

Review

Annelids in Extreme Aquatic Environments: Diversity, Adaptations and Evolution

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Abstract: We review the variety of morphological, physiological and behavioral modifications that annelids have acquired to cope with environments either unsuitable for, or on the limits of, survival for most animals. We focus on polychaetes (excluding sipunculans and echiurans) and clitellates (oligochaetes and leeches) and source information mostly from the primary literature. We identified many modifications common to both polychaetes and clitellates, and others that are specific to one or the other group. For example, certain land-adapted polychaetes show reduction in nuchal organs, epidermal ciliation and receptor cells, and other coastal polychaetes use adhesive glands and glue-reinforced tubes to maintain position in surf zones, while oligochaetes, with their simple body plans, appear to be ‘pre-adapted’ to life underground. Modifications common to both groups include the ability to construct protective cocoons, make cryoprotective substances such as antifreeze and heat shock proteins, develop gills, transform their bodies into a home for symbiotic chemoautotrophic bacteria, metabolize contaminants, and display avoidance behaviors. Convergent evolution in both directions has enabled annelids to transition from salt water to freshwater, sea to land via beaches, freshwater to soil, and surface water to subterranean water. A superficially simple worm-like body and a mostly benthic/burrowing lifestyle has facilitated radiation into every conceivable environment, making annelids among the most common and diverse animal groups on the planet.

Keywords: adaptation; habitat; environment; morphology; physiology; behavior; invertebrate; Annelida

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1. Introduction

Annelida has traditionally included Polychaeta, Oligochaeta and Hirudinea, the latter two together in the Clitellata. However, recent phylogenomic studies have shown that the monophyletic clade Clitellata is nested within the Polychaeta, rendering the latter paraphyletic and its taxonomic scope the equivalent of Annelida [1–3]. However, maintaining a distinction between the “polychaetes” and the “clitellates” remains evolutionary significant, as the polychaete–clitellate transition is associated with the loss of a larval stage and the emergence of direct development as one of several key adaptations to freshwater and terrestrial habitats [4]. In this chapter, and for the sake of convenience, we will use the vernacular term “polychaetes” to discriminate non-clitellate annelids from Clitellata. As pointed out by Weigert and Bleidorn [2], this is common practice for paraphyletic groups such as “fishes”, “reptiles” “crustaceans”.

In this overview, we consider annelids living in extreme aquatic environments (i.e., extremophiles) outside the typical range of conditions experienced by the group. Most examples we provide are free-living forms; commensals and ectoparasites, such as hirudineans

and myzostomatids, are largely excluded as these groups combined represent only approximately 2% of the total Annelida species diversity estimated at 30,000 [5], and as such would have little impact on our general conclusions. The focus of this chapter is on aquatic polychaetes and oligochaetes, as these two groups have many more examples of extremophiles than any other annelid group.

2. What Is a Polychaete?

Polychaetes encompass the traditional 80 or so families of the former class Polychaeta, plus the former phyla Echiura (now sister to the polychaete family Capitellidae), Sipuncula (uncertain position), and Pogonophora and Vestimentifera (the latter two combined as the polychaete family Siboglinidae) ([6] and references therein). Polychaetes are characterized by several morphological characters including segmentation via a pre-pygidial growth zone, a dorsal brain and ventral nerve cord, nuchal organs, longitudinal muscle bands and the structural composition of the capillary chaetae [7,8], although some of these features may be absent. Nuchal organs for example have been lost in clitellates and a few traditional polychaete families [7,8]. In keeping with their paraphyletic status, there are no evolutionary novelties (autapomorphies) that separate uniquely ‘polychaetes’ from clitellates. However, polychaetes tend to have separate sexes (clitellates are hermaphrodites), appendages on the prostomium, peristomium or pygidium (all lacking in clitellates), and parapodia bearing complex and numerous chaetae (clitellates lack parapodia and most of them have few, simple chaetae; leeches lack chaetae altogether).

Annelids comprise a single large clade, Pleistoannelida, which includes the vast majority of taxa including Clitellata, Siboglinidae and Echiura; this large clade is comprised of two smaller clades, Sedentaria (including Clitellata) and Errantia [6]. A basal grade including the sipunculans and a group of small polychaete families represents an early annelid radiation [2,6,9]. Fossil Annelida date back to the Cambrian, although forms we recognize today mostly arose at the end of the Carboniferous, approximately 300 Ma [10].

3. What Is a Clitellate?

Clitellata is a large taxon comprising approximately one-third of all known annelid species. A recent estimate places its divergence from sedentarian polychaetes in the mid-Palaeozoic Era, at least approximately 400 Ma, with all major extant clitellate lineages arising over the next ~150 million years [11]. The vast majority of the limnetic and terrestrial annelids belong to Clitellata [8], but the estimated rise of the highly diverse earthworm lineage (largely the taxon Crassiclitellata) was not until approximately 200 Ma [11]. The origin of the family Enchytraeidae, with a majority of its species on land today, was probably approximately 250 Ma [11].

Hirudinea [comprising Hirudinida (true leeches), Acanthobdellida and Branchiobdellida] are predatory and parasitic clitellates previously considered as sister group to Oligochaeta. However, morphological and molecular studies support that they originated near the oligochaete family Lumbriculidae, making Oligochaeta paraphyletic [12,13]. In analogy to the polychaete–clitellate case mentioned above, we will use the vernacular term “oligochaetes” only to discriminate non-leech clitellates from Hirudinea.

All sexually mature clitellates possess a clitellum, i.e., a modification of the epidermis into a glandular “girdle” near the female pores. This structure secretes a mucous cocoon, in which eggs are laid and fertilized, and embryonal development then proceeds directly without any polychaete-type larval stage. Clitellates are distinguished from polychaetes not only morphologically (see above) but they show a unique combination of other distinctive features such as hermaphroditism, the organization of their reproductive system and sperm ultrastructure [14–18].

Considering their universal adaptations to freshwater and terrestrial life, clitellates can be said to be extreme annelids by default; Kuo [4] reviewed the evo-devo background to these adaptations. Although it is clear that Clitellata has its root in Sedentaria, its sister group is yet unknown [2], and it is unsettled whether the earliest ancestor with a

clitellum and a typical clitellate reproductive mode arose before or after the colonialization of freshwater. Molecular evidence supports that the borders between sea, freshwater and land have been crossed several times in the evolutionary history of Clitellata [11].

4. What Is an Extreme Environment? What Is an “Extremophile”?

An organism that thrives in an extreme environment is an “extremophile”. Given that all physical and geochemical factors of the environment in which annelids live are on a continuum, extremes in any one factor may make it difficult for an organism to function [19–21]. Whether a species is an extremophile will depend on the annelid group in question. For the predominantly marine polychaetes, freshwater and terrestrial conditions count as ‘extreme’ environments; for oligochaetes, which have had a long evolutionary history in continental environments, the sea may hold more possibilities for extreme conditions. Extreme living in environments that are on the limits for survival has evolved convergently and repeatedly in annelids. The list of examples in this chapter is not exhaustive, but chosen to illustrate, especially, the adaptations to a variety of extreme conditions that are on the limits for survival of most other organisms.

5. Terrestrial Freshwater

Annelids are commonly found living in terrestrial freshwater, from the sediments of rivers and lakes to moist soils. Freshwater can be considered to be extreme for the marine derived polychaetes and the oligochaetes that have transitioned from marine to terrestrial waters. Polychaetes struggle to survive in freshwater because most are osmoconformers; when exposed to low salinities, they swell uncontrollably. Certain intertidal and estuarine species can withstand short periods of stress caused by changing salinities, but fundamental osmotic modifications are required for longer periods. Those polychaetes that have been able to penetrate and live permanently in freshwater are most probably osmoregulators as adults, although how they accomplish this is unknown as the osmoregulation is thought to develop after the larval stages. Protection of embryos and larvae from osmotic stress can occur with or without modification of the most common reproductive mode among polychaetes, i.e., free spawning with planktotrophic larvae. Species retaining the common mode may simply migrate seaward to spawn in more saline coastal waters, while modified strategies include various forms of brooding either inside the parent body, inside their tube, or encapsulation of embryos in a gelatinous mass (below).

The most successful freshwater family among the polychaetes by far is the Nereididae, with approximately 60 named species able to tolerate freshwater conditions, more than the combined number of species in the next three most successful families, Spionidae (26), Fabriciidae (13), and Sabellidae (11; Table 1) [22]. Almost half of the terrestrial nereidids belong to the subfamily Namanereidinae, which are found in every continent except Antarctica. Some of the more unusual habitats include tree leaf axils and plant container habitats (*Namalycastis hawaiiensis*, *Namanereis catarractarum*), rice fields in SE Asia (*Namalycastis rhodochorde*), and cisterns (*Namalycastis indica*) (Figure 1). The subfamily includes the highest reported elevation for a polychaete, 1600 m a.s.l. in cave pools in Mexico [23]. Glasby and Timm [24] suggested that the ancestor of *Namanereis* colonized freshwater as a result of a single colonization event prior to the breakup of Gondwana, although two invasions, of Gondwanan and Tethyan ages, were postulated in a later study [25]. The nereidid, *Simplisetia limnetica*, a freshwater polychaete found in the upper freshwater reaches of the Hawkesbury River, Sydney, Australia, may protect its developing young from osmotic stress by brooding them in its sedimentary galleries, which are more saline than overlying waters [26]. The larvae of other estuarine nereidids, particularly *Hediste* species, use tides to the wash larvae seaward and provide better chances of survival.

Freshwater Sabellidae include seven species of the highly modified genus *Caobangia*, shell-boring symbionts of gastropods and bivalves restricted to south and southeast Asia [22]. The closely allied Fabriciidae are represented by three sympatric species of *Manayunkia* in Lake Baikal: *M. baicalensis*, *M. zenkewitschii* and *M. godlewskii*; each occupies

a slightly different niche [27]. Sitnikova [28] claimed that a fourth species was present in the deep-water zone of the lake (at approximately 350 m depth) but it was never described and has not been mentioned again in later literature (see also below). Possibly, this ‘fourth’ species is a vagrant, as huge masses of water can suddenly sink into the deeper parts of the lake, probably bringing with them animals that normally do not live at such depths. A similar situation exists with the presence of *Nais* species (Naidinae, Naididae) under the dimictic layer of the lake, which is also unexpected given that species of this genus have a diet based on microalgae (and there is no light at such depths).

Among the oligochaetes, the Lake Baikal species *Baikalodrilus discolor* is characterized by unusual low osmotic concentration in its hemolymph, by comparison with *Spirosperma ferox*, a close Palaeartic relative, which is considered as an adaptation to low electrolyte concentrations of Baikal waters (see [29] and above). Another species of *Baikalodrilus*, *B. digitatus*, has peculiar epidermal projections on the body wall the function of which remains unknown (Figure 2A).

Table 1. Extremophile annelids and their adaptations. P = polychaete, O = oligochaete, H = hirudinid, and A = aphanoneuran.

Extreme Environment	Adaptation	Annelid Examples
Freshwater	osmoregulation	Namanereidinae (P), Fabriciidae (P), Sabellidae (P). <i>Baikalodrilus discolor</i> (O)
Land (for polychaetes)	reduced (or an absence) of nuchal organs; epidermis lacking ciliation; fewer types of receptor cells; embryos develop directly inside cocoons	Hrabeiellidae (P), Parergodrilidae (P), Nerillidae (P)
Deep-sea brine pools	avoidance	<i>Methanoaricia</i> sp. (P)
Hypersalinity, aridity	encysting; asexual reproduction	<i>Manayunkia athalassia</i> (P), <i>Lamprodrilus mrazeki</i> (O), some <i>Aeolosoma</i> species (A)
Frozen terrane	blood ‘antifreeze’ and other cryoprotective substances; increase internal energy levels; dehydration to lower mean supercooling point	Dinophilidae (P), <i>Dendrobaena octaedra</i> (O), <i>Enchytraeus albidus</i> (O), <i>Mesenchytraeus solifugus</i> (O)
High temperatures	protective tubes and cocoons, heat shock proteins	<i>Eisenia</i> spp. and <i>Amyntas</i> spp. (O), Siboglinidae (P) and Alvinellidae (P)
High-energy coasts and fast-flowing streams	small body, flat body, adhesive glands, strong tubes	many polychaete families; <i>Trichodrilus</i> sp. (O)
Subterranean	loss of eyes, pigmentation, elongation of sensory appendages (and legs), ability to cope with limited food resources	<i>Namanereis</i> spp. (P), <i>Marifugia cavatica</i> (P), <i>Croatobranchnus mestrovi</i> (H), <i>Trichodrilus</i> sp. (O)
Low oxygen	gills, unsegmented posterior end, high O ₂ affinity respiratory pigments, diel and seasonal vertical migration, oxygen debts	<i>Capitella</i> spp. (P), <i>Rhyacodrilus hiemalis</i> (O), <i>Croatobranchnus mestrovi</i> (H), Phallo-drilinae (O), <i>Aulodrilus</i> sp. (O)
Deep-sea vents and cold seeps	symbiotic autotrophic bacteria, host body-cavity ‘homes’ for symbiotic bacteria, long tubes	Siboglinidae, Alvinellidae (P), genera <i>Olavius</i> spp. (O) <i>Inanidrilus</i> spp. (O), Phallo-drilinae (O)
Pollutants (organic and inorganic)	metabolism of PAHs; assimilation of metals into hard structures, e.g., jaws; biotransformation of aromatic hydrocarbons	<i>Capitella</i> spp. (P). Namanereidinae (P), <i>Thalassodrilides</i> cf. <i>briani</i> (O)



Figure 1. Habitat of *Namanereis catarractarum* (Nereididae) in the moist dead leaf axils of *Pandanus vitiensis* beside Savuro Creek near Suva, Fiji. (A) Collecting dead leaves for examination in the lab. (B) Worms (almost transparent, arrows indicating position) found at the base of dead leaves in the moist layer between the plant fibers. Photographs: C. Glasby.

6. Hypersalinity and Aridity

Hypersaline conditions occur on land and in the sea. On land, such conditions are often associated with aridity. The Australian fabriciid *Manayunkia athalassia* (Figure 2B) has been recorded from hypersaline ephemeral lakes adjacent to the Coorong Lagoon in South Australia and other undescribed species of the genus are known from records in similar habitats in Western Australia [30]. *Manayunkia athalassia* can tolerate salinities of up to three times that of normal seawater (27–95‰). The worms also appear to be resistant to desiccation over the hot, dry summer months in southern Australia, as they can be revived from dried mud samples with the addition of distilled water (Table 1) [31]. In the deep-sea of the Gulf of Mexico, the orbiniid *Methanoaricia* sp. can tolerate short stays in hypersaline brine pools associated with hydrocarbon seeps, but usually avoids the most extreme conditions by aggregating on top of the associated mussel beds (Table 1) [32].

Marine Naididae are common in shallow tropical seas (including the intertidal zones), sometimes even in habitats with hypersaline conditions, with documented records of the genera *Heterodrilus* and *Ainudrilus* from up to approximately 54‰ in Saudi Arabia and Kenya [33,34]. From the Kenyan site, a high-intertidal beach in a mangrove, Healy [35] also described a species of *Marionina* (family Enchytraeidae).

In North Africa, water evapotranspiration is important due to the semi-arid to arid climate. This often results in high water conductivity or even high chlorosities, which is probably a factor explaining why the oligochaete fauna is impoverished in these regions [36]. The species present are known to prefer highly mineralized or brackish waters; they include *Paranais birsteini* var. *maghrebensis* and *Nais elinguis* (Naidinae, Naididae) [37], *Epirodilus* spp. (Rhyacodrilinae, Naididae), forms of *Tubifex tubifex* (Tubificinae, Naididae), and *Cernosvitoviella immota* (Enchytraeidae) [38]. One species, *Aktedrilus yacoubii* (Naididae; Figure 3A), belongs to a mainly marine subfamily Phallo-drilinae [39].

Among aquatic oligochaetes, encysting is an extreme adaptative response to the drying up of the animal's environment. *Lamprodrilus mrazeki* (Lumbriculidae) is a rare example of encysting in aquatic oligochaetes when pools dry up in summertime (Table 1). Archityomy, i.e., asexual reproduction by fragmentation, then occurs in the cysts [40,41]. The ubiquitous freshwater *Lumbriculus variegatus* and *Tubifex tubifex* have been observed dormant in a mucous cyst in the sediment of temporary pools [17].

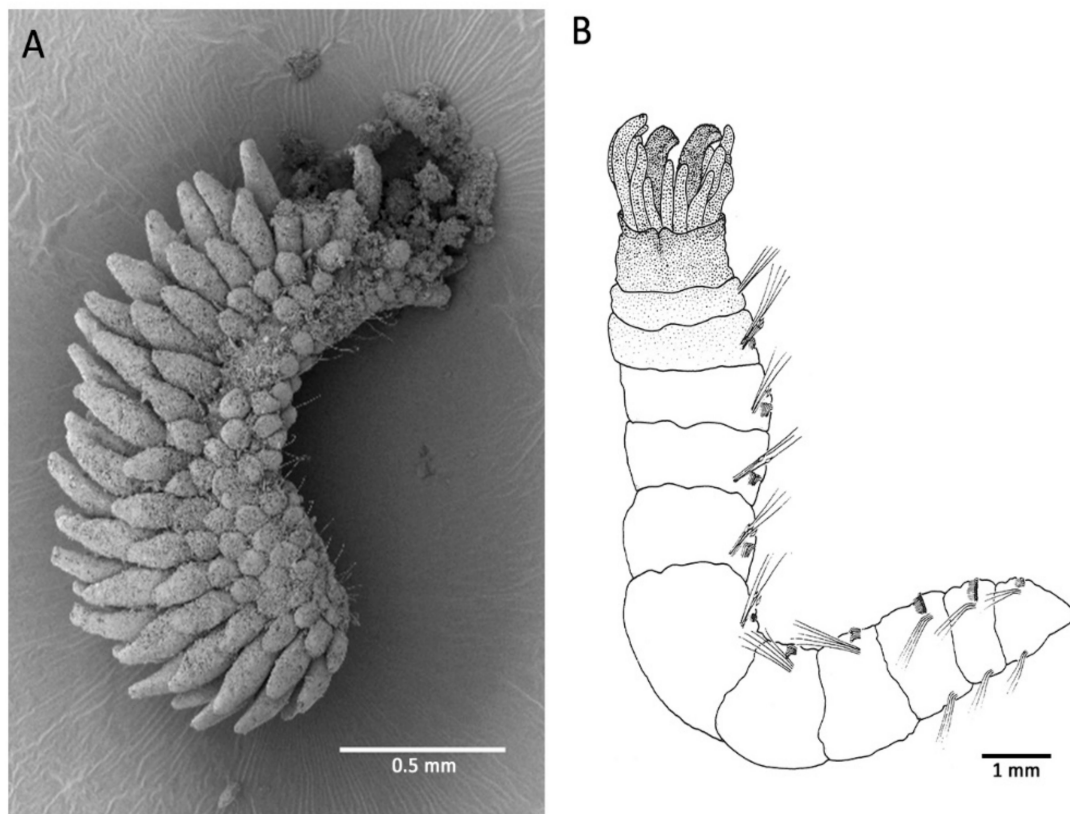


Figure 2. (A) The genus *Baikalodrilus* (Tubificinae, Naididae) is one of the most characteristic faunistic elements of the oligochaete community in Lake Baikal and constitutes a species flock in the lake with no less than 24 morphospecies known to date. *Baikalodrilus digitatus* is a species with epidermal projections of the body wall, giving the worm a resemblance to some nudibranchs. Photograph: P. Martin. (B), *Manayunkia athalassia* (Fabriciidae) from an ephemeral land-locked lake adjacent to Coorong, South Australia. After Hutchings et al. (1981: Figure 1a [31]).

A terrestrial habitat is considered extreme for polychaetes as, unlike oligochaetes, most typically lack protection for their eggs, and have vulnerable larval stages (but see below). There are only two entirely terrestrial families of polychaetes. Both are species poor and members live among other meiofauna in damp environments. The oligochaete-like *Hrabeiella periglandulata* (Hrabeiellidae) occurs in fresh, slightly acidic and well-drained soils in meadows and different types of forests (beech, fir, spruce) across Europe and northern Asia [42,43]. The Parergodrilidae are represented by two genera, the monotypic *Parergodrilus* (*P. heideri*), and *Stygocapitella* which is represented by 11 cryptic species. *Parergodrilus heideri* is found terrestrially in the humus-rich upper layers of soil in the Palearctic Region and *Stygocapitella* species are found worldwide, excluding the tropics, in the supralittoral zone of sandy beaches (i.e., semi-terrestrial) [44–49]. Both families have reduced (or an absence of) nuchal organs, the epidermis shows less (or no) ciliation, there are fewer types of receptor cells, and in Parergodrilidae embryos develop directly inside cocoons (Table 1) [45,49,50].

Most members of the non-clitellate Aeolosomatidae and Potamodrilidae, together comprising the taxon Aphanoneura, have an aquatic oligochaete lifestyle but some *Aeolosoma* can form desiccation-resistant cysts (a hardened membrane of mucus secreted by the worm) that allow them to survive adverse conditions and possibly enabling transport between water bodies by animals (Table 1) [51]. Herlant-Meewis [52] studied the encystment of *Aeolosoma hemprichi* in Canada, and concluded that it was induced by low temperatures, enabling hibernation during the winter season.

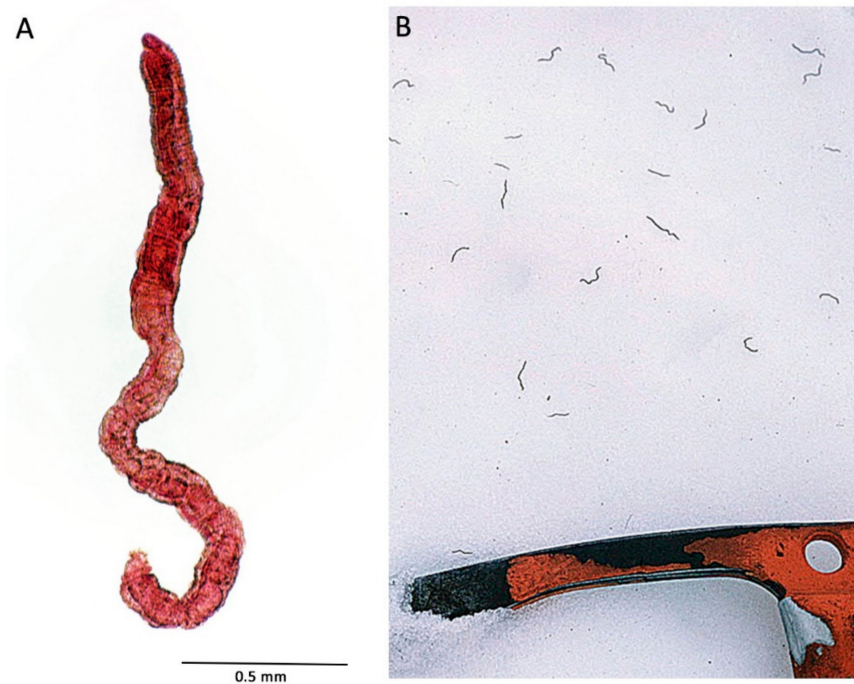


Figure 3. (A) *Aktedrilus yacoubii* (Phallodrilinae, Naididae), a stygobiotic oligochaete species from a resurgence in Morocco, illustrated as a freshwater representative of a mainly marine subfamily. Photograph: P. Martin. (B) The highly-pigmented aquatic “ice worms”, *Mesenchytraeus solifugus*, live in the melted ice cracks of North-American glaciers, tolerating only a narrow ± 7 °C range near freezing. Photograph: Dick Culbert, Stikine Icecap between Alaska and British Columbia; image cropped, otherwise unmodified, licensed under cc-by-2.0.

7. Extreme Temperatures, and Vents and Seeps

Aqueous environments are inherently less variable in temperature than subaerial environments. Therefore, it is not surprising to find more temperature extremophiles in terrestrial and supralittoral areas. Although many polychaete families show high diversity in sediments of polar seas, one appears to be particularly noteworthy. Dinophilidae, particularly *Trilobodrilus* species, inhabit interstitial coarse sands in the arctic, subarctic and boreal coasts, which can experience even colder temperatures than polar bottom waters, which largely remain above zero. In the laboratory, *T. axi* can withstand supercooled water without ice formation, with individuals of this species showing no damage after 5 h at -12 °C [53].

Holmstrup [54], referring to Zachariassen [55], noted that terrestrial oligochaete worms may have developed different strategies for survival in water-freezing temperatures. Sensitive species, likely to die if frozen, may promote supercooling by removal of ice-nucleating agents and proliferation of polyhydric alcohols and antifreeze proteins. Other species are more freeze tolerant and able to establish a controlled, protective freezing by dehydration of their extracellular fluids at high subzero temperatures by production of ice-nucleating agents. Holmstrup [54] studied the physiological mechanisms underlying the cold resistance of cocoons and juveniles of the earthworm *Dendrobaena octaedra* and found them not to produce cryoprotective, low molecular weight substances, but instead to use extensive dehydration to lower the mean supercooling point.

Sømme and Birkemoe [56] provided evidence that some arctic terrestrial Enchytraeidae also avoid freezing by dehydration at subzero temperatures and in this way survive temperatures as low as -15 °C. On the other hand, Slotsbo et al. [57] showed that the enchytraeid *Enchytraeus albidus*, which occurs in the supralittoral zone of arctic beaches, do use glyucose as a cryoprotective substance (Table 1).

The pigmented “ice worms”, *Mesenchytraeus solifugus*, live in ice cracks of some North-American glaciers, grazing on microalgae on ice surfaces on summer nights [58,59]; Figure 3B. They are aquatic rather than terrestrial animals, and they tolerate only a narrow ± 7 °C range near freezing [60]. The species is the only psychrophilic annelid, i.e., it lives and reproduces in the ice/snow of glaciers. It lacks cryoprotective agents but is able to increase its internal energy level when temperature falls, and all its biological processes are maintained even at 0 °C [61].

At the other end of the temperature scale, some earthworms, especially *Eisenia*, are well known for the ability to thrive in the high temperatures of organic compost, but the upper limit for survival is approximately 33 °C [62]. Studies of tropical earthworms have shown that cocoons of species of *Amyntas* can survive up to 38 °C (Table 1) [63].

In the marine realm, high temperatures are muted, although compared to surrounding conditions they may be regarded as ‘locally extreme’. Vestimentiferan siboglinids and alvinellids inhabiting deep-sea hydrothermal vents have the highest reported temperature tolerances for an aquatic annelid. The latter have developed strategies to cope with high (and variable) temperatures in these areas. Some species prefer temperatures between 40 and 50 °C, tolerating 55 °C for short periods [64]. Their tubes insulate the worm from high temperatures [65]. To cope with high temperatures, the alvinellids *Alvinella pompejana* and *Paralvinella sulfincola* have developed adaptations including a protective tube/cocoon made of positively and negatively twisted polymers layers comprising a stable glycoprotein matrix and elemental sulfur, a range of heat shock proteins and stress oxidative enzymes that remain stable and active at temperatures greater than 50 °C and, production of a thermally stable collagen (Table 1) [66–70]. To our knowledge, there are no records of oligochaetes from deep-sea hydrothermal vents with high temperatures (see McHugh and Tunnicliffe [71]), but nauidid clitellates (in *Tubificoides* and *Limnodriloides*) have been described in close proximity to hydrocarbon seeps on the continental slopes (at 540 to >2000 m depth) of the Gulf of Mexico [72] and off the US coast of the North-West Atlantic Ocean [73].

Many polychaetes living in “extreme” habitats, in particular elevated temperatures, occur in high abundances, have high growth rates, and may be numerically dominant. Several polychaete species living in the abyss display this behavior including the ampharetid, *Amphisamytha galapagensis*, which reaches densities of approximately 2200–3000 individuals per m² near hydrothermal vents in the Juan de Fuca area [71,74]. Hydrothermal vents are relatively short lived, subject to major disturbances and waxing and waning of fluid flow. Thus, the vestimentiferan siboglinid *Riftia pachyptila* grows extremely fast (the fastest growing invertebrate), but only in areas with relatively vigorous diffuse vent flow, and is relatively short lived [75,76]. Mass colonization of vestimentiferan siboglinids of new sites has been found, with growth to massive adult size completed in two years [77]. Other species living in extreme habitats live in very low densities, and presumably have also had to adjust their reproductive strategy to be able to reproduce. Cold seeps are relatively long lived and stable, so invertebrates living there such as frenulate siboglinids grow extremely slowly and are extremely long-lived [78–80]. Large individuals of *Lamellibrachia luymesii* with tube lengths over 2 m of are estimated to be older than 200 yr [79].

Hydrothermal vents are known in Lake Baikal, in Frolikha Bay, at approximately 420 m deep. Sediment temperatures under the bacterial mats that develop there are greater than 16 °C, a ‘local extreme’ compared to an ambient temperature of 3.47 °C [81]. On the contrary, the Frolikha vent houses rich freshwater benthic communities, which are built on ancient carbon and depend on in situ bacterial biochemosynthesis [82,83]. Densities of oligochaete species living near the vent have been found higher than at similar water depths and approximately nearly half of these species are only found in the dimictic zone of the lake, which extends up to 250 m deep in Lake Baikal [84,85]. Their presence at approximately 420 m depth, near the Frolikha vent, suggests that their bathymetric distribution is restricted by availability of food. Lake Baikal is indeed strongly oligotrophic and nutrient elements in the surface layer are recycled on average approximately four times before being removed to deep waters [86]. Hydrothermal vents in Lake Baikal would

instead appear as “food refuges” in an extreme environment from the point of view of food availability. In this respect, Lake Baikal shares similarities with the groundwater environment (see below).

8. Extreme Depths, and Other Depth-Related Factors

Great water depths are often associated with the marine environment, where depths can exceed 10 km. The pressure in deep water is extremely high, but this is largely unproblematic for soft-tissue animals (lacking free gases), as water volume is only slightly affected by it. Persistent low temperature and scarcity of food, however, are more challenging. The predominantly marine polychaetes are common in the deep-sea, where they occur in the water column and in the sediment of the deepest trenches, and as such are not dealt with in detail in this section. Many species of oligochaetes belonging to families Naididae (especially subfamily Phallodrilinae) and Enchytraeidae (genus *Grania*) occur in the deep-sea (species are listed in Erséus and Rota [87]), with the deepest record of a naidid from approximately 7700 m depth (*Bathydrilus hadalis*, in the Aleutian Trench, North Pacific Ocean [88]), and of an enchytraeid from approximately 2900 m (*Grania papillinatus*, off France in the North Atlantic [89]). For *B. hadalis*, even its clitellate-type cocoon has been described ([90] Figure 5).

Lake Baikal is one place on land where annelids can encounter extreme depths. The lake is unique because the water circulation carries oxygen to its deepest point (1642 m), which makes it the only freshwater lake in the world with an inhabitable abyssal area [91–93]. Oligochaetes are present at all depths although with an exponential decline of abundance and a decrease in sizes of animals with depth. No genuine deep-water oligochaete fauna seems to exist in Lake Baikal and the bathymetric distribution of oligochaetes is rather better explained by lower food availability at depth than by hydrostatic pressure ([85]; see also above).

Polychaetes (*Manayunkia* mentioned above) also occur in Lake Baikal, but they are primarily littoral species (3–20 m), although they are also present, but patchy, in the deep-water zone, below 250 m [27,28,94]. In the latter case, their presence is probably accidental because these sestonophagous, filter-feeding animals require an abundance of food particles which are probably limited at depth. Thus, the low salinity is more challenging for polychaetes (see above) than the extreme bathymetry of the lake. The strikingly low electrolyte content of Baikalian waters (not more than 150 $\mu\text{mol/L}$ sodium and 12 $\mu\text{mol/L}$ chloride) [95] can be considered as an extreme environment even for freshwater oligochaetes. *Baikalodrilus discolor*, which is one of the more characteristic faunal elements of the oligochaete community in Lake Baikal [96], presents a hemolymph with extremely low osmotic concentrations, which are considered as a physiological adaptation to the low electrolyte concentration of Baikal waters [29].

9. Subterranean and Cave Environments

The subterranean environment presents a difficult combination of extreme conditions including darkness, scarcity of food, limited variations in temperature, high physical fragmentation and, for the underground aquatic environment, low oxygen [97,98]. Only a few lineages are able to colonize and adapt to these inhospitable habitats [99]. Certain polychaete families have adapted to living in the water column of marine/anchialine caves, including the normally benthic Protodrilidae, Nerillidae, and Scalibregmatidae [100–102], while others live benthically and have secondary troglomorphic traits such as loss of eyes, pigmentation, and elongation of the sensory appendages [103]; Figure 4A–F. *Marifugia cavatica* (Serpulidae) is eyeless and lacks pigmentation, and is also considered to be a Tertiary relict of marine origin (Table 1) [104]; Figure 5B. The aptly named genus *Troglochaetus* (Nerillidae) is also found in the hyporheic zone of caves, wells and springs, with *T. beranecki* currently thought to occur in both Europe and North America. *Troglochaetus* has rudimentary parapodial cirri and, like all nerillids, development is direct, either via an external brood or in cocoons (Table 1) [105].

When polychaetes transition to underground environments, their typical sense organs (eyes, cirri) also tend to be reduced or absent, while other organs may be enlarged to compensate—for example, elongated parapodial cirri and antennae presumably both increase sensory awareness. Nereidid polychaetes adapted to living in the water column of marine/anchialine caves have been shown to have secondary troglomorphic traits such as loss of eyes or elongation of the sensory appendages (Table 1) [25,103].

Aquatic clitellates have a habitus that makes them pre-adapted to live in the subterranean environment [106]. In addition, they do not exhibit any peculiar morphological adaptations to subterranean life that can be seen in other subterranean organisms (loss of eyes, elongation of appendages and body, loss of pigmentation, increase in sensory structure). Therefore, the stygobiotic (i.e., obligatory hypogean) nature of the species can only be inferred from their exclusive presence in the subterranean environment. Despite their morphological pre-adaptation, only approximately 100 species of aquatic oligochaetes are exclusively present in groundwater out of approximately 1700 aquatic oligochaete species and 1100 freshwater species known to date [14,106]. However, biological and ecological traits that predispose oligochaetes and leeches to successfully colonize underground habitats are still mostly unknown. The ability to cope with limited food resources is probably an important adaptive factor.

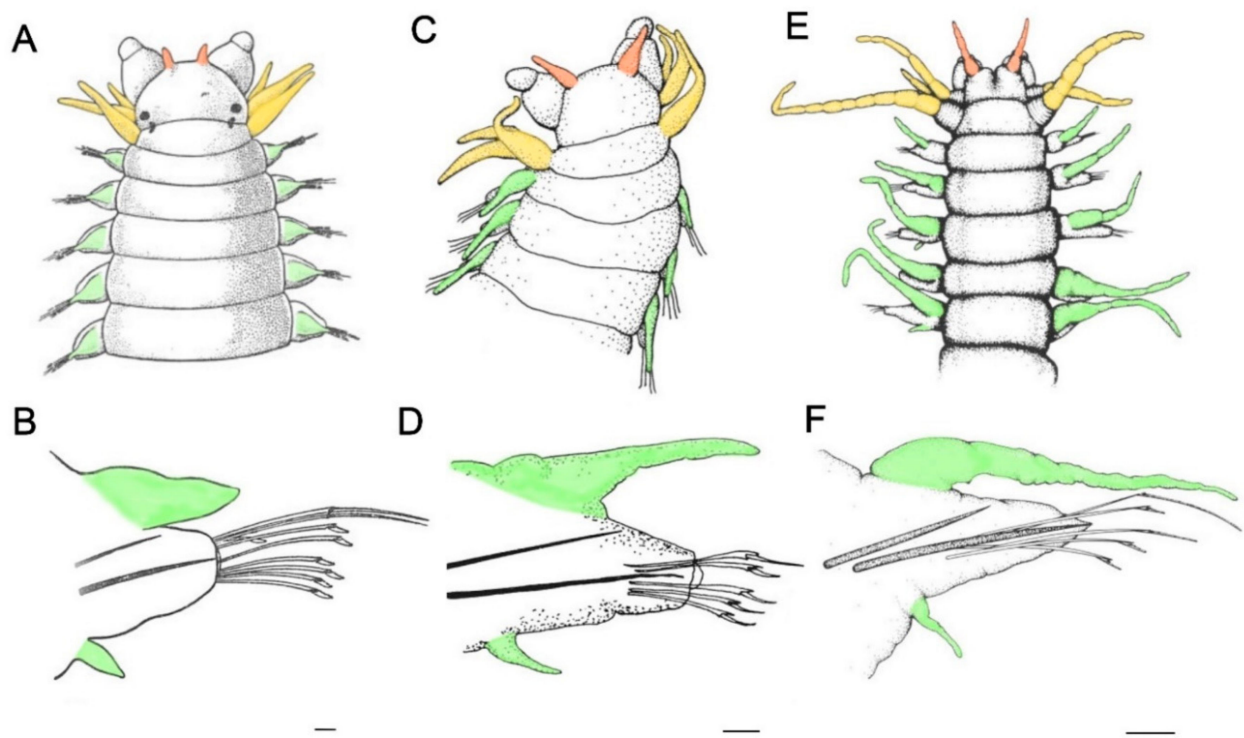


Figure 4. Typical morphology of *Namanereis* (Nereididae) exemplified by *Namanereis littoralis* (A,B), compared to the secondary troglomorphic traits in *Namanereis beroni* (C,D) and *Namanereis araps* (E,F), including loss of eyes, elongation of antennae, tentacular and parapodial cirri, and increase in length of the terminal blades of the articulated falcigerous chaetae (bar showing relative length). Adapted from Glasby et al. (2014: Figure 7 [25]).

On land, cave systems sometimes harbor physiologically or morphologically modified clitellates. An extreme example is the leech *Croatobranchnus mestrovi*, originally described by Kerovec et al. [107], but also known as *Erpobdella mestrovi* [108], which lives in deep shaft-like caves in the Velebit karst area in Croatia. It has been recorded as deep as 1320 m below surface in waters of 4–6 °C, and it walks around on the cave walls with leg-like appendages, which probably also function as gills (Table 1) [108] (Figure 5A).

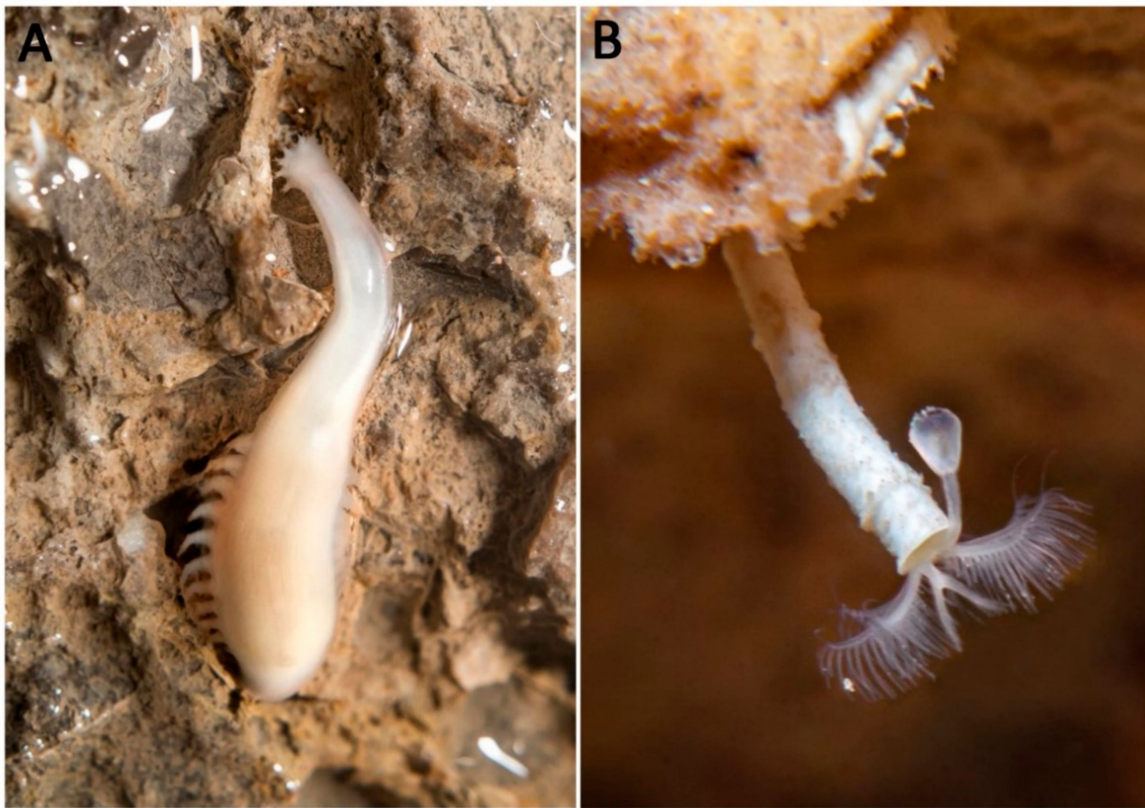


Figure 5. Two examples of subterranean annelids. (A) The leech *Croatobranthus mestrovim* lives in deep shaft-like caves in the Velebit karst area in Croatia. It has been recorded as deep as 1320 m below the surface, and it walks around on the cave walls with leg-like appendages. (B) The serpulid polychaete *Marifugia cavatica* attaches its calcareous tube to the walls of freshwater caves found on the eastern Adriatic coast and further inland; it is eyeless and lacks pigmentation. Photographs: Jana Bedek, archive of the Croatian Biospeleological Society.

Since photosynthesis is absent in the subsurface, life in this environment is highly dependent on trophic resources that can be imported from the surface environment. Yet food is not so much scarce as it is unevenly distributed. Moreover, among other ecosystems, the subsurface most resembles the hypolimnia of lakes (e.g., Lake Baikal) and the deep-sea in that, in this permanent and omnipresent darkness, the food that sinks from the surface into these habitats is patchily distributed. [99,106]. In Lake Baikal, food is clearly a limiting factor for some annelid species, as evidenced by the presence of some species near hydrothermal vents, where chemoautotrophic production is a substitute to primary photosynthesis production, located at depths where such species are never found [85]. As said earlier, the hypolimnion of Lake Baikal and groundwater are similar in environmental characteristics, which led Timm [109] to hypothesize that founders of some Baikalian oligochaete species flocks originated from the groundwater fauna.

Ironically, groundwater, as an extreme environment, turns out to be a refuge for annelids living in areas where conditions on the surface are even more extreme. In desert areas (Morocco, Arabian Peninsula), subterranean waters provide refuge for a diversified annelid fauna, including species of the oligochaete family Phreodrilidae whose presence in the northernmost part of an original geographical distribution assumed pan-Gondwanian is considered relictual, and the bifid-jawed polychaetes *Namanereis araps* and *N. socotrensis* whose present-day distributions on the Arabian Peninsula and Socotra Archipelago are suggestive of speciation following closure of the Tethys Sea [25,36,110,111]. These observations are interesting in that they demonstrate that an extreme environment loses its “extreme” nature once pre-adaptations, or exaptations, have allowed a population to pass the filter imposed by key ecological factors (in this case, the barrier of darkness) and actively colonize their new habitat [99].

10. High-Energy Habitats: Mobile Sediments and Surf Zone

Several families of polychaetes are specialized for living in unstable sedimentary environments of surf beaches. Species of the interstitial genera *Protodrilus* (Protodrilidae) and *Saccocirrus* (Saccocirridae) are swash zone specialists that are able to cling to sand grains using their caudal appendages and sticky mucous-exuding skin, and feed on plankton and carrion using elongated, highly motile ciliated feeding palps [112–115]. Larger-bodied forms such as Australian beachworms *Australonuphis* species (Onuphidae) also scavenge for dead morsels of food in the swash zone of surf beaches. Their great length, up to 2 m long, and muscular body help them to maintain station in the unstable substrate, and their prolonged anterior parapodia enable them to dig effectively and move rapidly toward stranded dead animals [116].

Other families also contain species adapted to high-energy conditions—the scalibregmatid *Axiokebuitta cavernicola* occurs only in coarse sands and gravel sediments in areas where there is active water movement produced by waves and tides and where the water turbulence precludes particle deposition [100]. Scalibregmatid polychaetes anchor themselves to coarse sediment by the adhesive papillae of the pygidium. These same worms use undulatory movements to swim for short distances.

Many species of Sabellariidae are adapted for life in the surf zone or shallow depths where current is strong for the animals to feed and capture sand grains for tube building [117]. They actively build tubes made of sand, shell fragments or other suitable particles glued together by a dark layer of mucoprotein secretions [118–120]. The tubes are attached to a variety of substrata, including rocks, seaweeds or invertebrates or other sabellariid tubes [30,121,122].

Several pholoin sigalionids (i.e., *Pholoe*, *Laubierpholoe*) are also known to inhabit interstitial sands of the surf zone including also *Imajimapholoe parva*, an intertidal member of the interstitial fauna, which is found in the nearshore surf zone in northern Japan. *Imajimapholoe parva* produces a sticky substance from their adhesive glands [123], which presumably helps them to stay within the coarse sediment.

In the surf zone, adhesive glands and a small flat body are adaptations to interstitial life [124]. The interstitial can be seen as an extreme environment due to the tiny size of the voids in which animals are constrained to live. Reduction in body size is a common morphological adaptation to this habitat (Table 1). In addition, as the marine littoral zone may function as a transitional zone between the marine and continental subterranean environments [106], adaptation to life in interstitial habitats can be considered for many marine meiobenthic species as a pre-adaptation to life in ground water, another extreme environment. Miniaturization and progenesis have both played a significant role in the evolution of annelids in interstitial environments [125–127].

The size of the marine interstitial *Psammodriloidea fauveli* Swedmark (Psammodriloidea), which is 25 times smaller than *Psammodrillus balanoglossoides* Swedmark, is not accompanied by a reduction in cell size but by anatomical changes and the absence of some organs as a result of progenesis [124].

The torrential regime of streams also constitutes in itself an “extreme” environment (water turbulence and sediment movement). In Maghreb countries (northwest Africa), it is responsible for strong variations in physico-chemical water parameters (temperature, salinity, dissolved oxygen, sedimentary load, etc.) [36]. As a result, streambeds are often an inhospitable environment for the oligochaete fauna, which is forced to find refuge beneath and alongside the riverbed (hyporheic zone). Due to greater environmental stability, groundwater (underflow, groundwater tables) probably plays an important role in maintaining a diverse aquatic fauna. In the high mountain Pyrenean torrents, the Enchytraeidae and the genus *Trichodrilus* (Lumbriculidae) are the only oligochaetes to resist the velocity of the current and the coldest temperatures [128]. Martínez-Ansemil and Collado [129] also showed that the Enchytraeidae dominate in streams with high current velocities associated with a mineral substrate of large granulometry. In the Maghreb countries, *Trichodrilus* is also commonly present and has been collected in streams where the temperature can reach

38 °C [130]. It thus appears that the ability of this genus to persist in streams with torrential flow depends less on its resistance to extreme temperatures than on its ability to withstand the power of fast-flowing water over a coarse, gravelly bottom (Table 1). The fact that *Trichodrilus* is frequently found in the hyporheic zone of the oueds is probably a strategy that allows the genus to cope with these extreme living conditions [36].

11. Low Oxygen: Organic Enrichment, Sulfidic, Methanic Sediments

Some groups of oligochaetes and polychaetes thrive in environments where levels of oxygen are low and hydrogen sulfide and methane are high. These conditions are common in coastal and terrestrial waters where there is organic enrichment, and in the deep-sea where there is mineral enrichment resulting from, for example, hydrocarbon seeps. Perhaps the best-known examples among polychaetes are the capitellids. *Capitella* spp. are often abundant in organically rich sediments (up to 47,000 ind.m⁻² in *C. telata*, see [131]). In the latter category, *Capitella* spp. can thrive in organically rich sediments by their fast response to large influxes of organic material and the resultant anoxia due to the lack of competition by less-stress-tolerant species as well as their early maturation and high reproductive potential [132]. Forbes et al. [133] suggested that *Capitella* spp. populations were strongly influenced by a physiology well adapted to exploit low oxygen and respond rapidly when more favorable oxygen conditions returned. Other intertidal capitellid species are able to tolerate periods of low oxygen levels or reduced salinities during low tide by building up oxygen debts which are repaid on the incoming tide (Table 1) [134]. Such physiology may allow some species to live in highly anaerobic sediments.

Cirratulids are often the dominant group in soft, nearshore sediments having reduced oxygen levels often associated with organically enriched sediments. For example, *Raricirrus beryli* inhabits upper slope sediments, sometimes near oil rigs, at continental shelf depths down to 500 m in the North Sea [135,136], and is a colonizer of organically enriched sediments in experiments near mud volcanos in the Bay of Cádiz, Spain [137].

Among Errantia, members of Namanereidinae (Nereididae) and Eunicidae are perhaps the best known for living in reduced sedimentary environments. For example, the *Marphysa sanguinea* complex is one of the few polychaetes able to endure the high organic loads of marine fish farms in the tropics [138] and among the nereidids, the intertidal *Namalycastis* species are commonly one of the few annelids found in the polluted, foul-smelling mangrove muds.

In aquatic oligochaetes, the ability of many species to thrive in heavily organically enriched sediments has long been known [139]. This ability has been widely exploited in research on pollution biology and its applications, for which oligochaete worms have proved useful. Rodriguez and Reynoldson [140] give a recent and detailed overview for many species. Other interesting examples are some marine naidids, e.g., members of the genera *Tubificoides* (Tubificinae) (e.g., [141]) and *Thalassodrilides* (Limnodriloidinae) (e.g., [142]), which are well known for their occurrence in eutrophic, often polluted, coastal sediments enriched with hydrogen sulfide. Of particular interest are also the marine gutless Phallophorinae, which actively migrate between the lower sulfidic and the upper oxygenated sediments and have evolved a mutualistic obligatory symbiosis with chemoautotrophic bacteria (Table 1) (see [143] and below).

A physiological strategy common to both oligochaetes and polychaetes to cope with reduce oxygen levels is modification of their respiration pigments, including hemoglobins. The orbiniid *Methanoaricia* shows a high hemoglobin–oxygen affinity and is able to withstand extended periods of anoxia [144,145]. The oligochaetes *Potamothenix hammoniensis* and *Tubifex tubifex* living in an oxygen-poor sediment or even periodically anoxic are known to be rich in erythrocrucorin [17]. In many annelids, erythrocrucorins provide large oxygen-carrying capacity through their high number of oxygen binding sites per complex and their high concentration in the blood [146]. Erythrocrucorin's high affinity for oxygen is usually seen as an adaptation to the hypoxic conditions prevailing in the habitat of animals using this protein.

Rhyacodrilus hiemalis is a freshwater naidid species endemic to Japan. It is known for its remarkable seasonal vertical migration in the sediment of Lake Biwa. During the cool season, it is a dominant littoral component of the oligochaete communities. During the summer, however, it can migrate up to 90 cm deep into the anoxic sediment, where temperatures are milder than in the littoral zone. In the absence of diel vertical migration, *R. hiemalis* is assumed to use anaerobic respiration when aestivating in this extreme environment, which could be based on glycolysis of glycogen [147].

The family Siboglinidae is specialized for life at the border of aerobic and anaerobic environments, including deep-sea vents and cold seeps. Siboglinids have a high concentration of hemoglobin in solution, which binds and transports both oxygen and sulfide, the latter in a non-toxic form that can be released to symbiotic chemoautotrophic bacteria [148]. Siboglinids utilize the organic material synthesized by the chemoautotrophic bacteria in their modified mid gut (trophosome) to produce their own organic compounds and derive energy. *Osedax* (Siboglinidae) utilize chemoheterotrophic bacteria to source their energy from whale bones and other bones on the seafloor.

While vestimentiferan siboglinids are arguably the most distinctive members of the faunal assemblage of hydrothermal vents, the polychaete family Alvinellidae is also well adapted to live in this harsh environment. Alvinellids differ in having functional feeding tentacles and a well-developed gut. They derive nutritional products from chemoautotrophic bacteria, which attach either to the inner part of the tube and/or mucous threads on the body secreted by the worm, and are ingested by the worm [149–151]. Further, the hemoglobins of Alvinellidae exhibit very high affinities for oxygen counterbalanced by a pronounced Bohr effect, which allows for an enhanced release of oxygen under low-pH conditions [152–154].

In both families, the relationship between the worm and its symbiotic bacteria has led to morphological adaptations in the worm. In siboglinids, the symbiotic bacteria live in a trophosome, a modification of the larval midgut; in alvinellids such as *A. pompejana* the epibiotic bacteria are housed in dorsal or posterior end expansions bearing modified geniculate setae [155].

Among the oligochaetes, one particular lineage (genera *Olavius* and *Inanidrilus*) of marine gutless Phallo-drilinae has evolved a mutualistic obligatory symbiosis with subcuticular chemoautotrophic bacteria, resulting in the complete loss of the worms' mouth and alimentary canal (e.g., [143,156]). These gutless phallo-drilines are particularly common in calcareous fine sands of shallow coral reef areas, but they may be found also in various other marine habitats, from the intertidal zone to several hundred meters depth. The symbiotic bacteria obviously provide nutrients to their hosts, which may migrate between the lower sulfidic and the upper oxygenated sediments in the sediment, implying "that sulfide is taken up in the anoxic deeper sediment layers, oxidized to sulfur by either nitrate from the environment or oxygen from the worm's hemoglobin, and the sulfur stored in the bacteria until the worms migrate to upper sediment layers where the sulfur could be fully oxidized to sulfate" ([143]: p. 256). In some cases, however, gutless worms may, in addition to the sulfide-oxidizing bacteria, have sulfate-reducing symbionts producing sulfide; these oligochaetes thus have established their own sulfur circuit by recycling sulfide internally [157].

Living in low oxygen sediments has produced one similar morphological response among gut-bearing oligochaetes and polychaetes: a proliferation of gills on the head or the posterior region, depending on which end of the body is closest to the oxygenated sediment/water-air interface. For example, the large, bright red gills of vestimentiferan siboglinid tube worms provide the huge surface areas required to extract oxygen from surrounding, often oxygen-poor, deep-sea waters. The animals extend their red branchial crown and white obturaculum into the water, leaving the rest of the body, from the collar backwards, inside the tube. The posterior end of both oligochaetes and polychaetes may be prolonged, or flattened, to increase the body surface area in order to maximize oxygen absorption.

Polychaetes, such as Sabellidae, Fabriciidae and Serpulidae, can also take up oxygen through their multi-functional, pinnulated tentacles surrounding the head, which also serve to collect food. In addition to modified posterior ends, gills and tentacles, parapodial structures can be modified (usually by way of enlarged and/or flattened lobes) to provide the additional surface area for oxygen uptake. For example, namanereidin polychaetes (*Namalycastis* species) inhabiting the decaying vegetation of mangrove zone use their highly vascularized, leaf-like posterior parapodial cirri for oxygen uptake [158]. Opheliids, capitellids and cirratulids are often abundant in low oxygen environments of the coastal zone; they use gills, and sometimes modified posterior ends to facilitate oxygen uptake.

Among oligochaetes, three morphological adaptations can be seen to cope with low oxygen content in the environment. Gills can sometimes be observed on some aquatic oligochaetes, but this is not a widespread adaptation. In the Naididae, they are known around the proctodeum in *Dero* and *Aulophorus*, or as external gills supported internally by hair chaetae in *Branchiodrilus* (Figure 6), or as finger-like gills dorsally and ventrally on the hind body of *Branchiura sowerbyi* [16]. In the Phreodrilidae, *Phreodrilus branchiatus* has finger-like gills present laterally [159]. Another type of morphological adaptation is the absence in species of the genus *Aulodrilus* (Naididae), of segmentation of their posterior end which is used as a respiratory organ (Table 1) [40]. In the Lumbriculidae, *Lumbriculus variegatus* and some *Trichodrilus* species, the circulatory blood vessel has developed networks of branched and blind lateral blood vessels that probably allow better irrigation of the segments and, hence, better oxygenation [17].



Figure 6. *Branchiodrilus* sp. (Naidinae, Naididae), a branchiate oligochaete showing external gills supported internally with hair chaetae (illustrated specimen from Cambodia). Photograph: P. Martin.

Another morphological strategy to maximize oxygen uptake exclusively employed by polychaetes is to live in very long tubes. Frenulate siboglinids use their long permeable tubes to reach oxygenated surface waters when the deeper layers are reduced. The animal's great length allows it to bridge the redox discontinuity, with oxygen uptake in the anterior body transported by its blood, bound to hemoglobin, to the symbiotic bacteria in the lower part of its trunk where sulfide or thiosulfate diffuse in from the sediment [148].

Sediment pore water and overlying sea water provide dissolved carbon dioxide, and organic nitrogen may be obtained as dissolved organic compounds or ammonia from the pore water. Similarly, *Spiochaetoperus* species (Chaetopteridae), which can be found in sediments from coastal to deep-sea hydrothermal vents, appear to use their long straw-like tubes to survive in the reduced muddy sediments adjacent a former bauxite refinery in Gove Harbour, northern Australia; they are the only macroinvertebrate able to tolerate the anoxic, alkaline muds resulting from waste water derived from the use of caustic soda to extract alumina from bauxite, although precisely how they do so is unknown (see also Extreme pH below; CJG pers. obs.).

12. Inorganic and Organic Contaminated Sediments

A few groups of polychaetes can tolerate heavy metal pollution. At Port Pirie in South Australia, sediments near an iron ore smelter operating since the beginning of the 1900s have extremely high levels of heavy metals—they are almost exclusively colonized by polychaetes. Ward and Hutchings [160] found that three or four species of polychaete were the most invertebrates at the most contaminated sites adjacent to the outflow pipes. One of these, a species of *Capitella*, occurred almost exclusively at the most contaminated site at a density of 322 worms per m², indicating that the species is self-sustaining and can tolerate very high concentrations of metals. Dense populations of *Capitella* can also build up rapidly in oil contaminated sediments [161], and members of this genus and *Ophryotrocha* (Dorvilleidae) are commonly encountered in the organically-enriched sediments of aquaculture facilities [132].

Heavy metals are a common component in sewage outfall discharges and a positive relationship between the concentrations of these components in the sediment and abundance of capitellids is shown in several studies. Densities of more than 300 ind. m⁻² were found to occur in a self-sustaining population in proximity to a south Australian lead-zinc smelting facility, where high concentrations of Pb (up to 5270 µg.g⁻¹) and Zn (up to 16,700 µg.g⁻¹) occurred in the sediment [160].

Among the oligochaetes, the marine Limnodriloidinae *Thalassodrilides* cf. *briani* (Naididae) was found to survive in polluted sediments with polycyclic aromatic hydrocarbons, in particular 1-nitronaphthalene, a toxic and carcinogenic chemical, and to biotransform them into substances that are not toxic to fish (Table 1) [162,163]. *Thalassodrilides* cf. *briani* increases the CYP (cytochrome P450) gene expression when exposed to polluted sediments with polycyclic aromatic hydrocarbons (PAH). Cytochrome P450 enzymes play important roles in the metabolism of exogenous compounds such as PAHs [163].

13. Extreme pH

Lake Van in Eastern Turkey is the largest soda lake in the world [164], with a pH of 9.5–9.9, a salinity of 21–24‰, and an extreme alkalinity for lakes with 155 m eq/L [165]. Its impoverished fauna includes a single clitellate, *Enchytraeus polatdemiri*, which occurs at profundal (8–115 m) depths in the lake [166]. This taxon is a member of the *Enchytraeus albidus* species complex, where other members are characteristic of high-intertidal habitats in seashores [167]. Other *Enchytraeus* species considered closely related to *E. polatdemiri* are also known from brackish-water lakes (see, e.g., [166,168,169]), giving further support to a marine rather than limnic origin of the Lake Van species.

14. Concluding Remarks

Polychaetes, clitellates, and the less diverse non-clitellate aphanoneurans present their own unique adaptations to cope with particular extreme environments, reflecting their existing body plans and morphological and physiological capabilities (Table 1). For example, some polychaetes construct protective tubes to cope with high-energy environments, oligochaetes are pre-adapted to life underground, and one leech is capable of growing legs to find its next meal. However, it is the shared similar strategies for coping with these adversities that is perhaps the most notable, particularly between polychaetes and clitellates—

both groups show the ability to construct protective cocoons, manufacture cryoprotective substances such as antifreeze and heat shock proteins, develop gills (greater capacity in polychaetes), transform their bodies into a home for symbiotic chemoautotrophic bacteria, metabolize contaminants, and avoid the most extreme of extreme conditions as much as possible by their local migrations and reproductive behaviors.

Annelids have largely retained a superficially simple worm-like body plan along with a mostly benthic/burrowing lifestyle, and yet they have been capable of immense radiation, both morphologically and physiologically. Over and over again, they have, by convergent evolution and in both directions, overcome and crossed the transitions from salt water to freshwater, sea to land via beaches, freshwater to soil, and surface water to subterranean water. Our overview has shown that these steps include a plethora of adaptations to extreme conditions and habitats not suitable for other animal life. Conceivably, it is the simplified “annelid” bauplan that has made it possible to cope with a multitude of living conditions. As one of the oldest group of invertebrates, annelids are indeed survivors and deserve their position among the most common and diverse animal groups on the planet.

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