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The Evolution of Parental Care in Freshwater Leeches*

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Summary: The life-history strategies of a selection of the most common European freshwater leeches (Euhirudinea) are described. On the basis of this information and results from the literature, the probable phylogenetic development of parental care in the Euhirudinea is reconstructed. The jawless worm leeches (Erpobdellidae) secrete a protective cocoon, cement it to the substrate and sometimes ventilate it before they leave the egg capsules. This behaviour represents the most ancient state in leech evolution. Members of the jawed Hirudinidae deposit desiccation-resistant cocoons on land. All known Glossiphoniidae (leeches equipped with a proboscis) have evolved the habit of brooding the eggs and young. These unique parental care patterns within one family of extant freshwater leeches can be arranged schematically in a series of increasing complexity which may reflect the evolution of brooding behaviour. Glossiphoniid leeches of the genus *Helobdella*, which have a world-wide distribution, display the most highly developed parental care system: they not only protect but also feed the young they carry. This results in the young being much larger when they leave the parent and, presumably, in higher subsequent survival. Isolated cocoons of all aquatic leeches are rapidly destroyed by predators, primarily water snails. In erpobdellids (but not glossiphoniids, which protect the cocoons) a large portion of the cocoons are lost due to predatory attacks. We conclude that the major selective pressure driving the evolution of parental care in leeches may have been predation on eggs and juvenile stages.

Introduction

Leeches (Hirudinea) are a class of segmented invertebrates related to earthworms that occur in habitats that range from aquatic (both freshwater and marine) to terrestrial environments. They are characterized by suckers at

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* Dedicated to Professor Dr. G. Osche on the occasion of his 75th birthday

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both ends of their flexible body and display a unique inch-worm like mode of locomotion. In spite of several early claims that some members of the Hirudinea may be vegetarians (Herter 1937) numerous studies have unequivocally shown that all leeches are either predatory or parasitic carnivores. The large diversity in behaviour and morphology among the ca. 650 leech species described when the last major monograph of this group of animals was published (Sawyer 1986 a, b, c) has been of both practical and theoretical interest to several branches of the biomedical sciences. The most famous species within the Hirudinea, the medicinal leech *Hirudo medicinalis*, was traditionally used for bleeding patients affected by all kinds of medical conditions and diseases. In the 19th century physicians and other medical experts believed that *Hirudo*-induced blood-letting would reestablish the disturbed balance of humours (blood, phlegm and bile). During the first part of the 19th century a large increase in the practice of leeching occurred so that this common species was almost entirely eliminated from the limnofauna of Europe. According to Herter (1937, 1968) it is estimated that in France alone, where leeching was very popular, some 50 million *H. medicinalis* were used by medical experts per year. For a variety of reasons, this practice more and more lost its popularity so that, in the 20th century, it became part of the folklore of traditional 'last century' medicine. However, because of their important salivary components, blood-sucking (sanguivorous) leeches such as *H. medicinalis* and related species have become of great interest for pharmaceutical companies seeking to expand their supply of various anticoagulants for use in microsurgeries to prevent blood clotting. As pointed out by Sawyer (1986 a) and Lent (1986), 'the return of the bloodsuckers' occurred in the western world during the early 1980s.

The scientific interest in leeches, notably *H. medicinalis*, goes back to the 1920s (Herter 1937). However, a revival of experimental leech biology occurred only about four decades ago when it was discovered that the exceptionally large nerve cells (neurones) of these worms can serve as an excellent model system for the neurobiologist (Leake 1983). Some members of the Hirudinea serve as vectors of protozoan blood parasites for aquatic vertebrates (fish, amphibians) (Siddall and Burreson 1995). The blood parasites may have co-evolved with their respective leech hosts as a consequence of long-term associations (Osche, 1965).

In freshwater streams, brooks and lakes, small leech species that are opportunistic predators or parasites of aquatic invertebrates are far more abundant than are the famous blood feeders that attack vertebrates, including man. These little known leeches, which inhabit the underside of stones and roots, are important components of freshwater ecosystems. The life-history strategies of most of the ca. 15 freshwater leeches that occur in Europe were the subjects of many studies by generations of naturalists (for a summary of early studies, see Herter 1937). The complex behaviour, including the brooding and parental care-patterns of some members of the Hirudinea, was described repeatedly. Two books on the biology of leeches published some decades ago (Mann 1962; Herter 1968) document that the phylogenetic significance of these behaviour patterns was not fully recognized. In a seminal paper by Sawyer (1971) the life cycles of representative leech species were compared and arranged in a series of increasing complexity. Fifteen years ago, we have modified and extended this picture of the phylogenetic development of brooding behaviour in leeches (Kutschera and Wirtz 1986 a). However, in spite of their importance for our understanding of the evolutionary history of the Hirudinea, the parental care patterns in leeches have received little attention, with some notable exceptions (Wilkialis 1970, 1984; Milne and Calow 1990).

In this review article we will first summarize some basic information on the little-known animals that are the subject of our report. In the following paragraphs we describe the life cycles of a selection of freshwater and terrestrial species. Our aim was to assess the phylogenetic relationships of leeches using observations and quantitative data that pertain to the reproductive behaviour of these segmented worms. We have summarized the relevant literature that was published on this subject over the past three decades but have also included previously unpublished observations and data to illustrate some important points.

The current taxonomy of leeches

Autrum (1936, 1939) was the first to summarize all pertinent publications on the taxonomic and phylogenetic relationships among the clitellates (Oligochaeta and Hirudinea). In general, the Clitellata can be defined as a monophyletic group of cylindrical (or disk-shaped) segmented invertebrates without parapodia that are characterized by a clitellum (Ax 1999, McHugh 2000). This structure is a glandular region in the anterior part of the body that secretes a cocoon for the reception of the eggs during the breeding season. All Clitellata are hermaphrodites. They are comprised of two separate groups, the Oligochaeta (earth-worms and other non-carnivorous detritus feeders) and the Hirudinea (leeches, i. e., carnivorous predators or parasites). The Oligocheata/Hirudinea can be distinguished as follows: number of body segments variable (10–130)/constant (33); chetae present/absent; two suckers absent/present.

In his classical monograph, Autrum (1936, 1939) stressed the close relationship between the Oligochaeta and the Hirudinea with special reference to the species *Acanthobdella peledina*, a rare ectoparasite on salmonid fish that was described in detail for the first time by Livanow (1906). In this publication, *Acanthobdella* was defined as an ancient (‘primitive’) leech that is in many ways intermediate between the Oligochaeta (characters: no anterior sucker, chaetae present on five anterior segments) and the Hirudinea (characters: posterior sucker present, chetae absent on 90% of the body segments). The observations and conclusions by Livanow (1906, 1931) were corroborated and considerably extended by Purschke et al. (1993). These authors confirmed that *Acanthobdella* represents the only living species of the relatively primitive Acanthobdellida, which are the sister group of the true leeches (Euhirudinea). In addition, Autrum (1939) discussed a second 'living relic', the aquatic oligochaete *Agriodrilus vermivorous* which has been described by Sawyer (1986 b) as a member of the Proto-Hirudinea. We will discuss the significance of this unique carnivorous oligochaete later.

The Euhirudinea or true leeches have been classified according to their mode of feeding as follows: Pharyngobdellida (pharynx unarmed, i. e., no jaws or a proboscis present), Gnathobdellida (oral sucker with jaws within the buccal cavity), and Rhynchobdellida (jawless pharynx; these worms utilize an evertible proboscis to penetrate the skin of their hosts). This scheme of classification (Autrum 1939) has been used in the literature without much modifications (Mann 1962; Herter 1968). In his comprehensive monograph on the biology and taxomomy of leeches, Sawyer (1986 b) revised the classification of the Euhirudinea as summarized in Table 1. The order Arhynchobdellida is comprised of leeches that are characterized by the lack of a proboscis: the non-sanguivorous (unarmed) Erpobdelliformes and the jawed (armed) Hirudiniformes. This latter group of leeches are well-known animals because they include the medicinal leech *Hirudo medicinalis* and related species. Members of the order Rhynchobdellida are marked by the possession of a protrusible proboscis. The only family of the suborder Rhynchobdelliformes that may be known to the non-specialist are the Piscicolidae, which comprise a number of marine and freshwater leeches that are ectoparasites of various fish species.

Over the past five years, the classification of the Euhirudinea introduced by Sawyer (1986 b) has been re-investigated. A cladistic analysis (Siddall and Burreson 1995) and molecular data (Siddall and Burreson 1998, Apakupakul et al. 1999) have essentially confirmed the taxonomic revision that was published fifteen years ago (Table 1). However, it should be noted that the suborder Rhynchobdelliformes (as a logical counterpart to the terms Erpobdelli- and Hirudiniformes) was not used by Sawyer (1998 b) and the authors cited above. In accordance with Westheide and Rieger (1996) we have incorporated this term into our classification scheme (Table 1). The three suborders of the Euhirudinea described here correspond to the classical German terms used by Autrum (1936) and others: we distinguish between *Schlund*-, *Kiefer*- and *Rüsselegel* (i. e., leeches with a strong unarmed pharynx, jaws or a proboscis). The most important families of the three suborders are the Erpobdellidae, the Hirudinidae and the Glossiphoniidae. Representative members of these leech families are depicted in Figures 1–4.

Table 1. Taxonomy of the leeches (Enhirudinea) with a list of the six most important families (Adapted from Apakupakul et al. 1999).

Class:	Hirudinea		
Subclass:	Euhirudinea		
Order:	Arhynchobdellida		Rhynchobdellida
Suborder:	Erpobdelliformes	Hirudiniformes	Rhynchobdelliformes
Families:	Erpobdellidae Salifidae	Hirudinidae Haemadipsidae	Glossiphoniidae Piscicolidae

We will restrict our discussion on the reproductive behaviour and parental care to these three major taxa within the Euhirudinea.

Parental care: some basic definitions

In the course of evolution those genetically based characteristics of an individual organism are selected for that allow it to bring more offspring into the next generation than the other members within the same population (Osche 1972). Essentially, there are only two different ways to bring more offspring into the next generation. These are to either increase the number of offspring produced or to invest more into the probability that offspring will indeed survive to reproductive age. Increased parental investment into offspring can take the well-known forms of protecting the offspring against predators and of providing them with nourishment, but can also take the form of more subtle activities such as, for instance, manipulating the physical environment of the offspring so as to increase their survival (e. g., Diesel and Schuh 1993).

The term 'parental care' is a descriptive word for such activities and carries no implication about the costs involved to the parent. In contrast, the technical term 'parental investment' refers to any characteristic or activity of parents that increase the fitness of offspring at a cost to any component of the fitness of the parent. Such costs could be to the parent's subsequent survival, fecundity, mating success, etc. Parental investment is usually (though not always) used to refer to the fitness cost of *individual* offspring, while the total costs of caring for *all* progeny are designated parental effort, which – with mating effort – is part of an organism's reproductive effort (Alexander 1974, Clutton-Brock 1991). In the German language, a distinction is made between *Brutfürsorge*, i. e., parental investment for offspring that the parent will never meet (such as selecting an oviposition site suitable for the development of the young or placing food next to the developing egg) and *Brutpflege*, which is parental care for offspring that live together with the parent. Futuyma (1998) pointed out that the study of the phylogenetic development of animal behaviour is as old as the analysis of evolution itself. However, the study of lower invertebrates (pre-arthropoda) has received only little attention in the literature dealing with the evolution of social behaviour (Clutton-Brock 1991).

In the following three sections we will describe the life cycles of representative European members of the leech families Erpobdellidae, Hirudinidae and Glossiphoniidae and discuss the behaviour of related species from Africa, Asia, Australia, North- and South America. On the basis of these observations and data the possible phylogenetic development of parental care patterns within the subclass Euhirudinea will be reconstructed.

Erpobdellidae: predatory worm leeches

The pharynx of these freshwater or amphibious hirudineans has no power of penetrating the skin of a potential host which is the prerequisite for a parasitic way of nutrition. These clitellates are carnivorous predators that are equipped with a powerful muscular pharynx. They swallow all kinds of small animals, such as oligochaetes, insect larvae and other invertebrates. Because of their earthworm (lumbriculid)-like habitus the Erpobdellidae are also known as the ‘worm leeches’ (Mann 1962).

The aquatic oligochaete *Agriodrilus vermivorous* is a cylindrical worm about 8 cm long and 2 mm wide. This unique animal lives exclusively in Lake Baikal at depths of 7–58 m and is a predator. In contrast to other lumbriculids, which almost exclusively feed on organic matter such as rotten leaves, *Agriodrilus* has a well-developed muscular pharynx. According to Sawyer (1986 b) the anatomy of the pharynx of this carnivorous oligochaete, which has been classified as the only extant member of the ‘Protohirudinea’, is very similar to that of leeches of the genus *Erpobdella*.

Two representative species of the Erpobdellidae, *Erpobdella octoculata* and *E. testacea*, are depicted in Fig. 1 A. Both leech species are widely distributed throughout freshwater habitats in Europe. The larger *E. octoculata* is one of the most widespread and abundant species in rivers, streams, lakes and gravel pits, whereas the smaller, less abundant *E. testacea* usually occurs in low-oxygen stagnant waters such as ponds where the leeches inhabit the leaves of semiaquatic plants (Elliot and Mann 1979, Sawyer 1986 b, Neubert and Nesemann 1999). In Lake Esrom, Denmark, the sympatric occurrence of these species was documented and analysed by Dall (1983). The co-existence of these very similar leech species was explained on the basis of different weight class compositions throughout the annual life cycles. The very common species *E. octoculata* usually spends day-light hours by sitting on the underside of stones. The leeches become active during the evening and night. They find their food by random probing of the environment and suck in only a small percentage of the potential prey with which they come into direct oral contact. According to Herter (1937, 1968) *E. octoculata* is reported in the earlier literature to feed on a wide variety of prey organisms including snails, crustaceans, insect larvae, mayfly nymphs, oligochaetes and triclads. However, detailed quantitative la-

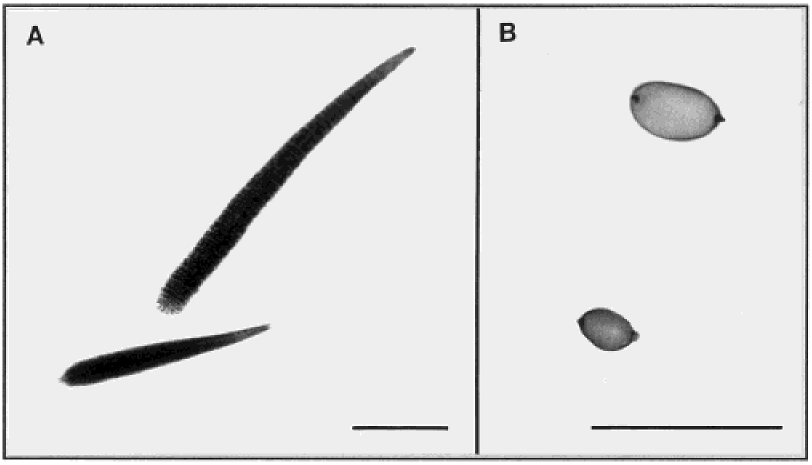

Fig. 1. Two representative 'worm leeches' (Erpobdellidae), *Erpobdella octoculata* (top) and *E. testacea* (bottom). The leeches are fixed with their posterior (hind) sucker to the substrate (dorsal view) (A). Cocoons of *E. octoculata* (top) and *E. testacea* (bottom) after they were fully hardened (about 3 days after deposition) (B). Scale bars: 1 cm.

boratory experiments have shown that *E. octoculata* feeds almost exclusively on insect larvae (*Chironomus*) and oligochaetes (*Tubifex*). This common worm leech is usually a macrophageous feeder, i. e., the prey organisms are consumed (sucked in) whole. Only very occasionally *E. octoculata* breaks off portions of the prey (Greene 1974, Young and Ironmonger 1980, 1982, Young and Procter 1985, Young and Spelling 1989). The reproductive behaviour of *E. octoculata* and related members of the Erpobdellidae has been studied in detail and can be summarized as follows (Brandes 1901, Mann 1962, Kutschera 1983, 1986, 1989 b).

Like earthworms, all leeches are protandrous hermaphrodites, i. e., the same animal functions first as a male (distribution of sperm) and thereafter as a female (production of eggs). Exchange of spermatophores during copulation usually takes place in the night, when the leeches are most active. The spermatophore is fixed on the epidermis of the partner, in most cases in the clitellar region. In all members of the Erpobdellidae (and Glossiphoniidae) studied so far the sperm passes through the epidermis into the body of the partner where it finds its way to the ovaries. This hypodermic insemination was described in detail by Brandes (1901). He coined the term 'pseudospermatophore' instead of 'spermatophore', because this transient structure has the function of an injection canula rather than that of a temporary recipient.

Within 1–2 days after copulation the leeches produce the first cocoon. The gravid *Erpobdella* places its clitellum over the substrate and secretes the cocoon. Formation and fixation of the cocoon has been described in detail (Kutschera 1983). *Erpobdella* cocoons are flat, lemon-shaped capsules that are characterized by two terminal plugs. After deposition, the cocoon is a soft, translucent, colourless bag that contains on average 10 very small eggs that are embedded into a viscous nutrient solution. After deposition, the parent begins to ventilate the fresh cocoon but leaves after about 10 minutes. Within a few hours the surface of the cocoon becomes hard, brown and almost opaque (Fig. 1 B). Three weeks later the young hatch through the two holes, which are created after the plugs are broken off, and begin an independent life.

In the laboratory, adult *E. octoculata* produced 0,5–1,0 (on average 0,7) cocoons per day over the whole summer (see Table 2). These data document that the representative aquatic worm-leech discussed here (Fig. 1 A) has a high, relatively constant rate of reproduction of several hundred young per leech and breeding season (Kutschera 1983). Based on an extensive study of the life cycle of *E. octoculata* Elliott (1973) concluded that the main regulatory mechanism for the size of a leech population was mortality of the eggs (i. e., fresh cocoons) which were eaten by conspecifics when the density of the worms was high. The eating of newly laid (soft) cocoons by other (non-breeding) *E. octoculata* was reported by Pawlowsky (1955). This author also remarked that parents do not eat their own cocoons. Kutschera (1983, 1989 b) confirmed this observation and described the intraspecific predation of cocoons in laboratory cultures of *E. octoculata* in detail. He concluded, in accordance with Elliott (1973), that the leech populations are self-regulated, because intraspecific predation of freshly laid cocoons was most severe at high population densities. In addition, water snails, which are very abundant in the leeches habitat, destroyed many freshly laid (as well as hardened) cocoons in leech populations kept in aquaria.

Laboratory experiments on intra- and interspecific predation on freshly laid and older (hardened) cocoons of *E. octoculata* carried out by Young (1988) confirmed and extended the observations summarized above. Freshly laid flaccid cocoons were eaten by a dytiscid beetle, fish species and conspecifics (non-breeding *E. octoculata*). Older (hardened) cocoons were severely damaged by water snails but not by other predators.

In North America, *E. punctata* is one of the most commonly encountered and widely distributed freshwater leeches. Sawyer (1970) studied the reproductive behaviour of this species and made essentially the same observations as those described above for the European *E. octoculata*. Intraspecific and snail predation of cocoons were the most important causes of mortality. Sawyer (1970) estimated that in natural populations up to 30% of the *Erpobdella* cocoons are destroyed by water snails. Similar observations were made for other Erpobdellidae such as *E. testacea*, *E. lineata* and *Trocheta bykowskii* (Sawyer 1986 b, Kutschera 1986). It should be noted that the two most species-rich genera of freshwater leeches *(Erpobdella* and *Trocheta*) are closely related taxa. This was recently confirmed by a detailed molecular phylogenetic analysis (Trontelj and Sket 2000).

In summary, the results described in this section demonstrate that our representative member of the Erpobdellidae (Fig. 1 A, B) produces many cocoons that are left by the parent; the unprotected offspring is in danger of being eaten by numerous predators, including conspecifics.

The second family of the suborder Erpobdelliformes listed in Table 1 (Salifidae) is comprised of four genera and several species. The reproductive biology of these leech species is largely unknown (Sawyer 1986 b).

Hirudinidae: amphibious and terrestrial scavengers and blood feeders

The second suborder of the Arhynchobdellida (hirudineans without a proboscis) are the Hirudiniformes, i. e., leeches that resemble more or less the famous species *Hirudo medicinalis*. Table 1 indicates that two major families can be distinguished: the Hirudinidae and the Haemadipsidae. In Europe only three species of the Hirudinidae have been investigated in more detail: the ‘horse leech’ (*Haemopis sanguisuga*), the sanguivorous species *Limnatis nilotica*, and the medicinal leech *H. medicinalis*. Figure 2 A shows the common species *Haemopis sanguisuga*. This large leech is widely distributed in the Palaearctic region from western Europe to eastern Siberia, mostly along the shores of small lakes or ponds. *H. sanguisuga* can swim in the water and creep on land, i. e., it is an amphibious animal. In contrast to the blood suckers *H. medicinalis* and *L. nilotica*, the ‘horse leech’ has only very weak jaws with blunt teeth, so that this species can not penetrate the skin of a potential host; it is a macrophagous species. The adult *H. sanguisuga* is a carnivore or scavenger that feeds opportunistically on any prey it can overpower (earthworms and other oligochaetes, aquatic and land snails, insect larvae, tadpoles and small fish). It has been observed to feed on dead frogs and toads (U. Kutschera, unpublished results). Due to its blunt teeth the ‘horse leech’ is unable to suck vertebrate blood. Its common name is a classical misnomer, due to a confusion with the sanguivorous species *L. nilotica*. This blood sucker enters the nasal cavities of drinking cattle, horses and other mammals (including humans). In the circum-Mediterranean countries, where this leech is widely distributed, *L. nilotica* parasitism of the throat and nose of domestic animals is a familiar problem.

In spite of the fact that *H. sanguisuga* is a common species throughout Europe only very few reports on the reproductive biology of this leech were published when the last major monograph appeared (Sawyer 1986 a, b). Because of this lack of information several aspects of the life-history of *H. sanguisuga* were investigated in more detail by Kutschera (1990). The basic results can be summarized as follows. In early spring the leeches mate by true copulation: an eversible male copulatory organ is inserted

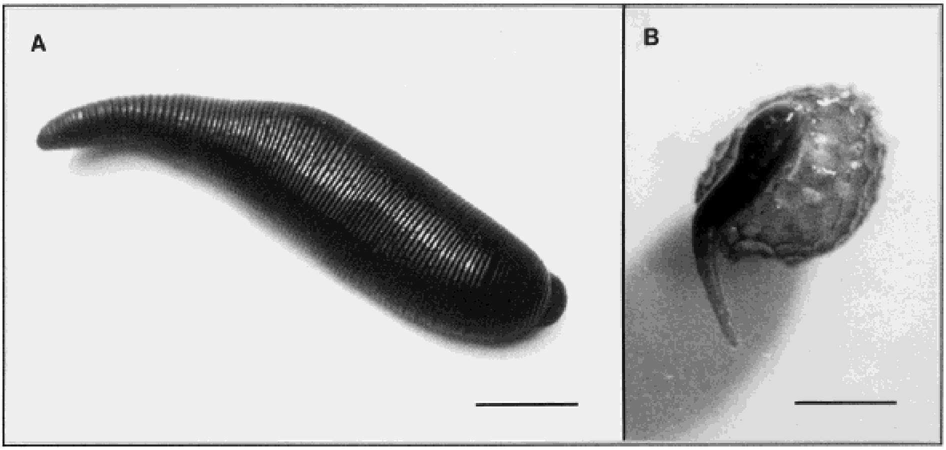

Fig. 2. Dorsal view of a mature individual of the 'horse leech' (*Haemopis sanguisuga*), a member of the Hirudinidae (leeches that are similar to the well-known species *H. medicinalis*) (A). The cocoons of *H. sanguisuga* are deposited on land. One juvenile leech crawls out of the hardened egg capsule (B). Scale bars: 1 cm.

into the female gonopore of another leech. About 3 months after copulation the leeches produce cocoons. They deposit their spongy egg-capsules on land, i. e., above the shoreline, mostly among rotten leaves or under rocks. The lemon-shaped cocoons of *H. sanguisuga* (Fig. 2 B) are about 8–9 mm long and 4–5 mm wide. At both ends they are equipped with a plug. In order to determine whether or not the chitinous, sturdy cocoons can withstand desiccation, several freshly laid specimens were collected from the moist underground, placed into a petri dish and exposed to dry air. After one week the *H. sanguisuga*-cocoons had lost about 90% of their water and looked like dry berries. After addition of a small amount of tap water they imbibed (like dry seeds of higher plants) and rapidly re-gained their original shape. From these dried/re-watered cocoons 4–6 young (about 10 mm long) emerged through the holes that were created due to the loss of the terminal plugs of the 'lemon'. The juvenile leeches (Fig. 2 B) hatched 4–5 weeks after cocoon deposition; they crawled into the water and fed on *Tubifex*-worms. Terrestrial cocoon deposition was also documented for the two related jawed species, *H. medicinalis* and *L. nilotica* (Herter 1968). It may be a general feature of the Hirudinidae. The terrestrial deposition of sturdy, desiccation-tolerant cocoons in which the developing young are protected from aquatic predators (such as water snails) can be interpreted as parental investment. It is clearly a more sophisticated mode of reproduction than that described for the Erpodellidae.

The Hirudinidae are semi-aquatic (amphibious) leeches that spend part of their life out of the water. In Table 1 a second family, the Haemadipsidae, is listed. These blood sucking tropical land leeches are fully adapted to a life on the damp forest floor. They deposit their cocoons, which have an outer coat of hardened froth, among moss, leaves or humus (Sawyer 1986 b). These observations document the close phylogenetic relationship between the amphibious Hirudinidae and the terrestrial Haemadipsidae.

Glossiphoniidae: aquatic blood suckers equipped with a tubular proboscis

The suborder Rhynchobdellida is comprised of all those leech species that are characterized by the possession of a proboscis (Table 1). This structure lies freely within a membranous sheath. The proboscis pore, through which the hollow muscular feeding organ is protruded, is positioned in the middle of the anterior sucker of the leech. The two most important families of the Rhynchobdelliformes, the Glossiphoniidae and the Piscicolidae, will be discussed here with special reference to the first taxon.

The Glossiphoniidae or flat leeches (Herter 1968) contain both the smallest and the largest leech species described so far. According to Sawyer (1986 a, b) the European leech *Alboglossiphonia heteroclita* has a length (at rest) of less than 1 cm (extended up to 1,3 cm). The related tropical glossiphoniid *Haementeria ghilianii* is 20–30 cm long and can reach a length of up to 50 cm (fully extended). When this giant leech was discovered in the 19th century near the origin of the Amazon this finding was announced as a sensation in the scientific literature (Filippi 1849).

All members of the Glossiphoniidae produce thin-walled, transparent cocoons that contain numerous large yolky eggs. They cover the cocoons and developing eggs with their disc-shaped body and later carry the young on their belly. This highly developed brooding behaviour was recognized by the pioneers of leech biology (Autrum 1939; Herter 1937, 1968; Mann 1962) but its phylogenetic and taxonomic significance was not recognized. Sawyer (1971) compared the reproductive behaviour of glossiphoniid leeches and, on this basis, proposed a novel (phylogenetic) mode of classification, which replaced that by earlier leech scientists (Autrum 1939; Herter 1968; Mann 1962). According to Sawyer (1986 b) the Glossiphoniidae can be divided into three subfamilies: Glossiphoniinae (mating by hypodermic insemination, cocoons attached onto the substrate), Haementeriinae (mating like Glossiphoniinae, cocoons attached directly to venter of patent) and the monogeneric Theromyzinae (a unique genus that shows a mixture of characters, see Discussion and Conclusions).

In this section we will summarize the reproductive biology of the two most widely distributed European glossiphoniid species, the large snail leech (*Glossiphonia complanata*) (Glossiphoniinae) and the two-eyed flat leech (*Helobdella stagnalis*) (Haementeriinae). The life cycle of a typical member of the Glossiphoniinae is illustrated by the snail leech *Glossiphonia complanata*, an abundant European, Asian and American species that

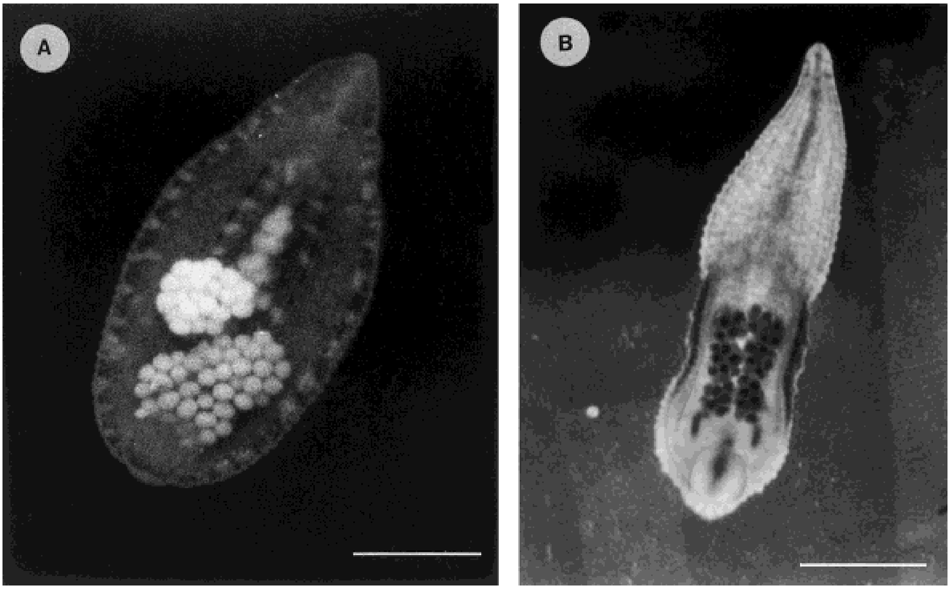

Fig. 3. Ventral views of mature individuals of members of the Glossiphoniidae. Snail leech *Glossiphonia complanata* that had just produced a third cocoon fixed to the substrate (glass pane). The cocoons are covered by the body of the parent (A). Two-eyed flat leech *Helobdella striata* with six cocoons attached to the belly of the parent. Both glossiphoniids perform ventilatory undulations with their body in order to enhance the oxygen content of the water surrounding the eggs and developing young. The *Helobdella* displays a ventral inflection of the lateral body margins (temporary brood pouch for the protection of the cocoons). Scale bars: 1 cm.

sucks the body fluids of molluscs (primarily aquatic snails). The snail leech reproduces only once per year, usually during the spring (March/April). This behaviour has been analysed in detail (Dall 1982, Kutschera 1984, 1992 a). When adult *G. complanata* are collected and then cultivated in aquaria (at room temperature) they readily start to transfer pseudospermatophores. A few days after copulation the leeches begin to produce 1–5 cocoons. The gravid worms can easily be recognized by the enlarged white ovaries containing numerous eggs that are visible through the body walls. It has been shown that the stimulus for egg production is a rise in water temperature (Dall 1982, Young 1983). Freshly laid cocoons, which are secreted by the clitellar glands that surround the female gonopore, are white and contain 2–30 large yolky eggs (Fig. 3 A). They are fixed to the substrate and covered by the body of the parent. When the leech is removed from its cocoons the parent rapidly creeps back and covers its brood again with its flat body.

Isolated cocoons (without parent) are rapidly eaten by water snails: they have no chance of survival in the habitat of the leeches. The snail leech actively defends its thin-walled cocoons against water snails. This behaviour was documented repeatedly (Kutschera 1984, 1992 a) and demonstrates that the major selection pressure to protect the brood probably is predation by snails. Four to 7 days after cocoon deposition the eggs hatch; the larvae attach to the ventral surface of the parent with their posterior sucker. The leech starts again to creep around and to fan the attached larvae with continuous waves of contractions with its body flanks.

Artificial detachment of the larvae usually results in the death of the brood (Calow and Riley 1982), although Kutschera (1984) was able to raise at least some isolated *G. complanata* under semi-sterile conditions. De Eguileor et al. (1994) have shown that the weight loss of brooding parents, as described by Milne and Calow (1992), is not only due to their inability to feed and to increased metabolic expenses for the body movements necessary to ventilate the offspring but also to an additional phenomenon. These authors demonstrated that brooding *G. complanata* seem to produce a sort of 'placenta' between parent and larvae. There appears to be a passage of nutrients from the body wall of the leech to the sucker of the larvae. Within the next days the larvae develop into juvenile leeches that are fixed with their posterior sucker at the venter of the parent. The young are carried around for another 1–2 weeks until the yolk in their crop is depleted. Thereafter, they leave the parent, which starts to feed again after the brooding period is over (3–4 weeks after cocoon deposition).

An even more advanced mode of parental care is established in freshwater leeches of the genus *Helobdella*. We will briefly describe the behaviour of *H. stagnalis*. In Fig. 3 B a related species, *H. striata*, is shown. The parental care patterns of these leeches have been analysed and were found to be very similar (Kutschera and Wirtz 1986 a, b, c).

The two-eyed flat leech *H. stagnalis* is one of the most common European hirudineans and has a world-wide distribution (except Australia). These small grey leeches can be found in stagnant and running waters where they feed on oligochaetes, insect larvae and water snails. The life cycle and prey selection in natural populations of *H. stagnalis* has been described repeatedly (Davies and Reynoldson 1975, Davies et al. 1979, Tillman and Barnes 1973). Reproduction occurs once (or twice) per year. Water temperature is the major factor controlling breeding in *H. stagnalis*, and the rising temperature in the spring may be the stimulus for copulation and egg production. A few days after reciprocal transfer of pseudospermatophores the leeches produce cocoons. Between 2 and 6 thin-walled, transparent cocoons, each containing 6–15 eggs, are pressed from the female gonopore and fixed to the ventral side of the parent. This sequence of events was described in detail by Sawyer (1972) and by Kutschera and Wirtz (1986 a). The flexible egg sacks are carried around by the brooding leech, which fans the cocoons with continuous waves of lateral contractions of its body flanks (Fig. 3 B). When the parent encounters a water snail (which devours unprotected cocoons rapidly) it forms a temporary brood pouch in which the cocoons are held. Due to this behaviour, egg predation by water snails and other aquatic carnivores is entirely prevented by the brooding leech. During the first 6–12 days after cocoon deposition the larvae hatch and adhere to the belly of the parent with a structure that was described as an 'embryonic attachment organ' (Nagao 1958). Over the next days the larvae, which may receive some nutrients from the parent (De Eguileor et al. 1994), consume their yolk supply and develop into juvenile leeches. They are attached with their posterior sucker to the ventral side and carried around for another 3–4 weeks. During this post-embryonic brooding period the parent continues to feed on a variety of small aquatic organisms. In our experience, *H. stagnalis* prefers to suck the body fluids from oligochaetes (*Tubifex* worms), insect larvae (*Chironomus*) and crustaceans (*Asellus*). These observations are in accordance with extensive feeding studies of lake dwelling leeches (Young and Ironmonger 1980, 1982; Young and Spelling 1989).

The young leeches that remain attached to the venter of the feeding parent regularly join the adult by inserting their proboscises into the prey. However, the juveniles not only participate in the meal by the parent but we also discovered that the young are frequently fed by the parent – without the adult leech feeding at the same time. In Fig. 4 A–D we have depicted this unique behaviour, which can readily be observed with every brooding (hungry) *H. stagnalis* that is kept in a small glass jar. When a suitable organism (*Tubifex* worm or *Chironomus* larvae) is offered, the parent will capture the prey, insert its proboscis and then offer it to its young (Fig. 4 A, B). The juvenile leeches rapidly insert their proboscises and together keep the prey so that it can not escape. The parent then withdraws its proboscis and performs fanning movements with its body flanks. This ventilation of the brood in order to enhance the oxygen supply of the water takes about 20–30 min (Fig. 4 C). Thereafter, the empty prey is discarded; the gut of the young (but not that of the parent) is coloured dark red due to the uptake of blood (Fig. 4 D). Due to this access to food the young grow considerably in size during the 3-week-period of post-embryonic parental care. They leave the parent when they have reached about one third the body length of the adult.

This complex behaviour, first described in detail for *H. stagnalis* and *H. striata* (Kutschera and Wirtz 1986 a, b, c), was later confirmed to occur in two North American species, *H. californica* (Kutschera 1989 a) and *H. triserialis* (Kutschera 1992 b). However, it should be noted that in the latter species, which exclusively feeds on water snails (Kutschera 1987), the juvenile leeches suck the blood from prey animals that have been killed by the parent. This behaviour has also been described for the related *H. robusta*, an endemic species which was found in a man-made waterway in the Sacramento delta of California (Shankland et al. 1992). The life cycle and feeding behaviour of the African leech *H. conifera* was examined in detail by Davies et al. (1997). This *Helobdella* species feeds, like *H. triserialis* and

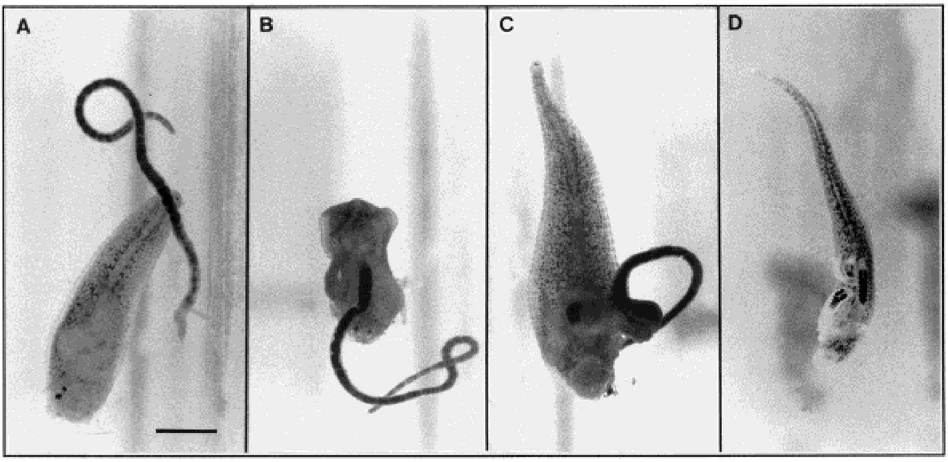

Fig. 4. Ventral view of a mature individual of the two-eyed flat leech *Helobdella stagnalis* that feeds its young carried on the venter of the parent. The leech is attached with its posterior sucker to the glass plate of an aquarium. The parent captures a prey organism (*Tubifex* worm) (A) and pushes it to the young (B). During communal feeding (C) the parent performs fanning movements with its body flanks. After the pale (empty) worm was discarded the gut of the young (but not that of the adult) was coloured red (D). The juvenile leeches, but not the parent, have taken up food. Scale bar: 0,5 cm.

H. robusta, exclusively on water snails; the young of brooding species participate in the meal of the parent. It should be noted that Pederzani (1980) mentioned similar observations carried out on several specimens of a *Helobdella* species of unknown taxonomic status. This enigmatic leech, which is very similar to *H. striata*, was introduced from South America via aquatic plants into several warm-water aquaria in Berlin (Germany).

The genus *Helobdella* has been recorded from all continents with the exception of Australia (Sawyer 1986 a, b). Recently, the first record of this genus on this continent was reported by Govedich and Davies (1998). The newly described species *H. papillornata* has a highly developed parental care system; it feeds exclusively on gastropod snails. Juvenile leeches are supplied with food by the parent.

This brief survey shows that all eight *Helobdella* species that have been investigated in the laboratory so far show very similar life cycles. Brooding of the young takes 3 to 5 weeks during which time period the juvenile leeches co-feed with the parent or are fed by the adult leech as exemplified by the type species *H. stagnalis* (Figs. 4, 5 C). As a result of this protection and consistent food supply the young are much larger (and have a better chance of survival) when they leave the parent to lead an independent life, as compared with members of the Glossiphoniinae or the Erpobdellidae (Fig. 5 A, B, C). The major selection pressure that gave rise to the phylogenetic development of these highly developed parental care systems has been identified as the (potential) predation by water snails.

Two members of the Haementeriinae, *Marsupiobdella africana* from South Africa and *Maiabdella batracophilia* from South America, evolved independently a permanent brood pouch (Van der Lande and Tinsley 1979, Sawyer 1986 b) in which the juvenile leeches are carried until they leave the parent. However, the direct (or indirect) feeding of the young as described for *Helobdella* species has not been observed. Sawyer (1986 b) introduced the subfamily Haementeriinae which comprises all Glossiphoniid species that attach their cocoons directly to the venter of the parent. The type genus *Haementeria* was selected because the well-investigated giant hematophagous leech species *H. ghilianii* displays complex parental care patterns, notably the creation of a temporary brood pouch (Sawyer et al. 1981). However, feeding of young as in *Helobdella* species has not been observed (Wilkialis 1984, Sawyer 1986 a, b). With respect to the care provided by the parent, members of genus *Helobdella* display the most advanced behaviour. It would therefore be appropriate to replace the term Haementeriinae by Helobdelliinae. However, as pointed out by Sawyer (1986 b), a clear phylogenetic trend towards bloodsucking on mammals is obvious when all known Glossiphoniidae described in the literature are considered, culminating with the giant species *H. ghilianii*. Since the highly evolved strategies in feeding behaviour of the genus *Haementeria* may exceed that of all the *Helobdella*-species the taxonomic terms coined by Sawyer (1986 b) are acceptable.

As indicated in Table 1, the second major family within the Rhynchobdelliformes are the Piscicolidae. These fish leeches exclusively suck the blood from vertebrates (fish); they occur in both fresh water and marine habitats. Members of the Piscicolidae produce hardened cocoons that are attached to the substrate (stones, water plants). No parental care has been reported from these fish parasites.

Discussion and Conclusions

The three European leeches *Erpobdella octoculata*, *Glossiphonia complanata* and *Helobdella stagnalis* occur regularly in the same body of water, often side by side under the same stones (Young et al. 1995). However, they probably differ in many ecological parameters such as, for instance, the intensity of predation on different age classes. As every organism has a limited amount of energy to invest into offspring, there is an inverse relation between the number of offspring produced and parental investment per offspring (Wilson 1975). Our three exemplary leech species well illustrate this relation. *Erpobdella octoculata* provides little parental investment and produces many small eggs, while *Glossiphonia complanata* and *Helobdella stagnalis* invest much more into a much smaller number of offspring (Table 2).

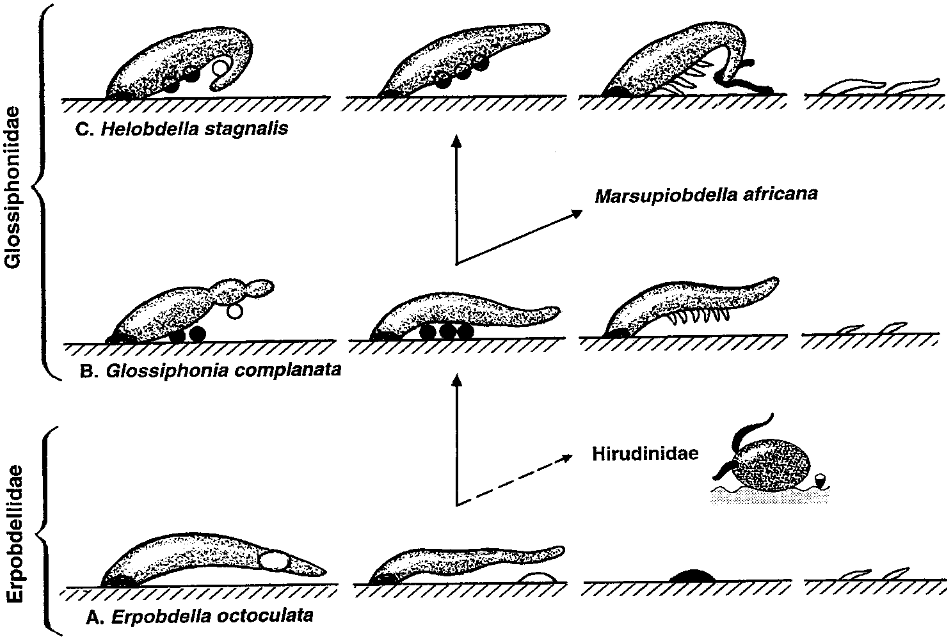

Fig. 5. Scheme of the life cycles of representative extant leech species to illustrate the probable phylogenetic development of parental care patterns in the Euhirudinea. The Erpobdellidae (*E. octoculata*) produce flat cocoons that are ventilated as they harden and darken (A). Members of Glossiphoniidae show increasing degrees of parental care. The Glossiphoniinae (*G. complanata*) cover their cocoons and remain attached above the eggs (B). The Haementeriinae (*Helobdella stagnalis*) are mobile during brooding of the eggs, larvae and young. They provide food for their offspring so that the juvenile leeches leave the parent at an advanced stage of development (C). In addition, the terrestrial cocoon deposition of the Hirudinidae and the parental care of *Marsupiobdella* are indicated. (Adapted from Kutschera and Wirtz 1986 a and from Kutschera 1990).

Thirty years ago, Sawyer (1971) proposed that within extant glossiphoniids, the degree of protection provided by the parent to the offspring can be arranged in a hypothetical series of increasing complexity, culminating in the development of a permanent brood pouch in the African leech *Marsupiobdella*. As a result of our discovery of the feeding behaviour in *Helobdella* species we revised and extended the original scheme, as proposed by Sawyer (1971). In Fig. 5 A–C we present an up-dated and modified version of our phylogenetic hypothesis published fifteen years ago (Kutschera and Wirtz 1986 a). Our current picture of the probable phylogenetic development of these complex brooding patterns can be summarized as follows.

In accordance with Sawyer (1986 a, b) we propose that predaceous worm leeches of the genus *Erpobdella* are more closely related to some extant oligochaetes than are other members within the Hirudinea. All jawless worm leeches (Erpobdellidae) studied so far forage in a random manner during the night. Prey-captures generally take place when ‘circumnavigating’ body movements brings the leech’s mouth into chance contact with a prey organism (*Tubifex* worms, *Chironomus* larvae). This behaviour is reminiscent to that of earthworms, which feed on plant material obtained from the soil surface (Edwards and Bohlen 1996). Carnivorous oligochaetes of the genus *Erpobdella* (Fig. 5 A) suck off fresh cocoons of its own species (as well as those of other Erpobdellidae, see Kutschera 1986). However, the brooding leech does not attack its own cocoon, i. e., the drive to eat fresh egg capsules is blocked after cocoon deposition (Sawyer 1970, Kutschera 1983, 1986, 1989 b). The unprotected, fresh *Erpobdella* cocoons are in danger of being eaten by many potential predators, notably conspecifics and water snails. After hardening the dark-brown egg capsules are attacked (and in part destroyed) by water snails. The heavy loss of unprotected offspring is countered by mass production of cocoons (Table 2).

All leech species classified as Arhynchobdellida (Table 1) deposit cocoons that develop a hard surface in order to protect the enclosed eggs that are embedded into a proteinaceous fluid. The eggs are small (diameter ~ 50 µm) and are not provided with yolk. They develop into 'cryptolarvae' that feed on the nutrient solution and thereby grow until the young leeches hatch through the holes of the egg capsule (Fig. 2 B). The terrestrial deposition of cocoons within the Hirudinidae is interpreted as a means to reduce the destruction of the offspring by aquatic predators such as snails, insect larvae and fish (*Brutfürsorge*) (Fig. 5 A).

Within the Hirudinea, parental care is known to occur only in the family Glossiphoniidae (Sawyer 1986 a, b). This observation strongly suggests

Table 2. Comparison of the main parental care patterns of the leeches *Erpobdella octoculata*, *Glossiphonia complanata* and *Helobdella stagnalis* (see Fig. 5 A–C). The results are based on leech populations raised in aquaria at room temperature. The animals were collected in ponds and streams in southern Germany (Freiburg i. Br.); they were fed twice per week with *Tubifex* worms or water snails. The experimental breeding seasons lasted from April to September during the years 1980–1985 (unpublished results).

	E. octoculata	*G. complanata*	*H. stagnalis*
Cocoons/season	~ 120	~ 3–4	~ 5–6
Egg production/season	~ 1000	~ 60	~ 50
Egg size	small (~ 50 µm)	large (~ 600 µm)	large (~ 500 µm)
Yolk	no (albumen)	yes	yes
Duration of parental care	~ 10 min (ventilation)	~ 30 days	~ 45–50 days
Egg mortality	high	low	close to zero
Care for larvae	no	yes	yes
Larval mortality	high	low	close to zero
Care for young	no	protection	protection and food provision
Mortality of young over the first 3 weeks	high	very low	close to zero
Growth of young	slow, dependent on own capture of food	slow, no food supply	rapid, due to feeding by parent

that this complex behaviour arose *de novo* in that group during the evolution of the leeches.

In all members of the Glossiphoniidae the cocoon is a transparent, thin (flexible) membrane that surrounds the large, yolky eggs (diameter ~ 0,5–2,5 mm, depending on species). This leech family can be divided as follows (1.–3.). Sawyer (1986 a, b) defined the subfamily Glossiphoniinae (1.) as those species which attach their cocoons directly to the substrate and cover them with their body (snail leech, *Glossiphonia*, turtle leech, *Placobdella*, tadpole leech, *Hemiclepsis*). In Fig. 5 B the life cycle of the type-species *G. complanata* is shown as a representative example. The monogeneric subfamily Thermoyzinae (2.) was separated from the Glossiphoniidae because the bird leeches (*Thermyzon*) are unique among the glossiphoniids with respect to their mode of cocoon production (Wilkialis and Davies 1980; Sawyer 1986 b). The subfamily Haementeriinae (3.) is defined as those glossiphoniid species that always attach their cocoons onto the ventral surface of the parent. This manner of parental care occurs in the giant tropical leech *Haementeria ghilianii* and all *Hellobdella-* as well as the *Alboglossiphonia*-species investigated so far.

In Fig. 5 C we have summarized the reproductive and brooding behaviour of *Helobdella stagnalis*. The cocoons are attached to the venter of the parent, carried around and thereby protected from predators. During the post-embryonic brooding period of 3–4 weeks the young co-feed with the parent or are fed by the adult leech.

The phylogenetic scheme shown in Fig. 5, that is based on life history strategies of three representative species, has recently been corroborated by taxonomic and cladistic studies. Siddall and Burreson (1995, 1996) have pointed out that the behaviour of secreting a protective cocoon and cementing it to a solid substrate represents the original state in leech evolution, exhibited by *Acanthobdella* as well as *Agriodrilus* and retained in the Erpobdellidae and the fish leeches (Piscicolidae). As the cladogram (Fig. 6) shows, the unique behaviour among the Glossiphoniidae to protect the cocoons and fanning them with their body flanks (parental care) is correlated with the loss of the protective hardened egg capsules. Terrestrial deposition of desiccation-resistant cocoons is restricted to the Hirudinidae. In summary, the phylogenetic tree depicted in Fig. 6 provides independent evidence for the hypothesis that the evolution of brooding behaviour within the Euhirudinea (Glossiphoniidae) was to a large extent driven by one major selective pressure: predatory attacks by water snails and other aquatic carnivores (Sawyer 1971, 1986 b; Kutschera and Wirtz 1986 a).

To our knowledge, the observations described here for the genus *Helobdella* are the only ‘prearthropodian’ examples of parental animals feeding their young. In the arthropods, such behaviour is known for many insects (Tallamy 1984, 2000; Trumbo 1996), a spider (Tretzel 1961), a crab (Diesel 1989) and several amphipod and isopod species (referenced in Thiel 1999 a, b).

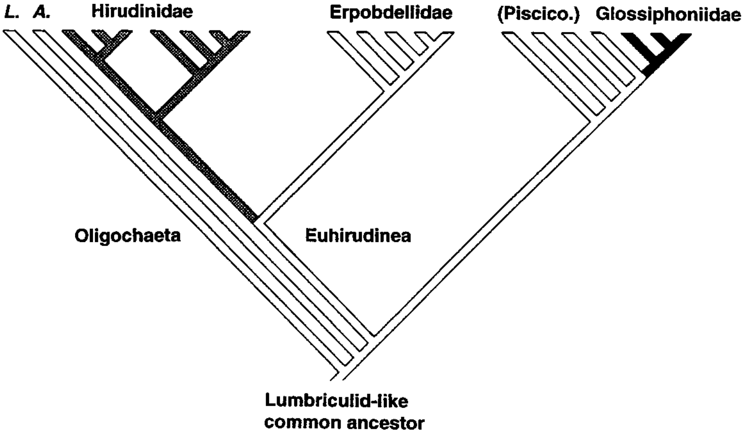

Fig. 6. Cladogram that illustrates the evolution of cocoon deposition characteristics within the Euhirudinea. White: Cocoons cemented-abandoned; grey: terrestrial deposition of desiccation-resistant egg capsules; dark: membranous (thin-walled) cocoons that are brooded by the parent. A. = *Acanthobdella*; L. = Lumbriculidae (earthworms); Piscico. = Piscicolidae (fish leeches). (Adapted from Siddall and Burreson 1996).

The evolution of parental care has been analysed in some detail in vertebrates such as fish, frogs, birds and mammals (Clutton-Brock 1991). Our systematic study of the reproductive behaviour in freshwater leeches demonstrates that much has yet to be learned about the phylogenetic development of the parental care patterns in aquatic (and terrestrial) invertebrates. Unfortunately, this fascinating subject has not received much attention by evolutionary biologists (Futuyma 1998, Stearns and Hoekstra 2000).

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