Nikolaj A. Livanow (1876 – 1974) and the living relict *Acanthobdella peledina* (Annelida, Clitellata)

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Abstract
The Clitellates are segmented worms (Annelida) that are characterized by a glandular girdle responsible for cocoon production. They are usually classified as the Oligochaeta (earthworms and allies) and the Euhirudinea (true leeches); these carnivorous clitellates use two suckers for attachment and crawling. In 1850, A. E. Grube discovered a primitive leech with only one (posterior) sucker and earthworm-like cephalic chaetae for attachment to its host. The anatomy of this living relict (Acanthobdella peledina) was described by N. A. Livanow in 1906. Our knowledge of A. peledina is based on Livanow's detailed and comprehensive monograph in which this fish parasite is identified as an ancient hirudinean. In this article we describe the life and major scientific works of N. A. Livanow and summarize his contributions to annelid systematics. We also review the life cycle and phylogenetic position of the connecting link, A. peledina, based on anatomical studies and DNA sequence data. It is concluded that both Livanow's hypotheses concerning the phylogenetic relationships within the clitellata and his interpretation of the living fossil A. peledina were correct. In addition, the second Acanthobdella species, A. livanowi Epshtein 1966, is briefly described and commented on.

Introduction

One century ago a seminal paper was published in the German periodical *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* that later became a citation classic in the literature on the taxonomy of the "segmented worms" (class Annelida). The *Zoologische Jahrbücher* were founded in 1886 by J. W. Sprengel and are nowadays continued under the new title, *Zoology*. In 1906, the Russian zoologist N. A. Livanow published a comprehensive monograph entitled "*Acanthobdella peledina* Grube, 1851" (230 pages, with numerous figures and plates) that was supplemented and updated by the author Livanow in a famous publication of 1931. In this second article, which was largely based on his classical original paper, the relationships between the Hirudinea (leeches) and the Oligochaeta (earthworms and related taxa) were analysed, and a phylogenetic hypothesis was proposed (Livanow 1906, 1931).

In the year 2001, an international team of invertebrate zoologists published a paper in the journal *Molecular Phylogenetics and Evolution*, wherein the authors confirmed the basic conclusions of the Russian scientist that were drawn exclusively on the basis of anatomical studies, combined with the strict use of the comparative method. In the title of this multiauthor-article the Russian zoologist is explicitly acknowledged: " Validating Livanow: Molecular data agree that …" (Siddall et al. 2001). In spite of the fact that N. A.

Livanow is still frequently cited in the scientific literature, nothing is known in the Western world about the life and work of this eminent biologist. The aim of this historical account is to describe the career and achievements of Livanow, with special reference to the "living fossil-leech" *Acanthobdella peledina* (Grube 1850).

Nikolaj A. Livanow: a short biography

The biographical data summarized here were obtained from several journal articles published in Russian. The senior author (V. M. Epshtein) translated the pertinent literature into English so that a brief summary of the life and scientific work of Livanow could be compiled.

Fig. 1: Nikolaj Alexandrovich Livanow (1876 – 1974) in his laboratory.

The Russian zoologist and evolutionist Nikolaj Alexander Livanow (1876 – 1974) was born 20. November 1876 in Saratow. A few months after his birth the family moved to the town Wjatka, where Nikolaj's father was employed as a school inspector.

When he lived in Wjatka and Kazan he attended a Gymnasium and left school in 1895 with excellent credits (Livanow was awarded the prestigious "gold medal"). In the same year, he began his studies in natural science at Kazan University and received his diploma (1st. grade) in 1899. In 1902 the 26-year old biologist published a monograph on leeches of the genus *Hemiclepsis* (Livanow 1902); this contribution was his first scientific publication. His pioneering paper on *Acanthobdella peledina* was published in 1905 in German (a Russian version appeared one year later). In 1907 Livanow was promoted to the rank of a Magister of Science at the University of St. Petersburg and became an assistant at Kazan University. Due to the generosity of his supervisor, Prof. E. A. Meyer, Livanow was permitted to work from 1907 to 1910 at the Biological Station in Naples (Italy), where he studied the invertebrate fauna of the Mediterranean.

In 1914/1915 Livanow left Kazan to live in Moscow, where he was a lecturer in the department headed by Professor A. N. Severtzoff (Levit et al. 2004). Thereafter, Livanow was employed at the Petrowskaja Academy as an assistant of Professor L. S. Berg. One year later he returned to Kazan, where Livanow was appointed to the position of Professor and head of the Chair of Zoology of Invertebrates (1918). Thirty years later he retired (1948) but lectured on a variety of topics until 1970. On 7. December 1974 Livanow died at the age of 98 years.

During his active time as Professor of Invertebrate Zoology, Livanow went on expeditions to the White Sea (1920 – 1922), the North Sea (1928), and Lake Baikal (1931). He received many honours and ranked among Russia's most famous naturalists.

Livanow published articles and book chapters on the following topics: systematics, morphology and anatomy of invertebrates (Hirudinea, Oligochaeta, Polychaeta, Echiuroidea, Nemertini, Planaria, Pogonophora), the evolution of the nervous system, and general aspects of evolutionary morphology. Fifty years ago he published a textbook in Russian, entitled *The Direction of Evolution in the Animal World* (Livanow 1955), that became widely known. This monograph was translated into German, the language of science during the 1950s.

At the age of 94 (1970) Livanow published his last contributions to the zoological sciences, a book chapter on general rules in organismic evolution (Livanow 1970a) and a theoretical journal paper on the origin of the metazoa (Livanow 1970b). The Russian biologist remained active into his ninety-seventh year.

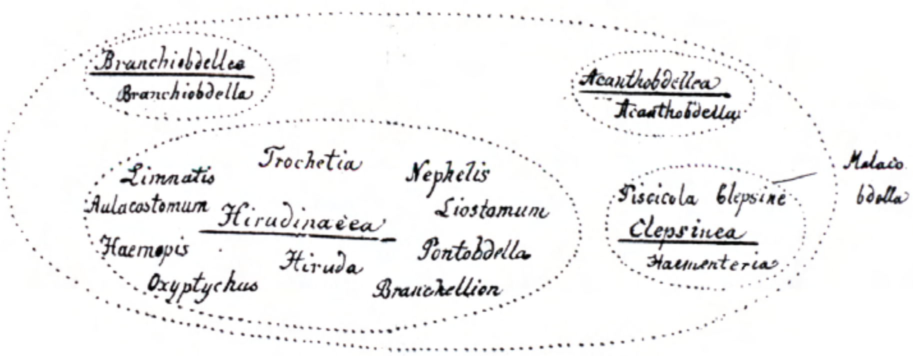

Fig. 2: Systematic position of the family Acanthobdellea (one genus, Acanthobdella). Scheme that is part of a larger drawing entitled "Survey of the families and genera (of annelids) according to their relationships" (Adapted from Grube 1850).

Acanthobdellidae: ancient leeches with chaetae

In 1850, the zoologist A. E. Grube published a comprehensive paper entitled "The Families of the Annelids". The class Annelida *sensu* Cuvier was defined by this author as a group of metamerically segmented worms in which the nerve cord is located ventrally. According to Grube (1850) the annelids are comprised of the orders Polychaeta, Oligochaeta, Hirudinea (Discophora) and Onychophora. Today we know that onychophorans (velvet worms such as *Peripatus*) are not annelids. They are classified as Proarthropoda, a sister group of the Euarthropoda (insects, crustaceans etc.). However, the other three orders established by Grube have "survived", i.e., the basic classification of this early annelid researcher is still valid (Herter 1968; Sawyer 1986 a, b, c; Mann 1962; Edwards and Bohlen 1996; McHugh 2000; Kutschera 2006).

Under the headline "Discophora" (i. e., Hirudinea), the naturalist A. E. Grube (1850) summarized the following taxa: Hirudinacea, Clepsinea, Branchiobdellea and Acanthobdellea. According to Nesemann and Neubert (1999), the Phylum Annelida contains the Subphylum Clitellata, a term that was coined by Michaelsen (1919). The clitellates are comprised of the classes Hirudinea, Branchiobdellida and Acanthobdellea; this modern taxonomy largely corresponds to Grube's original classification (Hirudinacea + Clepsinea: true leeches; Branchiobdellea: epizoic annelids that live on freshwater crustaceans; Acanthobdellea: leeches with chaetae). On the last page of his monograph, Grube (1850) introduced the family Acanthobdellea Gr. with one genus, *Acanthobdella* Gr., and one species (*A. peledina*, Grube 1850). In this original description, the author refers to an obscure publication (Middend. Sibir. Reise Bd II. Th. I. Annelid. p. 20. Taf. I. Fig. 1. a, 1. b), which we have identified as a chapter in a book edited by A. T. v. Middendorff (Grube 1851). In accordance with Nesemann and Neubert (1999), we have used the correct taxon name, *A. peledina* Grube 1850, and we do not refer to A. E. Grube's subsequent paper of 1851, as other zoologists have done (Livanow 1906; see Sawyer 1986 a, b, c).

In his monograph, Grube (1850) repeatedly referred to the taxon Acanthobdella. On pages 280/281 he defines the genus as follows: "Discophora (i. e., Hirudinea) with chaetae instead of an anterior sucker". In a hand-written scheme he depicted the taxa Branchiobdellea, Hirudinacea/Clepsinea and Acanthobdellea according to their presumed relationships (Fig. 2).

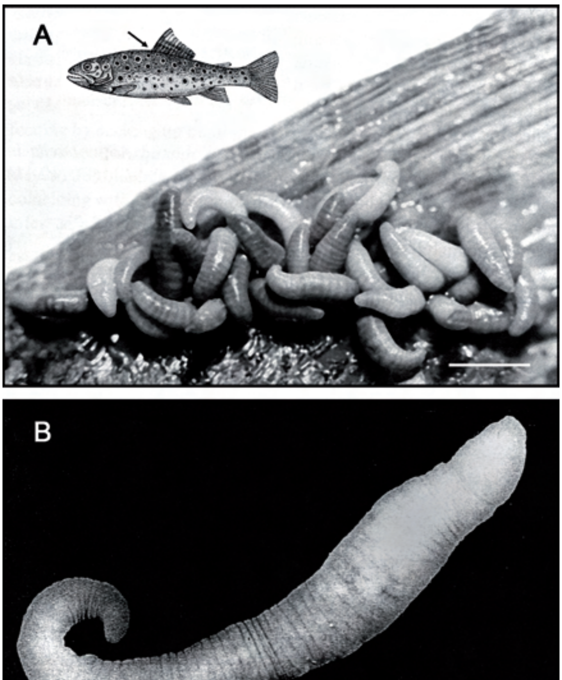

Fig. 3: The ancient leech Acanthobdella peledina. About 35 live individuals attached to the base of the dorsal fin of a salmonid fish (A). Alcohol-preserved leech (B). Bars = 1 cm (A) and 5 mm (B). (Adapted from Sawyer 1986 b and Epshtein 1987).

However, Grube (1850) pointed out that it is necessary to elucidate the anatomy of *Acanthobdella* to further explore the systematic position of this ancient leech with chaetae.

By the end of the 19th century, field naturalists had discovered that *Acanthobdella* inhabits cold water lakes in the northern regions of Europe. It is a parasite on salmonid fishes that attaches its head region to a host by the use of its hook-shaped chaetae (Fig. 3).

However, no details about the life cycle of this rare annelid were provided by these early biologists.

The pioneering work of A. N. Livanow and its confirmation

The Russian biologist Livanow (1906) was the first to study the internal organisation of *Acanthobdella peledina*, using classical histological techniques and the light microscope. He collected living specimens during the summer of 1902 in the Onega Lake close to Wytegra. About 100 leeches were picked up by him from salmonid fishes and preserved in a fixative. The anatomy of *A. peledina* was reconstructed based on stained sections. Livanow's monograph is of such a high quality that it formed the basis for much theoretical speculation over the subsequent decades. Figure 4 shows the anatomy of *A. peledina*;

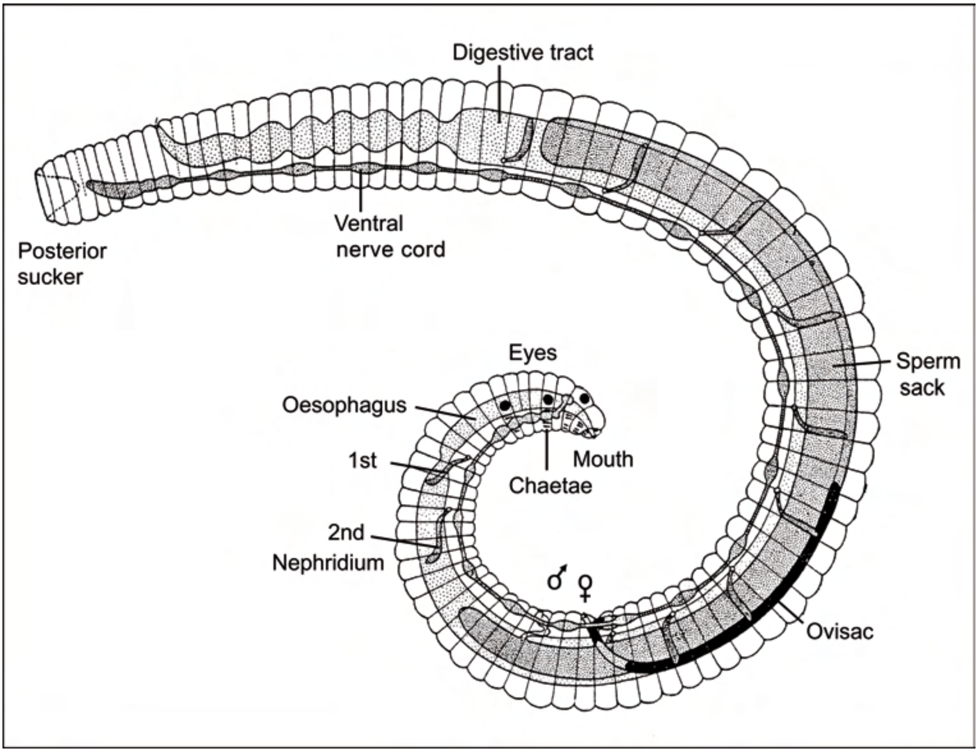

Fig. 4: Diagram of the anatomy of Acanthobdella peledina, reconstructed from histological studies of alcohol-preserved individuals (Adapted from Livanow 1906).

this scheme is based on drawing 1 in Livanow's original publication. Adult living specimens of this species are 20 – 35 mm long and about 3 mm wide. In the middle of the cylindrical body each segment is comprised of four annuli. Additional information on the morphology and anatomy of *A. peledina* was provided by Epshtein (1987), Franzén

(1991), and Purschke et al. (1993). These authors confirmed Livanow's classical results (with the exception of a few unimportant details) that can be summarized as follows.

The mouth pore of *A. peledina* is a small opening on the ventral side of the unspecialized head, which is characterized by three pairs of eyes and five transverse rows of chaetae (Fig. 4, 5 C). Each row consists of four pairs of hook-shaped chaetae. According to Dahm (1962), these chaetae occur on somites 1 – 5 of the anterior end of the body in a species-specific pattern. In all *A. peledina* populations investigated so far 5 x 8 (i.e., 5 x 2 · 4) = 40 hook-shaped chaetae were counted (Livanow 1906, Epshtein 1987, Purschke et al. 1993). These investigators agree that the 40 "hooks" (Fig. 5 D) are functionally equivalent to an anterior sucker, which is a specific feature of the "true leeches" (Euhi-

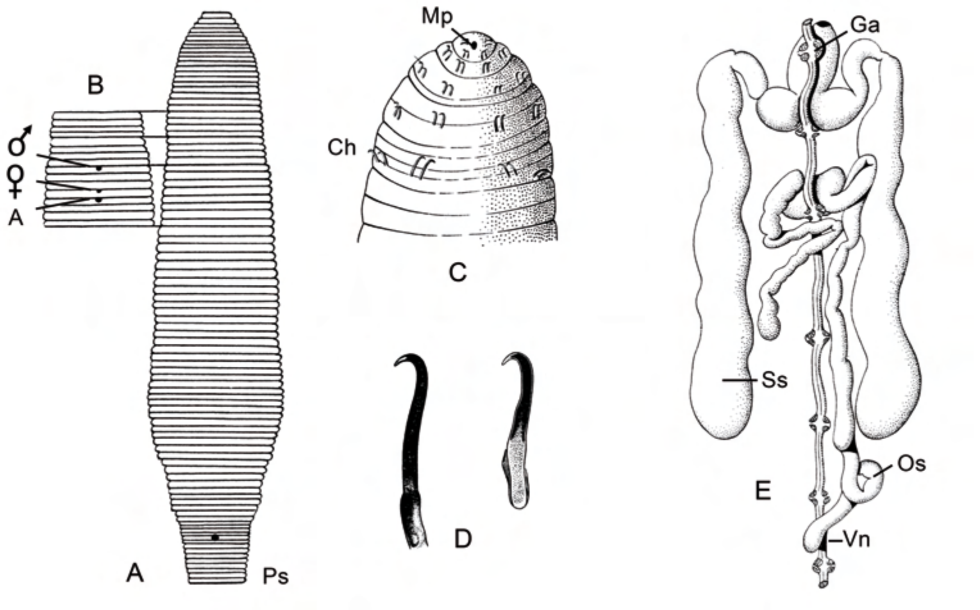

Fig. 5: Morphology and anatomical details of Acanthobdella peledina. Dorsal view of an adult individual (A), ventral view with male and female gonopores (B). Head with mouth and chaetae (C), isolated hook-shaped chaetae (D). Genital system, ventral view (E). A = accessory genital pore (area copulatrix), Ch = Chaetae, Ga = ganglion, Mp = mouth pore, Os = Ovisack, Ps = posterior sucker, Ss = sperm sack, Vn = ventral nerve cord (Adapted from Epshtein 1987).

rudinea). It should be noted that this conclusion is in accordance with the hypothesis of Grube (1850), who speculated that the chaetae of *A. peledina* may fulfil the role of the missing oral sucker in this ancient hirudinean.

According to Sawyer (1986 a) the digestive tract of *A. peledina* is, with respect to its shape, intermediate between that of oligochaetes and members of the Euhirudinea. Ten pairs of nephridia have been documented; in the region of the clitellum these organs (that are responsible for water balance) are absent. The central nervous system consists of a supraoesophageal ganglionic mass (brain), the suboesophageal ganglionic mass, the ventral nerve cord (chain of free ganglia), and the ganglionic mass close to the posterior sucker. The body of *A. peledina* consists of 29 segments and contains 31 pairs of ganglia (Fig. 4, 5 E).

Like all members of the Clitellata, *A. peledina* is a protandric hermaphrodite. The male genital organs consist of paired sperm sacks, and the female organs are made up of paired ovisacs. In Figures 4 and 5 A the positions of the genital openings are indicated by the biological symbols for male and female, respectively. In addition, the area copulatrix, which fulfils an unknown function during sperm transfer, is indicated in Fig. 5 B.

The results summarized here document that *A. peledina* is characterized by a mosaic of "oligochaetous" (i.e. earthworm-like) and hirudinean features, as described by Livanow (1906) and corroborated by subsequent investigators (Dahm 1962; Epshtein 1987; Sawyer 1986 a, c; Purschke et al. 1993).

Behaviour and life cycle

The ancient leech *A. peledina* inhabits cold-water lakes of alpine Scandinavia and northern Alaska/Eurasia. Sawyer (1986 b) summarized the literature on the biology of *A. peledina* and concluded that this archaic freshwater leech is a semi-permanent parasite, restricted almost exclusively to salmonid fishes. Most common hosts are brown trout (*Salmo trutta*) and grayling (*Thymallus thymallus*). The ectoparasite may occur anywhere on the body of its host, but usually the leeches attach to the base of the dorsal fin by the posterior (caudal) sucker (Fig. 3 A, B). After attaching the chaetae of the head region to the skin of a

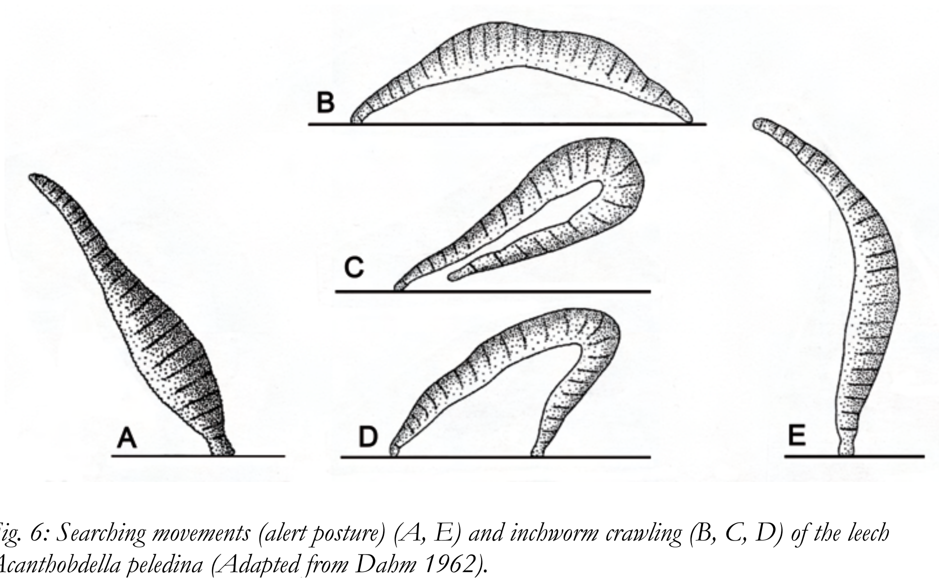

Fig. 6: Searching movements (alert posture) (A, E) and inchworm crawling (B, C, D) of the leech Acanthobdella peledina (Adapted from Dahm 1962).

fish the leech feeds on blood and tissue of its vertebrate host.

Dahm (1962) observed and documented the behaviour of adult *A. peledina* individuals that were attached to a salmonid fish. After the fish had been killed by the experimenter, the leeches continued to feed on their host. About one hour later, the *Acanthobdella* individuals left their dead host and moved around by "inchworm crawling" (Fig. 6). The caudal (posterior) sucker is used by the leech as a holdfast organ that sticks to the substrate via viscous mucoid secretions from adhesive glands (Livanow 1906). *A. peledina* individuals, isolated from a fish, perform searching movements that are reminiscent to those of fish leeches of the genera *Piscicola* or *Hemiclepsis* (Herter 1968, Sawyer 1986 a, b).

The life-cycle of *A. peledina* was elucidated by Andersson (1988), who studied free-living populations in a Lake in the northern part of Sweden and groups of leeches kept in freshwater aquaria. These containers were maintained at 4 °C and 10 °C, respectively. Copulation occurred more often at 4 °C than at the higher temperature. Details of the mode of sperm transfer are not known. Figure 7 A gives an impression of the sexual behaviour of this annelid. About one week after copulation the free-living fish parasites

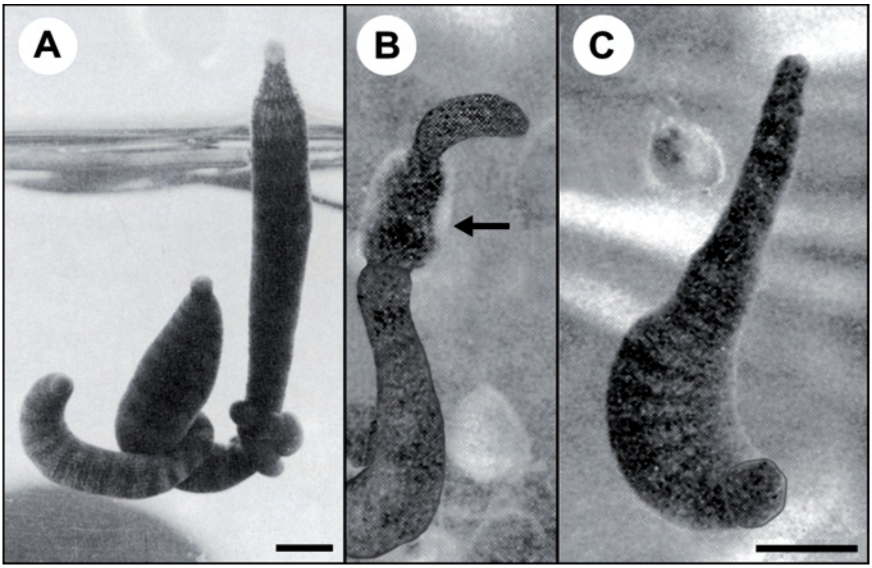

Fig. 7: Copulation (A), cocoon production (B) via the clitellum (arrow) and behaviour after cocoon fixation (C) in the leech Acanthobdella peledina . Note the fresh (transparent) and fully hardened (dark) cocoon attached to the glass plate of the aquarium (B, C) (Adapted from Andersson 1988).

produce cocoons. During the process of cocoon secretion via the clitella glands the leech is attached to a solid substrate with its caudal sucker. The worm rotates the anterior part of its body to shape the inner wall of the cocoon (Fig. 7 B). Thereafter, the soft translucent cocoon is attached to the substrate and later becomes hard and dark brown (Fig. 7 C). The entire process is reminiscent to that observed in earthworms (Edwards and Bohlen 1986) and leeches of the genus *Erpobdella* (Sawyer 1970, 1971, 1986 a, b; Kutschera 1983, 1989). This mode of cocoon production is considered to be the original state in leech evolution (Sawyer 1971, Siddall and Burreson 1995, 1996, Kutschera and Wirtz 2001, Borda and Siddall 2004 a, b, Kutschera 2006) and is also retained in members of the fish leeches (Pisciolidae).

The cocoons of *A. peledina* are about 5 mm long and contain 13 – 33 eggs (Andersson 1988). At 4 °C, the young (length ca. 2 mm) hatched after 7 months. They react to the water movement caused by a fish with intensified searching movements (Fig. 6 A, E), and try to fasten their hook-shaped chaetae on the ventral side of the host.

The life cycle of *A. peledina* in nature can be summarized as follows. Cocoons are deposited during August /September. Thereafter, free-living young leeches can be observed over a period of several months. The first infested fishes were found by the end of September of the following year. Young *A. peledina* remain attached to their host over the subsequent year and reach maturity. Thereafter, the adult individuals leave their host, produce cocoons and die a few months later (Andersson 1988). It should be noted that the data base on which this deduction rests is rather poor. Young (2002) provided a much more detailed account of the life cycle of the freshwater leech *Erpobdella octoculata*. However, these common clitellates are much more abundant than the "living relict" *A. peledina* so that studies of large leech populations in natural habitats were possible.

The significance of *Acanthobdella*: historical controversies

As a result of Livanow's monograph (1906), a controversial discussion commenced on the taxonomic status of this ancient leech that continues to the present (Siddall et al. 2001, Borda and Siddall 2004 a, b). The eminent zoologist Michaelsen (1919) was led to a study of the relationships between leeches and oligochaetes by noticing a figure in a paper on Sudanese Hirudinea. The schematic drawing represented an organ that was interpreted by the author as a diverticulum of the alimentary tract of leeches. Similar organs had been described in certain leeches from Sumatra, in which they are paired, and the external pores are situated ventrally. The organ strongly resembles the spermathecae of certain oligochaete species in the families Enchytraeidae and Lumbriculidae, in which the spermathecae communicate internally with the alimentary tract. Similar relations have also been found in certain species of other families of Oligochaeta.

As a result of his studies, Michaelsen (1919) reached the conclusion that the Hirudinea are, in reality, Lumbriculidae which have undergone special modifications in adaptation to a predatory mode of life. This conclusion receives much support from a careful comparison of the structure of two intermediate types of annelids: the Branchiobdellidae, and *Acanthobdella peledina*. The former are parasitic in the gill chambers and on parts of the surface of crawfishes and, as their name indicates, were formerly regarded as leeches. However, in the meantime their close relationship with the Oligochaeta has been documented (Brinkhurst 1999, Siddall and Burreson 1996). On the ventral surface of *A. peledina* (head region) are paired bundles of chaetae, and the characters of the reproductive organs and the body cavity appear to be closer to those of the Oligochaeta than to those of the leeches. Michaelsen (1919) concluded that, although there is some justification for including these two groups in the family Lumbriculidae, it is preferable to recognize them as two distinct families of Oligochaeta, i.e., Branchiobdellidae and Acanthobdellidae.

In addition, Michaelsen (1919) noted that there is a wide range of variation among different representatives of the Oligochaeta, and that most of the characters which one is accustomed to think of as typical of the Oligochaeta are not present in all members of the group. He also showed that many of the characters of Hirudinea, which one is likely to assume as distinguishing them from Oligochaeta, may be found present in certain members of the latter group. Absence of chaetae occurs in a genus of the oligochaete family Enchytraeidae, as well as in Branchiobdellidae, and they are greatly reduced in numbers and size in various other taxa. As previously mentioned, four pairs of well-developed chaetae are present on each of several anterior somites in *A. peledina*.

According to Michaelsen (1919), the most significant characteristics which distinguishes the Hirudinea from the Oligochaeta is the position of the "spermaries" in somites posterior to the one which contains the ovaries. This relative position of the two kinds of gonads is the opposite of that normally found in Oligochaeta, and in the apparent "connecting forms", Branchiobdellidae and *Acanthobdella*. To account for this reversal of relations, Michaelsen (1919) refers to instances where Oligochaeta are found with a considerable number of consecutive somites containing gonads and also to papers by different authors, in which gonads of certain oligochaete species have been shown to produce one kind of germ cells at one time, and at other times to produce those of the opposite kind. From individuals with series of gonads of this type, he regards it not improbable that there may have been derived descendants in which the relative position of the gonads of the two sexes is in the reverse order from that of the ancestors. On the basis of these and additional observations, Michaelsen (1919) regarded it desirable to modify the classification of the Annelida. He proposed the class Clitellata that includes two orders, Oligochaeta and Hirudinea; they can be distinguished by the differences in the degree of development of the body cavity and the relative order of the gonads.

Livanow (1931) did not accept Michaelsen's (1919) opinion that *Acanthobdella* is a oligochaete that had evolved hirudinean-like features (e. g. posterior sucker) convergently to the "true" leeches (Euhirudinea). The Russian zoologist described *A. peledina* as a "living fossil" leech that is an early offspring of the line of descent (with modifications) that led over millions of years to the Euhirudinea. Autrum (1936) considered *A. peledina* as the most primitive living leech species that represents a connecting link between the Oligochaeta and the Euhirudinea. This conclusion was also reached by Sawyer (1986 a, b), who interpreted *A. peledina* as a "living fossil (or relict) of special phylogenetic interest" that "connects leeches to oligochaetes".

In summary, the conclusions of Michaelsen (1919) regarding the position of *A. peledina* have not survived (Ax 1999, Brinkhurst 1999, Martin 2001, Westheide and Rieger 1996). However, this pioneer in annelid research coined a key term that is still in use today. He introduced the taxon (class) Clitellata, which was comprised of the orders Oligochaeta and Hirudinea (inclusive of *Acanthobdella* and the Branchobdellidae) (Autrum 1936; Sawyer 1986 a, b; Mc Hugh 2000). Today we know that Michaelsen's clitellates are a monophyletic group of segmented worms. This topic is discussed in the last section of this article.

Conclusions: Validating Livanow with molecular data

The classical paper of Livanow (1906) had far-reaching implications for the question as to the evolutionary relationships between oligochaetes and hirudineans. Sawyer (1986 a, b, c) was the first to summarize all pertinent data on the "living fossil-leech" *A. peledina* and concluded that this fish parasite represents an "intermediate form" between the Oligochaeta and the true Hirudinea. Siddall and Burreson (1995, 1996) analyzed the phylogenetic relationships among clitellates and suggested that *Acanthobdella* may be regarded as a sister group to the Euhirudinea, as proposed by Livanow (1906, 1931). These authors became the pioneers in a research program that is based on mitochondrial DNA sequence data for the elucidation of the phylogenetic relationships within the Clitellata (Siddall and Burreson 1998, Apakupakul et al. 1999). Methods introduced by these scientists are also of importance for the identification of new (or imported) annelid species within the framework of "DNA barcoding" studies (Trontelj and Sket 2000, Pfeiffer et al. 2004, 2005).

In a series of papers it was shown that the "living relict" *A. peledina* is in fact a primitive but typical hirudinean and that the Acanthobdellida is a sister taxon to the Euhirudinea (plus Branchiobdellida) (Apakupakul et al. 1999, Siddall et al. 2001, Borda and Siddall

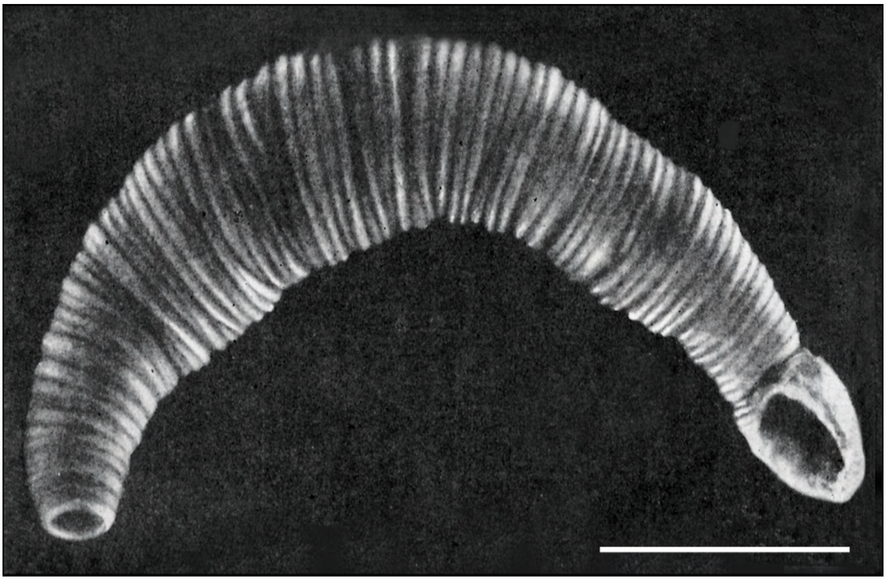

Fig. 8: The ancient leech Acanthobdella livanowi Epsthein 1966, adult individual, preserved in ethanol. The caudal sucker points to the left. Note the head region with the sucker-like disc that is equipped with chaetae.

2004 a, b). These reports document that Livanow's conclusions, which were exclusively based on anatomical studies, are in accordance with DNA sequence data. Independent evidence in support of a hypothesis is strong proof for the validity of a proposed evolutionary scenario. Other case studies where morphological and molecular data agree with each other are summarized in the recent literature on molecular phylogenetics and evolution of various taxa (Kutschera 2005, 2006, Kutschera and Niklas 2004).

Finally, it should be noted that 40 years ago a second acanthobdellid species, *A. livanowi* Epshtein 1966 (Syn.: *Paracanthobdella livanowi*, Epsthein 1987) was discovered (Fig. 8) and named in honour of the Russian zoologist (Fig. 1). The significance of this primitive leech with chaetae has been questioned (Brinkhurst and Gelder 1989, Brinkhurst 1999) so that more scientific work is required "in the wake of Livanow".

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