schröder, G. (1960). Polychaeten aus dem Roten Meer. *Kieler Meeresforsch* **16**, 69-125.
- Hartmann-Schröder, G. (1974a). Zur Kenntniss des Eulitorals der afrikanischen Westküste zwischen Angola und Kap der Guten Hoffnung und der afrikanischen Ostküste von Südafrika und Mocambique unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil II. Die Polychaeten des Untersuchungsgebietes. *Mitt hamb zool Mus Inst* **69**, 95-228.
- Hartmann-Schröder, G. (1974b). Polychaeten von Expeditionen der "Anton Dohrn" in Nordsee und Skagerrak. *Veröff Inst Meeresforsch Bremerh* **14**, 169-274.

- Hartmann-Schröder, G. (1980). Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 4. Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Port Samson im Norden und Exmouth im Süden). *Mitt hamb zool Mus Inst* **77**, 41-110.
- Hartmann-Schröder, G. (1981). Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 6. Die Polychaeten der tropisch-subtropisch Westküste Australiens (zwischen Exmouth im Norden und Cervantes im Süden). *Mitt hamb zool Mus Inst* **78**, 19-96.
- Hartmann-Schröder, G. (1982). Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 8. Die Polychaeten der subtropisch-antiborealen Westküste Australiens (zwischen Cervantes im Norden und Cape Naturaliste im Süden). *Mitt hamb zool Mus Inst* **79**, 51-118.
- Hartmann-Schröder, G. (1986). Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 12. Die Polychaeten der antiborealen Südküste Australiens (zwischen Wallaroo im Westen und Port MacDonnell im Osten). *Mitt hamb zool Mus Inst* **83**, 31-70.
- Hartmann-Schröder, G. (1993). Die Polychaeten der "Polarstern"-Reise ANT X / Ib zur Antarktischen Halbinsel und Isla de los Estados (Feuerland, Argentinien) 1991. *Mitt hamb zool Mus Inst* **90**, 127-150.
- Hennig, W. (1950). *Grundzüge einer Theorie der phylogenetischen Systematic*. Duetscher Zentralverlag, Berlin.
- Hennig, W. (1966). *Phylogenetic systematics*. Univ. Illinois Press, Urbana.
- Horst, R. (1917). Polychaeta Errantia of the Siboga-Expedition, Part 2: Aphroditidae and Chrysopetalidae. *Siboga Exped* **24**, 1-140.
- Imajima, M. & Hartman, O. (1964). The polychaetous annelids of Japan. Part 1. *Occ Pap Allan Hancock Fdn* **26**, 1-166.
- Jamieson, B. G. M. & Rouse, G. W. (1989). The spermatozoa of the Polychaeta (Annelida): An ultrastructural review. *Biol Rev Cambridge* **64**, 93-157.
- Johnson, H. P. (1897). A preliminary account of the marine annelids of the Pacific coast, with descriptions of new species. *Proc Calif Acad Sci (ser 3)* **1**, 153-198.
- Katzmann, W., Laubier, L. & Ramos, J. (1974). Une nouvelle espèce Méditerranéenne de Chrysopetalidae (Annelides Polychètes). *Annln naturh Mus, Wien* **78**, 313-317.
- Kinberg, J. G. H. (1858). Part 3: Annulater. *Kongliga Svenska Fregatten Eugénies Resa omkring jorden under befäl af C.A. Virgin åren 1851-1853. Vetenskapliga Iakttagelser*, 1-32. Almquist & Wicksells, Uppsala.
- Kirkegaard, J. B. (1992). Havborsteorme 1, Errantia. *Danm. Fauna* **83**. Dansk Naturhistorisk Forening, København.
- Kiseleva, M. I., 1959. Distribution of larvae of polychaete worms in the plankton of the Black Sea. *Trudy Sevastopol Biol Stantsii* **12**, 160 - 167.
- Kiseleva, M. I. (1992). New genus and species of the family Chrysopetalidae (Polychaeta) from the Black Sea. *Zool Zh* **71**, 128-132.
- Kiseleva, M. I. (1996). On a new name of the genus *Victoriella* (Polychaeta, Chrysopetalidae). *Zool Zh* **75**, 1092.
- Knoll, A. H. & Carroll, S. B. (1999). Early animal evolution: emerging views from comparative biology and geology. *Science* **284**, 2129-2137.
- Kojima, S., Segawa, R., Hashimoto, J. & Ohta, S. (1997). Molecular phylogeny of vestimentiferans collected around Japan, revealed by the nucleotide sequences of mitochondrial DNA. *Mar Biol* **127**, 507-513.
- Lamarck, Jean-B. de (1802). La nouvelle classes des Annélides. *Bull Mus Hist Nat, Paris An X: Disc. d'ouverture*, 27 Floréal.

- Lamarck, Jean-B. de (1818). *Histoire naturelle des Animaux sans Vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une Introduction offrant la Détermination des caractères essentiels de l'Animal, sa distinction du végétal et des autres corps naturels, enfin, l'Exposition des Principes fondamentaux de la Zoologie*, Vol. 5. Déterville & Verdière, Paris.
- Langerhans, P. (1880). Die Wurmfauna Madeiras. II. *Z wiss Zool* **33**, 267-316.
- Laubier, L. (1964). Contribution a la faunistique du coralligène. VI. Présence de *Chrysopetalum caecum* Langerhans dans l'endofauna coralligène. *Vie Milieu* **15**, 125-138.
- Laubier, L. (1968). Contribution a la faunistique du coralligène. VII. A propos de quelques annélides polychètes rares ou nouvelles (Chrysopetalidae, Syllidae et Spionidae). *Annl Inst océanogr, Monaco* **46**, 80-107.
- Levinsen, G. M. R. (1879). Om to nye slaegter af arctiske chaetopode Annelider. *Vidensk Meddr dansk naturh Foren København*. **1879-80**, 9-18.
- Levinsen, G. M. R. (1883). Systematisk-geografisk Oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. Første Halvdel. *Vidensk Meddr dansk naturh Foren København* **1882**, 160-250.
- Lynch, M. (1999). The age and relationships of the major animal phyla. *Evolution* **53**, 319-325.
- Matthew, G. F. (1899). Studies on Cambrian faunas. 3. Upper Cambrian fauna of Mount Stephen, British Columbia. The trilobites and worms. *Trans R Soc Can* **5**, 39-66.
- McHugh, D. (1997). Molecular evidence that echiurans and pogonophorans are derived annelids. *Proc Natl Acad Sci, USA* **94**, 8006-8009.
- Mileikovsky, S. A. (1962). On the morphology and systematics of polychaets belonging to the family Chrysopetalidae E. Ehlers, 1864 (genera *Palaenotus* L. Schmarda, 1861, *Heteropale* H.P. Johnson 1897 and others). *Zool Zh* **41**, 648-659.
- Mileikovsky, S. A. (1977). On the systematic interrelationships within the Polychaeta and Annelida. -An attempt to create an integrated system based on their larval morphology. In D.J. Reish & K. Fauchald (eds.). *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman*. Pp. 503-524. The Allan Hancock Foundation, University of Southern California, Los Angeles.
- Morgado, E. H. & Amaral, A. C. (1981). Anelídeos poliquetos associados a um briozoário. II. Palmyridae. *Bol Inst oceanogr, Sao Paulo* **30**, 87-89.
- Murina, V. V. (1986). On finding of pelagic polychaete larvae in the Black Sea. *Zool Zh* **65**, 1575-1578.
- Murina, V. V. (1997). Pelagic larvae of the Black Sea Polychaeta. *Bull Mar Sci* **60**, 427-432.
- Nylander, J. A. A., Erséus, C. & Källersjö, M. (1999). A test of monophyly of the gutless Phalloporinae (Oligochaeta, Tubificidae) and the use of a 573 bp region of the mitochondrial cytochrome oxidase I gene in analysis of annelid phylogeny. *Zool Scr* **28**, 467-482.
- Orensanz, J. M. (1972). Los anelidos poliquetos de la provincia biogeografica Argentina. I. Palmyridae (= Chrysopetalidae), Amphinomidae y Euphrosinidae. *Phusis* **31A**, 485-501.
- Parker, A. R. (1998). Colour in Burgess Shale animals and the effect of light on evolution in the Cambrian. *Proc Roy Soc London (Ser B)* **265**, 967-972.
- Pascual, M. & Núñez, J. (1998). Presencia de *Treptopale rudolphi* Perkins, 1985 (Chrysopetalidae: Polychaeta) en el Atlántico Oriental. *Rev Acad Canar Cienc* **10**, 21-27.
- Patterson, C. (1982). Morphological characters and homology. In K. A. Joysey & A. E. Friday (eds.). *Problems of phylogenetic reconstruction*. Pp. 21-74. Academic Press, London.

- Perkins, T. (1985). *Chrysopetalum*, *Bhawania* and two new genera of Chrysopetalidae (Polychaeta), principally from Florida. *Proc Biol Soc Wash* **98**, 856-915.
- Pettibone, M. H. (1963). Marine polychaete worms of the New England region. *Bull U.S. Nat Mus* **227**, 1-356.
- Pettibone, M. H. (1982). Annelida. In S. P. Parker (ed.). *Synopsis and Classification of Living Organisms*, vol. 2. Pp. 1-43. McGraw-Hill Book Company, New York.
- Pleijel, F. (1995). On character coding for phylogeny reconstruction. *Cladistics* **11**, 309-315.
- Potts, F. A. (1910). Polychaeta of the Indian Ocean. Part 2. The Palmyridae, Aphroditidae, Polynoidae, Acoetidae and Sigalinoidea. *Trans Linn Soc Lond* **2**, 325-353.
- Quatrefages, A. de (1866). Histoire naturelle des Annéles marine et d'eau douce. Annélides et Gephyriens. *Paris, Librairie Encyclopédie de Rôret*, vol. 2.
- Racovitza, É. G. (1896). Le lobe céphalique et l'encéphale des annélides (Anatomie, Morphologie, Histologie). *Archs Zool Exp Gén, Paris (Ser 3)* **4**, 133-343.
- Rioja, E. (1947). Estudios Anelidológicos. XVIII. Observaciones y datos sobre algunos anelidos poliuetos del Golfo de California y costas de Baja California. *An Inst Biol, México*. **18**, 517-526.
- Rouse, G. W. & Fauchald, K. (1997). Cladistics and polychaetes. *Zool Scr* **26**, 139-204.
- Runnegar, B. (1983). Molluscan phylogeny revisited. *Mem Aust Paleontol* **1**, 121-144.
- San Martin, G. (1986). *Acanthopale perkinsi* gen. et sp. n. (Polychaeta, Chrysopetalidae) from Cuba and Florida. *Zool Scr* **15**, 305-312.
- Schmarda, L. K. (1861). *Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857. Turbellarien, Rotatorien und Anneliden, 1(2)*. Wilhelm Engelmann, Leipzig.
- Schram, T. A. & Haaland, B. (1984). Larval development and metamorphosis of *Nereimyra punctata* (O.F. Müller) (Hesionidae, Polychaeta). *Sarsia* **69**, 169-181.
- Seilacher, A., Bose, P. K. & Pflüger, F. (1998). Triploblastic animals more than 1 billion years ago: Trace fossil evidence from India. *Science* **282**, 80-83.
- Sergeeva, N. G., Zaika, V. E. & Kiseleva, M. I. (1997). Life cycle and ecological demands of larval and adult *Vigtorniella zaikai* Kiseleva, 1992 (Chrysopetalidae) in the Black Sea. (Abstract). *Bull Mar Sci* **60**, 622-623.
- Shin, P. K. S. (1980). Some polychaetous annelids from Hong Kong waters. In B. Morton & Tseng (eds.). *Proceedings of the first international marine biological workshop*, Vol. 1. Pp. 161-172. Hong Kong University Press, Hong Kong.
- Siddall, M. E. & Burresson, E. M. (1998). Phylogeny of leeches (Hirudinea) based on mitochondrial cytochrome c oxidase subunit 1. *Mol Phyl Evol* **9**, 165-162.
- Smith, A. B. (1999). Dating the origin of metazoan body plans. *Evol Develop* **1**, 138-142.
- Southern, R. (1909). Polychaeta of the coasts of Ireland. Pelagic Phyllodocidae. *Sci Inv Fish Ireland, Dublin* **3**, 1-11.
- Swofford D. L., Olsen G. J., Waddell P. J., & Hillis D. M. (1996). Phylogenetic Inference. In: D. M. Hillis, G. Moritz, & B. K. Mable (eds.). *Molecular Systematics*. Pp. 407-514. Sinauer Associates. Sunderland, Massachusetts,
- Uschakov, P. V. (1955). Polychaeta of the Far Eastern Seas of the U.S.S.R. *Akad Sci USSR. Keys to the fauna of the USSR*. **56**, 1-433. [Translated, Israel Program for Scientific Translations, Jerusalem 1965].
- Valentine, J.W., & Erwin, D.A. (1987). Interpreting great developmental experiments: the fossil record. In R.A. Raff & E.C. Raff (eds.). *Development as an evolutionary process*. Pp. 71-107. Alan R. Liss, New York.
- Valentine, J. W., Jablonski, D. & Erwin, D. H. (1999). Fossils, molecules and embryos: new perspectives on the Cambrian explosion. *Development* **126**, 851-859.
- Verrill, A. E. (1900). Additions to the Turbellaria, Nemertina and Annelida of the Bermudas, with revisions of some New England genera and species. *Trans Connecticut Acad Arts Sci* **10**, 595-671.

- Walcott, C. D. (1911). Cambrian geology and paleontology. II. Middle Cambrian annelids. *Smithson misc Collns* **57**, 109-144.
- Watson Russell, C. (1986). *Paleaequor*, a new genus of polychaete worm (Chrysopetalidae). *Rec Aust Mus* **38**, 153-174.
- Watson Russell, C. (1987). Chrysopetalidae. In M. Baud & C. Cazaux (eds). Description and identification of polychaete larvae; their implications in current biological problems. *Oceanis* **13**, 596-753.
- Watson Russell, C. (1989). Revision of *Palmyra* (Polychaeta: Aphroditidae) and redescription of *Palmyra aurifera*. *The Beagle, Rec N Territory Mus Arts Sci* **6**, 35-53.
- Watson Russell, C. (1991). *Strepternos didymopyton* Watson Russell in Bhaud & Cazaux, 1987 (Polychaeta: Chrysopetalidae) from experimental wooden panels in deep waters of the western North Atlantic. *Ophelia Suppl* **5**, 283-294.
- Watson Russell, C. (1997). Patterns of growth and setal development in the deep-sea worm, *Strepternos didymopyton* (Polychaeta: Chrysopetalidae). *Bull Mar Sci* **60**, 405-426.
- Watson Russell, C. (1998). Description of *Arichlidon* new genus and two new species from Australia: *Bhawania reynsi* redescribed and assigned to *Arichlidon* (Chrysopetalidae: Polychaeta). *The Beagle, Rec N Territory Mus Arts Sci* **14**, 159-176.
- Webster, H. E. (1884). The Annelida from Bermuda, collected by Mr. G. Brown Goode. *Bull US Natl Mus* **25**, 307-327.
- Webster, H. E. & Benedict, J. E. (1887). The Annelida Chaetopoda from Eastport, Maine. *Rep US Commnr Fish Wash* **13**, 716-717.
- Wesenberg-Lund, E. (1949). Polychaetes of the Iranian Gulf. *Dan scient Invest Iran* **4**, 247-400.
- Wesenberg-Lund, E. (1950). The Polychaeta of West Greenland, with special reference to the fauna of Nordre Strømfjord, Kvane- and Bredefjord. *Meddr Grønland* **151**, 1-171.
- Wesenberg-Lund, E. (1953). The zoology of east Greenland. Polychaeta. *Meddr Grønland* **152**, 1-169.
- Westheide, W. (1997). The direction of evolution within the polychaeta. *J Nat Hist* **31**, 1-15.
- Westheide, W., McHugh, D., Purschke, G. & Rouse, G. (1999). Systematization of the Annelida: different approaches. *Hydrobiologia* **402**, 291-307.
- Westheide, W. & Watson Russell, C. (1992). Ultrastructure of Chrysopetalid Paleal Chaetae (Annelidae, Polychaeta). *Acta Zool* **73**, 197-202.
- Whittington, H. B. (1981). Cambrian animals: Their ancestors and descendants. *Proc Linn Soc, New South Wales* **105**, 79-87.
- Wills, M. A., Briggs, D. E. G. & Fortey, R. A. (1994). Disparity as an evolutionary index - a comparison of Cambrian and Recent arthropods. *Paleobiology* **20**, 93-130.

## APPENDIX

Checklist of chrysopetalid taxon names.

- Acanthopale* San Martin, 1986. Type species *Acanthopale perkinsi* San Martin, 1986, by monotypy.  
*A. perkinsi* San Martin, 1986.  
*Arichlidon* Watson Russell, 1998. Type species *Arichlidon hanneloreae* Watson Russell, 1998, by original designation.  
*A. acropetalon* Watson Russell, 1998  
*A. hanneloreae* Watson Russell, 1998.  
*A. reyssii* (Katzmann, Laubier and Ramos, 1974). As *Bhawania reyssii*.  
*Bhawania* Schmarda, 1861. Type species *Bhawania myrialepis* Schmarda, 1861, by monotypy.  
*B. ambionensis* Horst, 1917. —Hartman 1959.  
*B. brunnea* Morgado and Amaral, 1981. —Perkins 1985.  
*B. cryptocephala* Gravier, 1902. —Potts 1910; Fauvel 1932; Wesenberg-Lund 1949; Hartman 1959; Perkins 1985; Watson Russell 1986.  
*B. cryptocephala pottsiana* Horst, 1917. —Hartman 1959; Gibbs 1971; Perkins 1985; Watson Russell 1986.  
*B. goodei* Webster, 1884. —Imajima & Hartman 1964; Day 1967; Perkins 1985.  
*B. multisetosa* Hartman-Schröder, 1981. —Perkins 1985.  
*B. myrialepis* Schmarda, 1861. —Perkins 1985.  
*B. obscura* (Grube, 1868). As *Psectra obscura*. —Hartman 1959.  
*B. pottsiana* (Horst, 1917). As *B. cryptocephala pottsiana*. —Gibbs 1971; Watson Russell 1986.  
*B. riveti* (Gravier, 1909). As *Chrysopetalum riveti*. —Augener 1913; Hartman 1959; Perkins 1985.  
*Chrysopetalum* Ehlers, 1864. Type species *Chrysopetalum fragile* Ehlers, 1864, by monotypy.  
*C. debile* (Grube, 1855). As *Palmyra debilis*. —Fauvel 1923; Day 1967; Perkins 1985.  
*C. ehlersi* Gravier, 1902. —Hartman 1959; Perkins 1985.  
*C. elegans* Bush in Verrill, 1900. —Hartman 1942; Perkins 1985.  
*C. elongatum* (Grube, 1856). As *Palmyra elongata*. —Augener 1925; Perkins 1985.  
*C. europale* Perkins, 1985.  
*C. floridanum* Perkins, 1985.  
*C. fragile* Ehlers, 1864. Junior synonyme to *C. debile*. —Hartman 1959; Perkins 1985.  
*C. hernancortezae* Perkins, 1985.  
*C. heteropale* Perkins, 1985.  
*C. occidentale* Johnson, 1897. —Hartman 1959, 1961, 1968; Fauchald 1977a; 1977b; Perkins 1985.  
*C. paessleri* Augener, 1912. Junior synonym of *Chrysopetalum occidentale*. —Hartman 1959; Perkins 1985.  
*C. remanei* Perkins, 1985. —Hartman-Schröder 1960. As *Chrysopetalum debile*.  
*Dysponetus* Levinsen, 1879. Type species *Dysponetus pygmaeus* Levinsen, 1879, by monotypy. (= *Taphus* Webster and Benedict, 1887). —Levinsen 1883; Annenkova 1935.  
*D. bidentatus* Day, 1954. —Laubier 1964; Hartmann-Schröder 1974a; Perkins 1985; Dahlgren 1996.  
*D. bulbosus* Hartman-Schröder, 1982. —Perkins 1985; Hartmann-Schröder 1986; Hartmann-Schröder 1993; Dahlgren 1996.  
*D. caecus* (Langerhans, 1880). As *Chrysopetalum caecum*. —Augener 1913; Augener 1928; Fauvel 1923; Annenkova 1935; Hartman 1959; Laubier 1964, 1968; Perkins 1985; Dahlgren & Pleijel 1995; Dahlgren 1996.  
*D. gracilis* Hartman, 1965. —Dahlgren 1996; Aguirrezabalaga et al. 1999.

- D. hebes* (Webster and Benedict, 1887). As *Taphus hebes*. —Annenkova 1935; Pettibone 1963; Laubier 1964; Hartman 1965; Dahlgren 1996.
- D. paleophorus* Hartman-Schröder, 1974b. —Dahlgren (Paper III).
- D. pygmaeus* Levinsen, 1879. —Levinsen 1883; Annenkova 1935; Wesenberg-Lund 1950; 1953; Uschakov 1955; Pettibone 1963; Imajima & Hartman 1964; Laubier 1964; Dahlgren and Pleijel 1995; Dahlgren 1996.
- Heteropale* Johnson, 1897. Type species *Heteropale bellis* Johnson 1897, by monotypy. Junior synonym of *Paleanotus* Schmarda, 1861.
- Hyalopale* Perkins, 1985. Type species *Hyalopale bispinosa* Perkins, 1985, by monotypy.
- H. bispinosa* Perkins, 1985.
- Paleaequor* Watson Russell, 1986. Type species *Paleaequor setula* Watson Russell, 1986, by original designation.
- P. brevis* (Gallardo, 1967). As *Bhawania brevis*. —Shin 1980; Watson Russell 1986.
- P. heteroseta* (Hartman, 1945). As *Paleanotus heteroseta*. —Perkins 1985; Watson Russell 1986.
- P. nicoyensis* Watson Russell, 1986.
- P. psamathe* Watson Russell, 1986.
- P. setula* Watson Russell, 1986.
- Paleanotus* Schmarda, 1861. Type species *Paleanotus chrysolepis* Schmarda, 1861 by monotypy. —Augener 1913.
- P. bellis* (Johnson, 1897). As *Heteropale bellis*. —Augener 1913 (as *Paleanotus chrysolepis*); Hartman 1959, 1961; Perkins 1985.
- P. chrysolepis* Schmarda, 1861. —Augener 1913; Ehlers 1913; Day 1967; Gathof 1986.
- P. intermedius* Orensanz, 1972.
- P. macrophthalma* (Hartmann-Schröder, 1959). As *Chrysopetalum macrophthalmum*. —Hartmann-Schröder, 1980; Perkins 1985.
- P. purpurea* Rioja, 1947. —Hartman 1959; Mileikovsky 1962; Perkins 1985.
- P. schmardai* Mileikovsky, 1962. —Hartman 1965; Perkins 1985; Watson Russell 1997.
- Palmyra* Savigny in Lamarck, 1818. Type species *Palmyra aurifera* Savigny in Lamarck, 1818, by monotypy. —Watson Russell 1989.
- Palmyrides* Claparède, 1864. Type species *Palmyra (Palmyrides) portusveneris* Claparède, 1864, by monotypy. —Augener 1913; Fauvel 1923 (as *Chrysopetalum*).
- Palmyra (Palmyrides) portusveneris* Claparède, 1864. Probably belonging to *Paleanotus* (unpublished obs.). —Augener 1913.
- Palmyropsis* Claparède, 1864. Type species *Palmyra (Palmyropsis) evelinae* Claparède, 1864, by monotypy. Junior synonym of *Chrysopetalum*. —Perkins 1985.
- Palmyra (Palmyropsis) evelinae* Claparède, 1864. Junior synonym of *Chrysopetalum debile* (Grube, 1855). —Quatrefages 1866.
- Psectra* Grube, 1868. Type species *Spectra obscura* Grube, 1868, by monotypy. Junior synonym of *Bhawania* Schmarda, 1861.
- Strepternos* Watson Russell in Bhaud & Cazaux, 1987. Type species *Strepternos didymopyton* Watson Russell in Bhaud & Cazaux, 1987, by monotypy.
- S. didymopyton* Watson Russell in Bhaud & Cazaux, 1987. —Watson Russell 1991, 1997.
- Treptopale* Perkins, 1985. Type species *Treptopale rudolphi* Perkins, 1985, by monotypy.
- T. rudolphi* Perkins, 1985. —Pascual and Núñez 1998.
- Taphus* Webster and Benedict, 1887. Type species *Taphus hebes* Webster and Benedict, 1887, by monotypy. Junior synonym to *Dysponetus* Levinsen, 1879.
- Vigtorniella* Kiseleva, 1996. Replacement name for *Victoriella* Kiseleva, 1992. —Kiseleva 1996. Type species *Vigtorniella zaikai* (Kiseleva, 1992), by monotypy.
- V. zaikai* (Kiseleva, 1992). —Murina 1986 (as *Pelagobia serrata*), 1997; Kiseleva 1996.