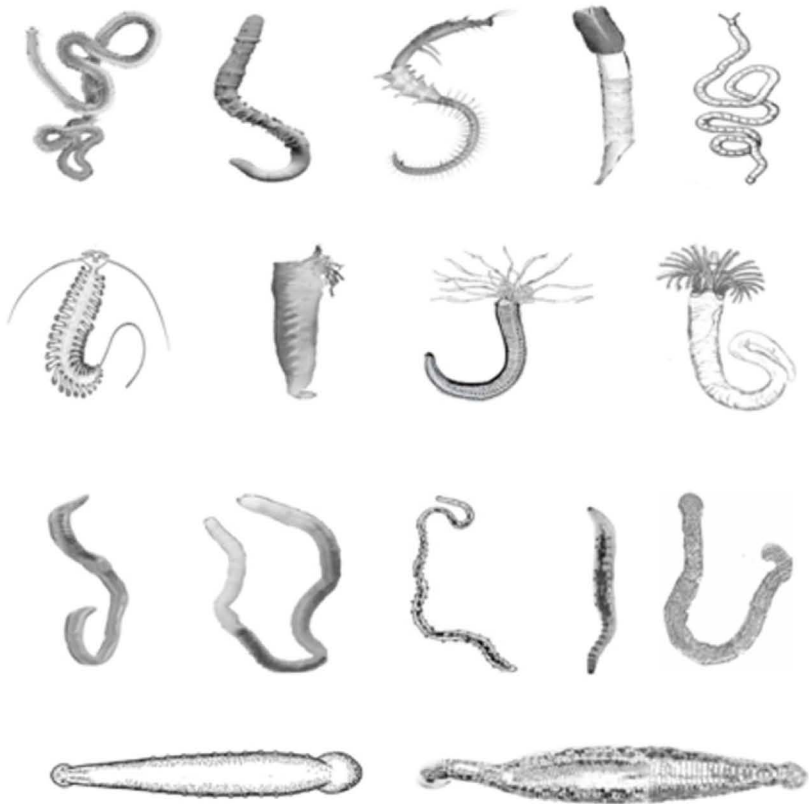


Series
Reproduction and Development in
Aquatic Invertebrates
Volume 4

Reproduction and Development in Annelida



T. J. Pandian



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Series on

**Reproduction and Development in Aquatic
Invertebrates**

Volume 4

**Reproduction and
Development in Annelida**

T. J. Pandian

Valli Nivas, 9 Old Natham Road
Madurai-625014, TN, India



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Cover page: Representative examples of annelid species. For more details, see [Figure 1.1](#)

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Preface to the Series

Invertebrates surpass vertebrates not only in species number but also in diversity of sexuality, modes of reproduction and development. Yet, we know much less of them than we know of vertebrates. During the 1950s, the multi-volume series by L.E. Hyman accumulated bits and pieces of information on reproduction and development of aquatic invertebrates. Through a few volumes published during the 1960s, A.C. Giese and A.S. Pearse provided a shape to the subject of Aquatic Invertebrate Reproduction. Approaching from the angle of structure and function in their multi-volume series on Reproductive Biology of Invertebrates during the 1990s, K.G. Adiyodi and R.G. Adiyodi elevated the subject to a visible and recognizable status.

Reproduction is central to all biological events. The life cycle of most aquatic invertebrates involves one or more larval stage(s). Hence, an account on reproduction without considering development shall remain incomplete. With the passage of time, publications are pouring through a large number of newly established journals on invertebrate reproduction and development. The time is ripe to update the subject. This treatise series proposes to (i) update and comprehensively elucidate the subject in the context of cytogenetics and molecular biology, (ii) view modes of reproduction in relation to Embryonic Stem Cells (ESCs) and Primordial Germ Cells (PGCs) and (iii) consider cysts and vectors as biological resources.

Hence, the first chapter on Reproduction and Development of Crustacea opens with a survey of sexuality and modes of reproduction in aquatic invertebrates and bridges the gaps between zoological and stem cell research. With capacity for no or slow motility, the aquatic invertebrates have opted for hermaphroditism or parthenogenesis/polyembryony. In many of them, asexual reproduction is interspersed within sexual reproductive cycle. Acoelomates and eucoelomates have retained ESCs and reproduce asexually also. However, pseudocoelomates and haemocoelomates seem not to have retained ESCs and are unable to reproduce asexually. This series provides possible explanation for the exceptional pseudocoelomates and haemocoelomates that reproduce asexually. For posterity, this series intends to bring out six volumes.



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Preface

Annelids are known for the unique spectacular epitoky, regeneration and clonal reproduction. These features have attracted attention more from academic interest. An objective of this book is to elevate annelids from academic interest to economic importance. Many books are authored or edited on annelids but are limited to a taxonomic group or a specific theme like phylogeny. This book is a concise, informative elucidation of reproduction and development in annelids covering from *Aeolosoma viride* to *Zeppelinina monostyla*.

The book is structured in nine chapters. In view of their importance, two chapters are devoted to regeneration and clonal reproduction, a chapter on epitoky and another on vermiculture. Some 81, 12 and 7% annelids are marine, freshwater and terrestrial inhabitants. Comprising 17,000 species, annelids are found mostly in aquatic habitats but a few in terrestrial habitats. Vertically distributed between 4,900 m depth and 2,000 m altitude, they are also found in unusual habitats like hydrothermal vents, subterranean aquatic system and migrating between the nutrient-rich anoxic and oxic zones in the sediments. For the first time, information on gutless oligochaetes and polychaetes, osmotrophism and anaerobiosis in some annelids is highlighted. In the absence of exoskeleton to escape predation, 42–47% polychaetes brood their eggs.

The second chapter deals with sexual reproduction. Polychaetes are gonochores. But clitellates are hermaphrodites characterized by internal fertilization and laying cocoon enclosing a few eggs. Updating has revealed the incidence of hermaphroditism in 207 polychaete species from 27 families. Hence, only 74% of annelids are gonochores. A directory is generated and lists 75 parthenogenic annelid species, of which 56 are earthworms. The first estimate has revealed the incidence of external fertilization in 54% polychaetes. The existence of poecilogony with triple morphs and simultaneous sex change between mating partners are projected.

Devoted to regeneration and clonal reproduction, the third and fourth chapters have brought to light a whole range of new findings. In oligochaetes, inadequate reserves in the chloragogue temporally separate the incidence of regeneration and reproduction. However, the sedentary polychaetes, which do not possess the chloragogue or its equivalent, undertake them together,

of course, at the cost of reduced reproduction. The number of species capable of anterior, posterior and anterior cum posterior regeneration is 149, 206 and 143, respectively. When these numbers are considered as fractions of 13,012 polychaete and 3,175 oligochaete species, the percentage values (1.57, 1.80, 1.42) indicate that the potency is 1.5–2.0 times more prevalent in oligochaetes than the respective ones (0.88, 1.22, 0.85) in polychaetes. The earlier loss of the regenerative potency in ‘older’ anterior segments than in ‘young’ posterior segments located adjacent to the generative pygidium may be a reason for the observed less prevalence of anterior regeneration.

Clonal reproduction can sustain a species for > 30–60 years. When stressed or induced, sexual reproduction is manifested, as Primordial Germ Cells (PGCs) are transmitted up to 1,000–3,000 clonal generations. Abundant food supply and low density trigger clonal reproduction but not intense predation; for example 290 tubicolous sabellids species, only 17 are cloners. Of 100 and odd annelid families, the incidence of clonal reproduction occurs only in 12 polychaete families and 5 oligochaete families. It ranges from 2% of spionids to 54% of naidids. Further, it occurs in 79 polychaete species but to as many as 111 oligochaete species. Clonal reproduction is considered to have been derived from regeneration. However, this view is not correct, for (i) in as many as 111 oligochaete species, cloning does obligatorily require the presence of neoblasts and (ii) even with anterior cum posterior regenerative potency, 34 out of 63 polychaete species, do not reproduce clonally. In most polychaetes, the stem cells responsible for cloning are located at the posterior end and also mid-body in a few.

The epitokes are divided into semelparous epigamics and iteroparous schizogamics. For the first time, a directory is documented listing epigamy in 61 species from 12 families and schizogamy in 45 syllid species. Again for the first time, the assembled information on vertical distance traveled by 28 epitokous species reveals that the larger glycerids, nereidids and eunicids use muscular energy to climb up < 50 m but the smaller phyllodocids and ctenodrilids may engage reduced buoyancy to climb the vertical distance of up to 4,000 m.

The sixth chapter deals with sex determination by genes harbored on chromosomes. Karyotyping and breeding experiments have found heterogametism in six polychaete species only. A directory is assembled for the chromosome numbers in annelids. By selective fertilization of large eggs by X-carrying sperm, *Dinophilus gyrocolliatus* have nullified the chromosomal mechanism of sex determination. In *Capitella capitata*, expression of W gene(s) is stable but that in Z chromosome is labile resulting in generation of phenotypic ZZ hermaphrodites and females.

Our understanding of endocrine sexualization in syllids and regulation of reproductive cycles in others is based on temperate polychaetes alone. A dozen neuroendocrines/hormones secreted mostly by the ‘brain’ regulate the reproductive cycle.

The ninth chapter on vermiculture (i) emphasizes the need for information on growth and reproduction in cultivable species, (ii) considers parthenogens and cloners, as they do not have adequate genetic diversity and cloners increases the number but may not the biomass and (iii) recognizes 'layers' as distinct from 'brooders'. There is an urgent need for research input to harvest tubificids and nauidids at appropriate intervals, as it may reduce the input of nitrogen fertilizers in ricefields. The fastest growing earthworms, nereidids, tubifex and pot worms are recommended as cultivable species. For the first time, the fast growing *Branchiura sowerbyi* fed on waste paper immersed in water is identified as potential candidate species for vermiculture.

This book is a comprehensive synthesis of 737 publications carefully selected from widely scattered information from 237 journals and other literature sources. The holistic approach and incisive analysis have led to several new findings and ideas related to reproduction and development of annelids. Hopefully, the book serves as a launch-pad to further advance our knowledge on annelids.

July, 2018
Madurai-625 014

T. J. Pandian



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Firstly, I wish to thank many authors/publishers, whose published figures are simplified/modified/compiled/redrawn for an easier understanding. To reproduce original figures from published domain, I gratefully appreciate the permission issued by Dr. S.M. Mandaville. For permissions issued to reproduce original figures from dissertations/protocols of his students, I remain thankful to Dr. S. Sudhakar, who has also provided me his consent to reproduce unpublished figures. Dr. P. Murugesan has kindly provided me a hand drawn figure. For advancing our knowledge in this area by their rich contributions, I thank all my fellow scientists, whose publications are cited in this book.

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1

Introduction

1.1 Annelidan Science*

Annelids are bilaterally symmetrical, triploblastic, schizocoelomatic, metamerically segmented vermiform invertebrates. Their segmented body has a well-developed ladder-like central nervous system with a bi-lobed cerebral ganglion and sense organs, a closed blood-vascular system, coelom, an excretory system and a fairly well developed endocrine system. Among aquatic fauna, they are a fascinating taxon displaying (i) epitoky, a spectacular unique phenomenon involving transformation from benthic to meroplanktonic reproductive morphism, (ii) osmotrophism displayed by the gutless tubificids acquiring cent percent nutrients across the body surface from ambient sea water, (iii) partial (tubificids) and complete (vestimentiferans) chaemoautotrophism by engaging symbiotic microbes to draw energy, (iv) poecilogony, another unique feature shared only by some gastropods (Pandian, 2017), (v) metamerism, the most distinguishing feature of annelids and (vi) regeneration, which may be followed by bidirectional (a genet divided into two ramets) and multidirectional (a genet divided into multiple ramets) asexual reproduction. They are classified into Archiannelida, Polychaeta, Oligochaeta and Hirudinea (Table 1.1). In polychaetes, a pair of bilaterally located parapodia facilitates burrowing and locomotion. It is, however, reduced to setae in oligochaetes and totally missing in archiannelids and hirudineans. The marine interstitial archiannelids are phylogenetically enigmatic annelids and include five families. The exclusively marine polychaetes include burrowing, crawling, digging, drifting (*Tomopteris* spp), and tubiculous forms (Fig. 1.1) commonly known as sea mice (*Aphrodita*), scale- (*Polynoe*), paddle- (*Notophyllum*), pile/rag/clam- (*Nereis virens*),

* Names of most annelids species are listed following Worms—World Register of Marine Species; however, some are named, according to author's citation.

TABLE 1.1

Systematic resume of Annelida (compiled from Barnes [1974] and others; terrestrial and amphibious taxa are indicated by bold and italic letters; representative family names alone are indicated)

Phylum: Annelida (15,000 [Wildlife J Junior, 2017], 16,763 [Chapman, 2009], 22,000 [Aguado et al., 2014])

Class: Archiannelida, *Polygordius*, *Nerilla* (60 species [Westheide, 1984])

Class: Polychaeta (8,000 [IASzoology.com], 10,000 species [Minelli, 1993], 13,000 [Australian Museum, 2015])

Sub class: Erranta

Families: Aphroditidae, Polynoidae, Siboglinidae, Phyllococidae, Amphinomidae, Nereididae, Pisionidae, Alciopidae (pelagic), Tomopteridae (pelagic), Hesionidae, Syllidae, Nephtyidae, Glyceridae, Eunicidae, Lysaretidae, Arabellidae, Lumbrineridae, Histriobdellidae, (Ectoparasites), Ichthyotomidae (Ichthyoparasites), Myzostomidae

Sub class: Sedentaria

Families: Orbiniidae, Spionidae, Siboglinidae, Magelonidae, Chaetopteridae, Cirratulidae, Flabelligeridae, Opheliidae, Capitellidae, Echiuridae, Cossuridae, Arenicolidae, Maldanidae, Oweniidae, Sabellariidae, Pectinariidae, Ampharetidae, Terebellidae, Sabellidae, Serpulidae, Fabriciidae

Class: Oligocheta (1,700 species [Martin et al., 2008])

Orders: Lumbriculida (145 species, Ferraguti et al., 1999 [*Lumbriculus*]), Moniligastridae

Order: Haplotaxida

Sub order: Haplotaxina

Sub order: Tubificina

Families: Enchytraeidae (670 species, Schmelz and Collado, 2015), Tubificidae (1,000 species, Martin et al., 2008), Naididae (175 species, Ferraguti et al., 1999), Phreodrilidae, Opisthocystidae, Dorydrilidae

Sub order: *Lumbricina* (33–670 species and subspecies in ~ 48 genera [Wikipedia])

Families: Allurioididae, **Glossoscolecidae**, **Lumbricidae**, **Megascolecidae** (*Pheretima*), **Eudrilidae**

Class: Hirudinea (700–1,000 species [Govedich and Bain, 2005])

Order: Acanthobdellida, Rhynchobdellida

Families: Glossiphoniidae (*Placobdella*), Piscicolidae (*Pontobdella*)

Order: *Gnathobdellida*

Families: *Hirudinidae*, **Haemadipsidae** (50+10 species [Won et al., 2014]) (*Hirudo*, *Haemopsis*)

Order: Pharyngobdellida: Primarily aquatic with some semi-terrestrial species

nuclear- (*Namalycastis*), fire- (*Amphinome*), blood- (*Glycera*), tube- (*Onuphis*), lug- (*Arenicola*), bamboo- (*Maldane*), trumpet- (*Pectinaria*), spagehetti- (*Terebella*), fan- (*Sabella*) and feather duster- (*Hydroides*) worms. The drifting holoplanktonic polychaetes are included in two families Alciopidae and

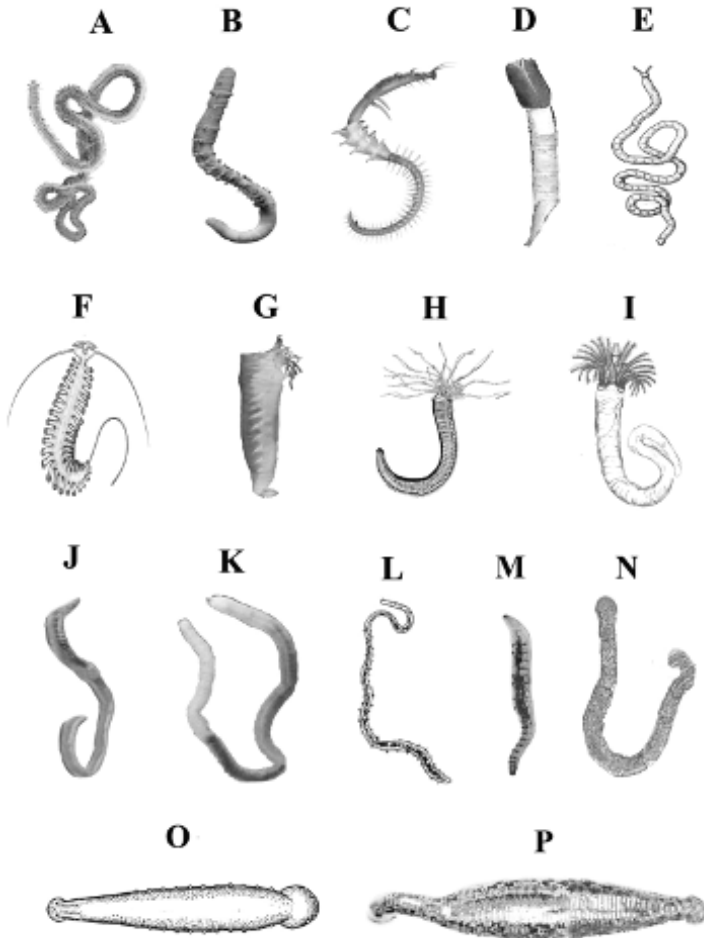


FIGURE 1.1

A. *Nereis*, B. *Arenicola*, C. *Chaetopterus*, D. *Riftia* (Public domain, Wikipedia), E. *Polygordius* (freehand drawing from Fraipont), F. *Tomopteris kils* (redrawn), G. *Ampharete*, H. *Amphitrite*, I. *Hydroides* (H and I freehand drawings from Dales, 1963), J. Earthworm, K. *Amphichaeta* (permission by limnes@chebucto.ns.ca), L. *Tubifex*, M. *Aeolosoma* (copyright free projects.ncsu.edu), N. *A. hembrichi*, O. *Piscicola* (freehand drawing from Mann, 1962), P. Human leech (A, B, C, F, G, J and O are all copyright free images from dreamstime.com).

Tomopteridae and are being expanded to Lopadorhynchidae, Pontodoridae, Iospilidae, Poeobiidae and Typhloscolecidae (Bonifazi et al., 2016). The fire worms (Amphinomidae) are known for their brittle poisonous setae and some blood worms can be venomous (Aguado et al., 2014).

Though the swarming palolo worms *Eunice viridis* are collected and consumed by Samoan Islanders (Caspers, 1984), annelids do not directly

contribute to the global fisheries. However, they serve as key bait in recreational fisheries. More than 65 million anglers from Europe, USA, Canada and Australia catch annually 2 million ton (mt) high value fishes (Pandian, 2015). Between 1966 and 1980, 27–38 million pileworms *Nereis virens* were harvested annually (Creaser and Clifford, 1982). The estimated market value of the bait worms for Europe alone is ~ US\$ 250 million (Olive, 1999). van der Have et al. (2015) have listed some 25 polychaete (pile-, lug-, blood-, sand- and nuclear-worms) species used as bait by anglers in Europe, Korea and China. The demand for these bait worms is so high that *N. virens* is cultured in the UK and Netherlands; the bloodworm *Diopatra bilobata* and Korean lug worm *Perinereis* spp are also cultured in Vietnam, Korea, China and Japan (for export). Among freshwater oligochaetes, *Tubifex* and the like serve as live feed for domestic ornamental fishes. Many publications (e.g. Marian and Pandian, 1984, 1985, Marian et al., 1989) and privately circulated books (e.g. Pandian and Marian, 1985a) are available describing the procedures for rearing and harvesting the worm are available.

Being ecosystem engineers, services rendered by the earthworms needs no emphasis. These worms accelerate degradation of organic matter and molecules produced by plants and other organisms, and render nutrients, especially nitrogen reusable by plants. Total production of mineral nitrogen by the worms ranges between 30 and 50 kg/hectare (ha)/year (y). By altering porosity, these worms contribute to soil structure and thereby water absorption and retention; for example, water infiltration rate through soil can be increased by the worms from 15 to 27 mm/hour (h), resulting in reduced runoff. In soil formation, they breakdown the primary minerals and incorporate them with organic matter. Their aquatic counterparts, the polychaetes and tubificids serve also as ecosystem engineers to turbulate (see Hutchings, 1998) and make the organic matter from sediments and deposits available for benthic productivity. For example, *Tubifex benedii*, *Amphichaeta sannio*, *Paranais litoralis* (naidid) and *Manayunkia aestuarina* (polychaete) jointly contribute 50–90% of the total invertebrate production in the Forth estuary, Scotland (see Giere, 2006). Inhabiting 1.6 km long, 3 m width and 30 cm depth of intertidal zone of the Pacific coast, USA, the small (25 mm long) opheliid *Euzonus mucronata* annually turbulates 14,600 ton (t) sediments. Hence, the indirect contribution by the annelids to the global benthic fisheries must be of high order. However, not much information is yet available on quantitative contribution by the polychaetes to the trophodynamics of many ecosystems (cf Pandian, 2016). Time memorial, leeches, especially *Hirudo medicinalis* have been used in hirudotherapy. *H. medicinalis* secretes hirudin, a 65 amino acid peptide that inhibits thrombin-catalyzed conversion of fibrinogen to fibrin and prevents host blood from clotting. By inflicting the deepest bite and the most-prolonged post-bite extravasation, a leech can engorge maximally with 50–100 ml human blood (Govedich and Bain, 2005).

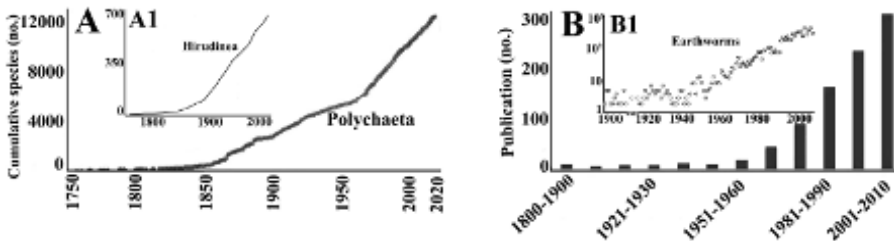


FIGURE 1.2

A. Described polychaete species during the period from 1750–2020 (from Polychaeta Statistics, modified). A1 in window shows the same relationship for hirudineans (modified from Sket and Trontelj, 2008). B. Number of publications relevant to polychaetes during the period from 1800–2010 (from Faulwetter et al., 2014, modified). B1 in window shows the same relationship for earthworms (modified from Sturzenbaum et al., 2009).

For polychaetes, relatively more information is available on the number of species and publications for the past two centuries. Syllidae, Nereididae, Spionidae and Serpulidae are speciose families each comprising > 500 species (Faulwetter et al., 2014). Described polychaete species number has remained < 2,000 until the 19th century and is expected to increase to ~ 13,000 species by 2020 (Fig. 1.2A). This trend also holds true to hirudineans (Fig. 2.1A1) and perhaps to oligochaetes. Publications relevant to polychaetes, which have remained less than a dozen per decade until 1960, have increased rapidly to ~ 300/decade during 2000–2010 (Fig. 1.2B). This type of spurt may hold true for earthworms (Fig. 1.2B1) and other clitellates also. Hence, this book provides only a ‘snap-shot’ of annelid reproduction and development rather than an in depth or exhaustive description of each item listed in the ‘Contents’.

1.2 Species and Structural Diversity

A vast majority of annelids are gonochores and reproduce sexually. Not surprisingly, this feature is reflected in their species diversity. For example, any macrofaunal sample from the Australian soft sediments is reported to hold from 24% (Bass Strait) to 36% (Port Phillip Bay) polychaete species (see Hutchings, 1998). Indicating the sustained contribution to annelidan taxonomy, the described species number has progressively increased from 8,700 (Barnes, 1974) to 14,000 in polychaetes, 4,000 + in oligochaetes and 800 in hirudineans (Rouse and Pleijel, 2006), 16,763 (Chapman, 2009, see also Westheide and Purschke, 2013) and to 22,000 (Aguado et al., 2014). More recently, Bleidorn et al. (2015) have considered that annelids comprise >

17,000 species (Table 1.2, see also p 5). This number may further increase, as the described polychaete species number alone, which was around 10,000, is estimated to shoot to 25,000 (Hutchings, 1998). Similarly, the number of hirudinean species has also increased from 500 (Barnes, 1974) to 700–1,000 (Govedich and Bain, 2005). Martin et al. (2008) reported that of 1,700 valid species of aquatic oligochaetes, of which the most speciose Tubificidea holds over 1,100 species. However, it must be stated that the annelidan taxonomy remains fluid but dynamic. Erected new species by mis/wrong identification is being continuously corrected. For example, a check-list of polychaete species from the Black Sea reveals that 51 species reported between 1868 and

TABLE 1.2

Distribution and number of annelid species in marine, freshwater and terrestrial habitats

Taxon	Habitat (no.)			Total (no.)	Reference
	Marine	Freshwater	Terrestrial		
Archannelida	60	–	–	60	Westheide (1985)
Polychaeta	> 13,000	~ 12†	2**	13,002	Australian Museum (2015), Erseus (1994)**
Hirudinea	102	482	92	684	Sket and Trontelj (2008)
Oligochaeta	+	+			Martin et al. (2008)
Moniligastrida			+		
Lumbriculida		145 + 24*		169	Feragutti et al. (1999)
Haplotaxina		++	+		
Tubificina	16†			16	Giere (2006)
Enchytraeidae			~ 670	670	Schmelz and Collado (2012)
Tubificidae	600	1,100 + 13*	+	1,713	Martin et al. (2008)
Naididae	–	175	–	175	Ferraguti et al. (1999)
Phrocodriliae	+	+			
Ophistocystidae					
Dorydrilidae		++			
Lumbricina		+	+		
Alluroidae		++			
Lumbricidae			432	432	Rhoden (2015)
Megascolecidae			+		
Eudrilidae			+		
	13,776	1,939	1,202	16,911	Bleidorn et al. (2015)

* subterranean species recognized by Chatelliers et al. (2009), + freshwater, ++ mostly freshwater, – absent, † riverine polychaetes

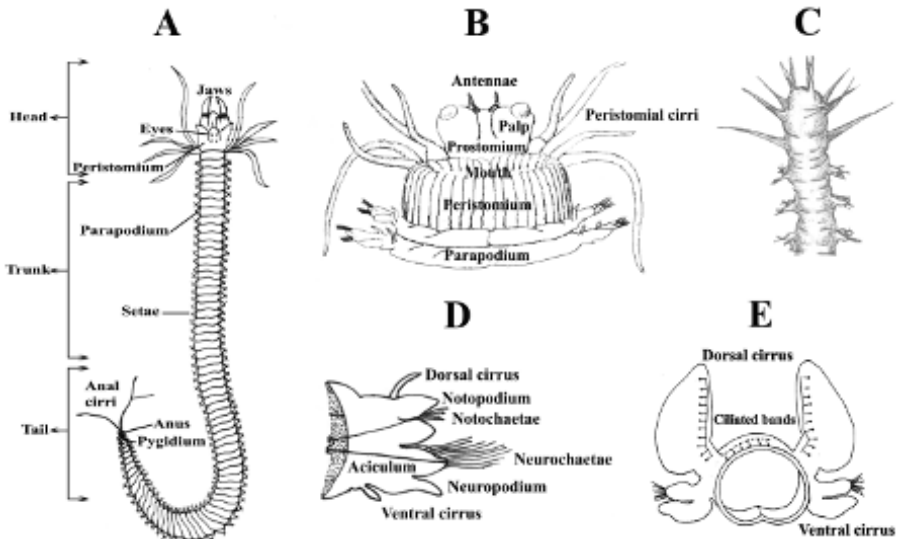


FIGURE 1.3

A. An errant *Nereis* showing head/peristomium, trunk and tail regions. B. Ventral view of *Nereis* head. (modified and drawn from Snodgrass). C. Anterior portion of *Hesionides*. Note the ventrally directed parapodia adapted for crawling. D. Ventral view of parapodium of *Nereis*. E. Surface ciliation in filter feeding *Phyllodoce* (modified and drawn from Segrove). Arrows indicate direction of water current (A. all are free hand drawings; A and D, courtesy Dr. P. Murugesan).

2011 has been synonymized with other species (Sahin and Cinar, 2012). In fact, many reviewers refer only generic names, as species-level revisions are an ongoing research.

The annelidan body is distinctly divided into a series of similar segments. These segments are arranged in a linear series along the antero-posterior axis. The prostomium and pygidium, which are not true segments, are located at the anterior and posterior ends of the body. The formation of new segments occurs just anterior to the pygidium. The oldest segments are therefore anterior and the youngest are posterior (Fig. 1.3). Considering polychaetes as representative taxon, the number of segments ranges from a few to as many as 300 in the orbinid *Nainereis dendritica*, the body length from 2 mm in the cirratulid *Monticellina serratiseta* to 3 m in an *Eunice* sp and the width from 0.4 mm in the cirratulid *Caulleriella lafolla* to 6 mm in the orbinid *Phylo nudus*. Obviously, thinning of the body facilitates burrowing to deeper depths. Table 1.3 and Fig. 1.3 briefly summarize the remarkable structural diversity in prostomium as well as structures like the parapodia associated with each segment of the body. Sensory organs attached to the prostomium and bilaterally located parapodia are greatly modified to suit the burrowing, crawling and tubicolous mode of life and to collect food, as well.

TABLE 1.3

Diversity of segmental structures in annelids

Polychaeta
<i>Crawlers</i>
Well developed preoral prostomium bears antennae, palps, eyes, nuchal organ. Fleshy biramous parapodia consisting of an upper notopodium and lower neuropodium terminate by an invaginated series of setae. Cirri form processes arise from the bases of these podia. The segment is supported by one or more chitinous rods (Fig. 1.3A, D)
<i>Drifters</i>
Structures like the crawlers. Transparent. Enormously large eyes in alciopids and membranous parapodial pockets in tomopterids (Fig. 1.1). Setae are absent
<i>Burrowers</i>
Reduced prostomium. Antennae, palps and eyes absent but carry food collecting structures (e.g. tentacles of <i>Amphitrite</i> , Fig. 1.1A). Reduced uniramous parapodia represented by transverse ridges, which may be modified into hooks
<i>Borers</i>
Spionid <i>Polydora</i> burrows into the shell aided by a viscous fluid, which dissolves the exposed calcite crystals of the shell (Pandian, 2017)
<i>Diggers</i>
Heads of the pectinariid worms bear rows of large conspicuous seta used for digging
<i>Tubicolous worms</i>
Carnivores: Segmental structures do not greatly differ from those of crawlers. Inhabit in vertically or horizontally straight hyaline/membranous tubes
Others: Prostomium and sensory structures reduced or absent. Specialized food collecting structures present. Sabellids build membranous sand grain tubes. Serpulids secrete calcareous tubes. Oweniids carry their tubes
Oligochaeta
No parapodia. Setae can be long or short, straight or curved, heavy or needle-like and blunt, pointed, forked, pinnate or plumose. The setal shaft is S-shaped with middle swelling or nodule. Longer setae are characteristics of aquatic species. Setal number is fixed at 8 in aquatic species and <i>Lumbricus</i> . In mature oligochaetes, certain anterior adjacent segments thickened and swollen by glands that secrete mucus for copulation and for formation of cocoon. Their glandular area is called clitellum, which forms a girdle around the body
Hirudinea
No head appendages but eyes are present. No parapodia and setae except in <i>Acanthobdella</i> . Dorso-ventrally flattened body with suckers at the anterior and posterior ends. Segment number is fixed at 34. Septa absent

1.3 Geographic Distribution

Geographic range is the horizontal and vertical areas, in which populations of a species are distributed. It is a species specific trait with evolutionary consequences inclusive of determination of life span and exposure to different environmental and biological factors. In freshwaters, the oligochaetes *Tubifex*

tubifex is cosmopolitan in distribution; so is the polychaete *Nereis virens* in the intertidal zone of marine environment. The archiannelids and polychaetes are exclusively marine, although a couple of polychaetes *Peregodrilus heideri* and *Hrabeiella periglandulata* are almost terrestrial inhabiting moist soil (see Rota et al., 2001), and a dozen of them inhabit rivers and estuaries. On the other hand, oligochaetes and hirudineans are found in marine, freshwater and terrestrial habitats. Experts have provided counts on the number of species for groups within, oligochaetes but a total of which does not tally with that reported for the class (Table 1.2). As a result, the sum of subtotals does not tally with recently reported 22,000 species of annelids (Aguado et al., 2014). For example, the estimate of 5,000 clitellate (Oligochaeta + Hirudinea) species by Martin et al. (2008) does agree with the subtotal estimates reported by different experts for the suborders and families. Despite this constraint, and considering 17,000 species number for annelids (Bleidorn et al., 2015), ~ 11.5 and 7% annelids are distributed in freshwater and terrestrial habitats, respectively; the remaining 81% are marine inhabitants. Reports on geographic distribution of a specific taxon in some of these habitats are available; for example, polychaetes in the Black Sea (Sahin and Cinar, 2012), naidids in African freshwaters (Grimm, 1987) and terrestrial enchytraeids in Latin America (Schmelz et al., 2013). A report on distribution within the major geographical zones is also available but only for freshwater hirudineans (Table 1.4). In general, the geographic range is increasingly limited in the following descending order: planktotrophy < lecithotrophy < brooding/viviparity < exclusive asexual reproduction. Within Cirratulidae, the range is extended from the Washington coast of North America to Puget Sound, Washington (DC) for *Chaetozone acuta*, which broadcasts small (50–60 µm) planktotrophic egg; but it is limited between California and Mexico in the west Pacific coast for *C. corona* spawning 75 µm egg, to arctics alone for *C. setosa* releasing 120–160 µm egg, and to the east and west coasts of North America around the equator for *Aphelocheata monilaris* spawning 275–300 µm egg (see Blake, 1996).

TABLE 1.4

Number of freshwater hirudinean genera and species present in major geographical zones (compiled from Sket and Trontelj, 2008)

Zone	Genera (no.)	Species (no.)
Palaearctic	45	187
Nearctic	24	79
Neotropic	27	107
Afrotropic	22	50
Indotropic	27	64
Australasian	15	34

Polychaetes dominate the benthic macrofauna (Gremare et al., 1998). From their long- (20 years) term study on polychaetes at two sites in the western English Channel, Quiroz-Martinez et al. (2012) have analyzed the dynamics of abundance as function of species diversity. With increasing abundance up to 8,000 individuals, species diversity is also increased from ~ 40 to ~ 60 in a site but ~ 25 to ~ 35 species in another site.

Understandably, vertical expansion especially into abyssal depth encounters more environmental challenges than horizontal distribution. The maximum depth, at which the soft-bodied annelids have been collected, is in the range of ~ 4,000 m (Table 1.5). This depth is comparable with the external shell-less molluscs like that aplacophorans (3,200–4,000 m) and cephalopods (2,430–4,850 m) (Pandian, 2017). However, the asteroid and ophiuroid echinoderms with internal skeleton penetrate to 6,035 m (Pandian, 2018). Strikingly, the shelled molluscs are capable of expanding up to 6,370 m (bivalves) and 9,050 m (prosobranchs) (Pandian, 2016). The presence of hard shell(s) enables these shelled molluscs to expand up to the greatest depths.

The abyssal depths, from which annelids have been collected, ranges from 1,500 m for the orbiniid *Phylo nudus* to 4,016 m for the cirratulid *Chaetozone gracilis* for polychaetes and 700 m for the naidid *Nais abissalis* to 1,680 m for four taxa of Tubicinae in Lake Baikal and to 4,900 m depth in the Indian Ocean for the tubificid *Abyssidrilus stilus* (Table 1.5). Describing the pattern and scale of biogeographic variability of abyss in the North Atlantic Ocean, Smith et al. (2006) have reported that the diversity of polychaete species declines perceptibly below 3,000 m depth. Bathymetric distribution of polychaetes seems to be determined by the availability of dissolved oxygen. For example, the Black Sea becomes anoxic and is contaminated with hydrogen sulfide below 150–200 m depth. The number of polychaetes species present in the sea progressively decreases from ~ 100 between 0 and 10 m to 0 below 150 m depth (Sahin and Cinar, 2012). Obviously, the polychaetes in the Black Sea are unable to switch over to anaerobiosis and colonize the anoxic depths. However, Hartman (1966, 1967) has indicated that Antarctic collections have included 23 polychaete species belonging to 14 genera from the depths of 4,930–4,963 in the South Sandwich trench. In freshwater, the naidids occur up to 50 m depth but rarely *Nais abissalis* has been collected from 700 m depth in Lake Baikal. Typically, they feed on phytoplankton (Brinkhurst and Gelder, 1991). With increasing depth, they do not find adequate phytoplankton below 100 m depth (Bondarenko et al., 1996). However, the other oligochaetes, feeding on detritus from sediments, represented by enchytraeids (1,600 m), haplotaxids, lumbriculids and tubificids have been collected from the depth of 1,680 m in Lake Baikal but with perceptible decline from ~ 1,700 no./m² at ~ 50 m depth to < 10 no./m² at 1,680 m depth (Martin et al., 1999). In contrast to the Black Sea, both water column and sediments of Lake Baikal is well oxygenated at all depths (Martin et al., 1999). Considering, hydrostatic pressure, light, temperature and food

TABLE 1.5

Vertical distribution of annelids (from Erseus, 1994*, Blake, 1996, Dean, 1995†, Martin et al., 1999**)

Species	Depth (m)	Location
Polychaeta		
Orbinidae (14–15 species)		
<i>Califa calida</i>	470–2,000	Off California
<i>Phylo nudus</i>	400–1,500	California
Paraonidae (85 species)		
<i>Arcidea monicae</i>	200–300	Mediterranean
	590–1,745	California
<i>A. wassi</i>	80–1,480	California
<i>A. ramosa</i>	10–2,000	California
	44–2,400	Western Pacific, Japan
<i>A. simplex</i>	100–3,000	California
Apisthobranchidae (5 species)		
<i>Apisthobranchus</i>	3,000	
Spionidae (90 species)		
<i>Spiophanes anoculata</i>	463–2,400	California
<i>S. kroeyeri</i>	3,500	Australia-Antartic
Poecilochaetidae		
<i>Poecilochaetus johnsoni</i>	90–189	California-Mexico
Chaetopteridae (30 species)		
<i>Phyllochaetopterus limicolus</i>	119–3,000	California
Cirratulidae (46 species)		
<i>Chaetozone spinosa</i>	280	Japan
	2,623–2,955	California
<i>C. gracilis</i>	4,016	Catalina Island
<i>Tharyx kirkegaardi</i>	1,260–2,400	California
	255–3,000	Atlantic
Cossuridae (16–17 species)		
<i>Cossura pygodactylata</i>	1–2,720	Western France
<i>C. candida</i>	11–2,400	Mexico, Baja California
<i>C. modica</i>	985–2,955	Oregon-California
<i>C. brunnea</i>	1,600–2,200	North Carolina-Mexico
<i>C. rostrata</i>	6–3,348	Oregon-Western Mexico
Oligochaeta		
<i>Nais abissalis</i> (Naichidae)	700	Lake Baikal**
<i>Propappus glandulosus</i> (Enchytraeidae)	1,600	Lake Baikal**
<i>Haplotaxis</i> sp (Haplotaxidae)	1,680	Lake Baikal**
<i>Stylodrilus asiaticus</i> (Lumbriculidae)	1,680	Lake Baikal**
<i>Balkaiodrilus maievici</i> (Tubificidae)	1,680	Lake Baikal**
<i>Abysso-drilus stilus</i> (Tubificidae)	4,900	Indian Ocean*
Ctenodrilidae		
<i>Raricirrus variabilis</i>	4,000	Virgin Islands†

availability, Martin et al. (1999) have found that other than oxygen level, food availability is the most dominant factor that determines the bathymetric distribution of the haplotaxids. Incidentally, the cocoons of *Tubifex tubifex* and *Potamothrix hammoniensis* deposited at the sediment surface are all eaten by the fish *Abramis brama* but > 99% of them survive, when deposited at 20 mm depth (Newrkla and Mutayoba, 1987). There are adequate indications that in the deep anoxic sediments, tubificids may become anaerobic (e.g. Narita, 2006). With abundance of food at 4,900 m depth, *A. stilus* may have switched to anaerobiosis. Interestingly, the highest altitude, at which the enchytraeid *Buchholzia appendiculata* has been collected, is ~ 2,000 m above sea level (asl) in the montane regions of South America (Schmelz et al., 2013). Amazingly, the oligochaetes have a range of vertical distribution of 6,900 m, i.e. from the depth of 4,900 m to an altitude of 2,000 m.

In the absence of moisture/water, the oligochaetan earthworms are unable to penetrate below 80 cm depth (e.g. *Glossodrilus*, Jimenez and Decaens, 2000). Soil moisture potentials, measured in -kPa unit, reduce the optimum for growth and reproduction at -2 kPa to almost 0 at -50 kPa (Johnston et al., 2014). In the presence of water at the peculiar subterranean habitats, the stigobiont oligochaetes are known to flourish (Chatelliers et al., 2009). With their elongated, segmented and flexible body shape, these stigobiont oligochaetes are pre-adapted to the subterranean habitats and do not exhibit troglomorphic features like the absence of body pigments and eyes, elongated appendages and increased sensory structures. The stigobiont oligochaetes belonging to 42 genera in 17 families are reported from the subterranean aquatic habitats. Of them, the number of species belonging to the lumbriculid *Trichodrilus* and tubificid *Rhyacodrilus* accounts for 23 and 11%, respectively (see Chatelliers et al., 2009).

In his informative taxonomic description of Californian polychaetes, Blake (1996) has provided useful data on body length and depth, at which orbinids, paranoids, spionids, cirratulids and others have been collected. When data on body length are plotted against depth, different trends become apparent (Fig. 1.4), clearly indicating that body size may not be a factor for polychaetes to penetrate into greater depths. Unlike oligochaetes, not all polychaetes switch over to anaerobiosis at hypoxic/anoxic depths (e.g. Black Sea, Sahin and Cinar, 2012). Hence, it is likely that the oxygen levels of water and sediments as well as respiratory structures may prove to be important factors in bathymetric distribution of polychaetes.

Endemism: Depending on limited powers of motility and larval dispersal being at the mercy of waves and currents, many annelids are endemic. Not surprisingly, of 155 oligochaete species, 114 are endemic to the truly ancient and long-lived Lake Baikal (Martin et al., 1998). Data on the distribution of stigobiont oligochaetes in the subterranean habitat suggest pronounced endemism. More than 60% species are known only from the type locality (see Chatelliers et al., 2009). Likewise, hydrothermal vent-inhabiting

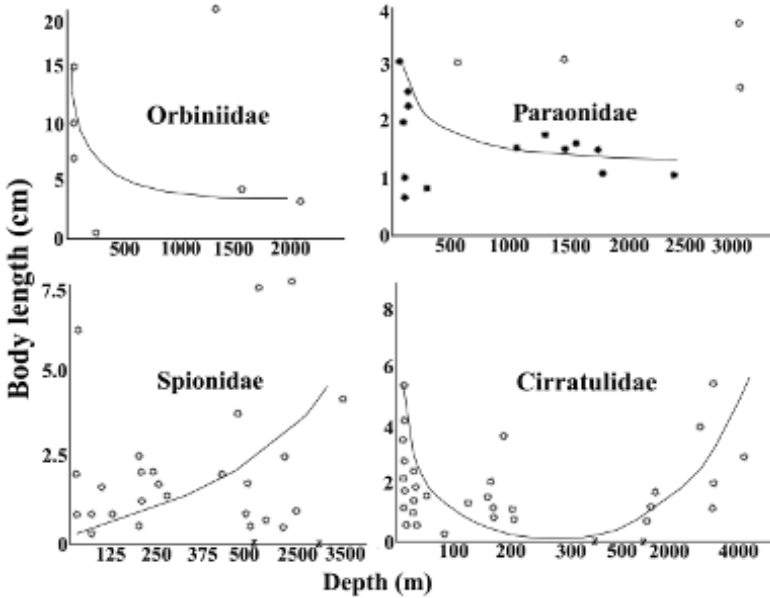


FIGURE 1.4

Vertical distribution of polychaetes belonging to four selected sedentarian families (drawn from data reported by Blake, 1996).

vestimentiferan polychaetes are also endemic. Though polychaetes are continuously occupying a wide vertical depth range, for example *Cossura candida* from 11 to 2,400 m depth off California, Mexican waters (Table 1.5), many of them are reported as endemic. From 19 expeditions carried out during the last 124 years for polychaete taxonomic research around the southernmost tip of the South American continental shelf, Martin et al. (2005) have recorded 431 species belonging to 108 genera and 41 families. Subregions on the Pacific and Atlantic sides are characterized by the presence of 10% endemic species. Investigation on the geographic distribution of the endemic 178 polychaete species between 18° and 56° S of South America has revealed the marked peak endemic hotspot between 36° and 41° S, corresponding to a peak in species richness (Moreno et al., 2006).

Symbiosis: Many annelids symbiotically inhabit as (e.g. *Dipolydora commensalis* on hermit crab within the shell, Lindsay and Woodin, 1993) or as endosymbiont in another polychaete, e.g. *Veneriserva pygoclava meridionalis* in aphroditid host *Laetmonica product* (Micaletto et al., 2002) and within the canals of aquiferous systems of sponges. For example, 33 syllid species constituting > 9% of all the known symbiotic polychaetes are reported to inhabit the canal system of sponges. As many as 600 *Haplosyllis spongicola*

happily inhabit within a small (16.5 cm³) *Ciona* sp but without disturbance to the host. *H. spongicola* can inhabit in 36 species of host sponges (Lopez et al., 2001). The earthworm *Eudrilus eugeniae* symbiotically engage *Bacillus endophyticus* to draw riboflavin, an essential nutrient for regeneration (Samuel et al., 2012, Subramanian et al., 2017).

1.4 Gutless Oligochaetes

Since the discovery of a couple of gutless tubificids in coralline sands of Bermuda (Giere, 1979), over hundred species belonging to two phallodrilan genera *Olavius* and *Inanidrilus* (= *Phallodrilus*) with no digestive system and excretory organs have been described (Erseus, 2003). In *I. leukodermatus*, the integument surface of the long, slender worm is much annulated and highly folded into numerous tiny irregular ridges. These expansions increase the worm body surface nearly 10 times (Giere, 1981). Unlike in other annelids, the epidermal layer is unusually thick with extensions crossing the cuticle (microvilli) and ending in epicuticular projections. Consequently, a wide cuticle-epidermal interface is present. All the studied phallodrilan 30 species are reported to incorporate a fairly thick layer of extracellular bacteria beneath the cuticle. Only in two species *Olavius algarvensis* and *O. ilvae* from the Island Elba, Italy, the microbes are enclosed by the epidermal cells and thus attain an intra-cellular position (Giere and Erseus, 2002). In these gutless tubificids, the symbiotic microbes belonging to the following phytotypes are present: 1. Large, oval-shaped γ *Proteobacteria*, which are shown to be sulfide oxidizers (Dubilier et al., 1995). 2. Small rod shaped α *Proteobacteria*, which reduce sulfate into sulfide. This unique 'cyclotrophism' by these symbiotic microbes enables the gutless tubificids to thrive not only in sulfide/oxic interfaces but also in oxic layers (Giere et al., 1991). 3. Some phytotypes, including *Spirochaeta* also occur; however, their symbiotic function is not known (Giere, 2006). Yet, the quantum of symbiotic microbes harbored in relatively smaller area of these gutless tubificid oligochaetes is too small, in comparison to the massive trophosome filled with prokaryotic symbionts in the hydrothermal vent-inhabiting vestimentiferan siboglinid polychaetes. Hence, the overall contribution by the symbiotic microbes is ranked low (Giere et al., 1984).

Interestingly, these gutless tubificids draw nutrition through (i) osmotrophism and (ii) symbiosis. With relatively larger body surface area to volume ratio and thin cuticle, the oligochaetes are well adapted to uptake nutrients from ambient water across the body wall. Absorption of many amino acids and glucose by osmotrophic fauna may proceed from extremely low concentration against concentration gradients of 4–6 orders magnitude; on accumulation, these organic substances are metabolically used (see Pandian,

1975). Southward and Southward (1980) have estimated that the gutless worms can absorb glucose to meet 30% of the metabolic needs. The pore water within the sediments, from which the gutless tubificid *I. leukodermatus* have been collected, contains an extremely high concentration of glucose and fairly high levels of amino acids. *I. leukodermatus* is able to absorb mainly hexoses (but not pentoses) at the rate of $\sim 150 \mu\text{g}$ glucose/h. Among amino acids, aspartate is preferably absorbed in comparison to glutamate (Giere et al., 1984). As in hydrothermal vent inhabiting vestimentiferans, the tubificids display substantial activity of ribulose-1,5-biphosphate-carboxylase, a marker enzyme of the Calvin-Bensen cycle, known to be present only in bacteria and plants. The high levels of ATP-sulfurylase and sulfide oxidases indicate that enzymatic sulfur metabolism is carried by the symbiotic bacteria. These enzyme studies suggest that the gutless tubificids are able to draw ATP through the symbiotic microbes and oxidize sulfide for the fixation of inorganic CO_2 from ambient water. Hence, the gutless tubificids like *I. leukodermatus* can also thrive in sediments containing high concentrations of hydrogen sulfide. The preferred zone of *I. leukodermatus* lies between 5 and 7 cm depth, which correspond to +50 and -50 mV , i.e. in and around the redox discontinuity (RPD) layer (Fig. 1.5), where extremely high concentrations of sugars and amino acids are present in the pore water within the sediments. The worm keeps migrating between the upper oxic and lower anoxic depths. At the lower anoxic depth, it acquires and accumulates reduced sulfur but the necessary binding of oxygen occurs at the upper micro-oxic sediment layers (Giere et al., 1991). Strikingly, these gutless tubificids have successfully conquered and colonized an ecological niche, so far unoccupied by any other interstitial fauna (Giere et al., 1984).

In these gutless tubificids, the location of the microbial symbionts and complicated mode of reproduction suggests vertical transmission. In

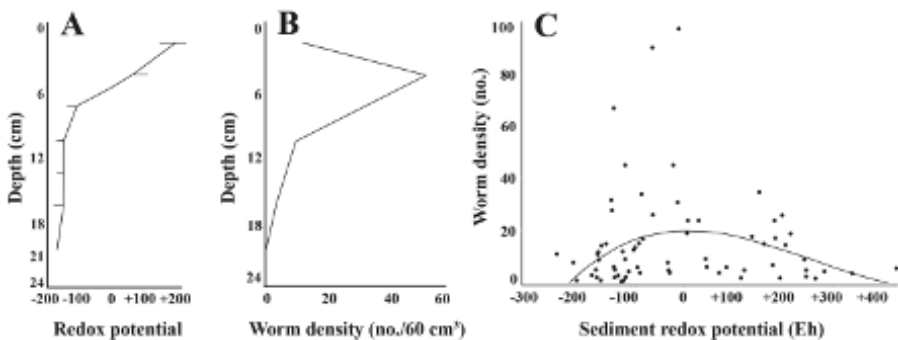


FIGURE 1.5

Vertical distribution of the gutless oligochaete *Inanidrilus leukodermatus* as functions of A. redox potential and B. worm density, and C. worm density as function of sediment redox potential (compiled, modified and redrawn from Giere et al., 1991).