Naturwissenschaften (2007) 94:967–974
DOI 10.1007/s00114-007-0278-3

ORIGINAL PAPER

The European land leech: biology and DNA-based taxonomy of a rare species that is threatened by climate warming

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Received: 12 March 2007 / Revised: 11 June 2007 / Accepted: 21 June 2007 / Published online: 24 July 2007

Abstract The European land leech *Xerobdella lecomtei* was discovered in 1868 and is one of the rarest animals on Earth. During the 1960s, several individuals of these approx. 40 mm long, cold-adapted terrestrial annelids that inhabit the moist soils of birch forests around Graz, Austria, were investigated. Only one original research paper has been published on the biology of this species. Between 2001 and 2005, we re-investigated the morphology of preserved specimens and searched for living individuals in their natural habitat that appeared to be intact. We found only one juvenile individual (length approx. 10 mm), indicating that this local leech population became largely extinct over the past four decades. The feeding behaviour of our 'lonesome George of the annelids' was studied and is described here in detail. After its death, the *Xerobdella* individual was used for chemical extraction and molecular studies (deoxyribonucleic acid [DNA] barcoding, based on one gene, the mitochondrial cytochrome *c* oxidase subunit I). In addition, novel DNA barcodes for a land leech from Madagascar and a recently discovered species from Europe were obtained. Our phylogenetic tree shows that *X. lecomtei* is not a member of the tropical land leeches (family Haemadipsidae), as previously thought, but represents a separate line of descent (family Xerobdellidae). The decline of the local leech population around Graz correlates with a rise in average summer temperatures of +3°C between 1961 and 2004. This warming led to a drastic reduction in the moisture content of the soil where *X. lecomtei* lives. We suggest that human-induced climate change without apparent habitat destruction can lead to the extinction of populations of cold-adapted species that have a low colonization ability.

Keywords Climate warming · DNA barcoding · Land leeches · *Xerobdella*

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Introduction

Tropical land leeches (Haemadipsidae) are found in Sri Lanka, India, Burma, Malaysia, the Islands of the East Indies, China, Japan, Australia and Madagascar. In these areas, these aggressive blood-sucking parasites are confined to habitats that have a heavy rainfall because moist conditions are necessary for their terrestrial way of life. In some regions of India, haemadipsids have been described as a 'formidable pest' (Bhatia 1975; Sawyer 1986). These agile annelids suck the blood of mammals (cows, horses and humans); many tropical places are dominated by land leeches to the extent that they are almost un-inhabitable. However, not all terrestrial leaches are tropical; that is, there are species that live in temperate climates.

In 1868, Georg Ritter von Frauenfeld (1807–1873) published a short report on the occurrence of a new leech species that was discovered in Austria (province Steiermark) in the moist soil on a mountain, far away from any freshwater pond or stream. This unusual annelid, the European land leech (*Xerobdella lecomtei*), was described on the basis of three approx. 40 mm long alcohol-preserved specimens (v. Frauenfeld 1868). Three decades later, Penecke 1896 reported that *Xerobdella* individuals, found in relatively cold alpine regions, are sometimes attached to the skin of the montane salamander *Salamandra atra*. He concluded that the European land leech is a facultative blood sucker on terrestrial amphibians. In 1909, Schuster discovered remnants of partly digested oligochaetes in the gut of two sectioned *Xerobdella* individuals and suggested that the land leech feeds on earthworms.

Between 1922 and ca. 1940, the zoologist Erich Reisinger (1900–1978) collected several adult land leeches in the birch forests around Graz (Austria). He analysed the feeding and reproductive behaviour of this rare annelid on animals kept in glass jars in the laboratory. Amphibians (*S. atra* etc.) were not attacked by hungry *Xerobdella*, but the leeches voraciously fed on earthworms and other terrestrial oligochaetes (Reisinger 1951). In addition, this author discovered that *Xerobdella* is a cold-adapted terrestrial annelid, which prefers temperatures of 10–15°C. At 25°C, the land leeches rapidly died.

The *Xerobdella* population around Graz was analysed a second time between ca. 1960 and 1970. Within this decade, more than 20 individuals were collected, preserved in liquid fixatives and used for an anatomical study (Moosbrugger and Reisinger 1971). After the death of Reisinger (1978), only four adult *Xerobdella* individuals remained in the Institute of Zoology (Karl-Franzens-University of Graz). In 2001, we wanted to use part of this stored material for an ongoing deoxyribonucleic acid (DNA)-barcoding study on European leeches (determination of mitochondrial cytochrome *c* oxydase subunit I [COI] gene sequences for identification of species, see Pfeiffer et al. 2004, 2005; Siddall and Budinoff 2005; DeSalle et al. 2005; Bely and Weisblat 2006; Waugh 2007; Kutschera 2007). However, we were unable to extract amplifiable DNA fragments from these poorly preserved samples. Because only one original report has ever been published on the biology of *Xerobdella* (Reisinger 1951), we engaged in expeditions to the birch forests where the leeches were collected four decades ago. These extensive searches for the European land leech were largely unsuccessful. Between 2001 and 2005, we found only one living juvenile *Xerobdella* individual. Hence, the *Xerobdella* population analysed by Reisinger 1951 became largely extinct over past decades, although the habitat of this rare annelid has not been destroyed.

In this report, we describe the morphology of preserved individuals of the original population and the biology and feeding behaviour of this single specimen. After its death, our ‘Lonesome George of the annelids’ (Nicholls 2006) was used for DNA extraction and sequencing to explore the systematic position of this enigmatic animal as well as its supposed phylogenetic relationship to the tropical land leeches (Blanchard 1917; Sawyer 1986; Nesemann and Neubert 1999). Based on a recent study that documents the human-induced climate change in Austria over the last four decades (Kabas 2005), we propose a hypothesis that may account for the almost complete extinction of this local population of land leeches.

Materials and methods

Leech specimens and field work

Four formaline-preserved adult specimens of *X. lecomtei* from the Reisinger collection were stored without refrigeration for time periods from 30 to 40 years. In 2001, these animals were transferred to 70% ethanol and 2 years later investigated under a light microscope. One living juvenile *X. lecomtei* individual was collected in 2002 in a sample of relatively moist soil (region around Graz, Austria) and was maintained in a closed plastic container (approx. 10×15×5 cm) at the University of Kassel (Institute of Biology, cold room; temperature =10–15°C). The terrarium was equipped with moist filter paper and leaves of birch (*Fagus sylvatica*) trees from the leech’s natural habitat (Moosbrugger and Reisinger 1971). Over a period of 10 months, this individual was fed nine times by the addition of one earthworm (adult *Lumbricus castaneus* or juvenile *L. terrestris*, length approx. 30–40 mm). The feeding episodes were recorded with a camera as previously described (Kutschera and Wirtz 2001; Kutschera 2003). One representative episode was selected and is illustrated by a schematic drawing. After its death, the *Xerobdella* individual was stored in 95% ethanol at −20°C.

Land leeches from Madagascar were collected in the vicinity of the town of Antananarivo (see map in Goodman and Benstead 2003). Individual leeches were picked up from leaves in forests. About 40 individuals, juveniles and adults, were collected; the length of living leeches at rest was 5 to 16 mm. All specimens were immersion fixed and preserved in 95% ethanol. The land leeches were assigned to the taxon *Mallagabdella fallax* according to the key of Richardson (1978). Alcohol-preserved individuals of the European species *Hirudo verbana* (Kutschera 2006), *Trocheta pseudodina* (Pfeiffer et al. 2005) and *Haemopis elegans* (Grosser 2004) were obtained from M. Roth (Giessen, Germany) and C. Grosser (Leipzig, Germany).

DNA extraction

All leeches were stored in 95% ethanol at −20°C until used for extraction of total DNA. The caudal sucker was removed and utilized for all analyses. This organ was specifically used to minimize the possibility of contamination from prey (or host) DNA stored in the gastric region of the leeches. From these tissues (about 10 to 80 mg per sample), total DNA was extracted using the QIAamp Tissue Kit (Quiagen GmbH, Hilden, Germany) as described by Pfeiffer et al. (2004). The resulting DNA was diluted in 50 µl of double-distilled water and used for further analyses. All DNA extractions were repeated at least two times with different specimens (Pfeiffer et al. 2004). In the case of *X. lecomtei*, only one juvenile specimen was available for DNA extractions, which were repeated from small tissue samples excised from the flanks of the body. It should be noted that molecular studies based on a single specimen are not uncommon (for a recent example, see Giribet et al. 2006).

PCR amplification, sequencing and data analysis

We examined sequence diversity in a specific 648-bp fragment of the mitochondrial COI gene (Pfeiffer et al. 2004). This sequences was amplified using the 'universal primers' designed by Folmer et al. (1994): LCO 1490: 5′-GGTCAACAAATCATAAAGATATTGG-3′ and HCO 2198: 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′.

Amplification reactions for COI included 10× polymerase chain reaction (PCR) buffer (10 mM $MgCl_2$, pH 8.3) and Q-solution, 100 µM of each deoxyribonucleotide triphosphate, with 1 U of *Taq* polymerase and 10 pmol of each primer and 4 µl of the DNA extract. The total volume of this solution was 20 µl. The amplifications were carried out with initial denaturation at 95°C for 10 min, followed by 38 cycles of one denaturation step at 94°C for 40 s, primer annealing at 38°C for 40 s and primer extension at 72°C for 45 s in a Thermocycler (Biometra, Göttingen, Germany).

Two microliters (20–50 ng) of the PCR products were cycle sequenced as previously described (Pfeiffer et al. 2004). DNA sequences were analysed on an ABI Prism 3100 genetic analyzer (Applied Biosystems, Foster City, USA) according to manufacturer's instructions and were aligned subsequently by eye in BIOEDIT (Hall 1999). Sequence divergences among individuals were quantified using the Kimura-2-parameter distance scheme (Pfeiffer et al. 2004) and graphically displayed in a neighbour-joining tree (Saitou and Nei 1987; Waugh 2007). The novel sequences have been deposited in GenBank (accession nos. EF 125040–EF 125044).

Results

Morphology of adult leeches

Four decades ago, Moosbrugger and Reisinger (1971) collected, preserved and investigated several adult *Xerobdella* individuals. In 2001, only four formaline-preserved specimens were found in the archives of the Institute of Zoology (Graz, Austria). Because no photograph of this rare annelid has ever been published, we document here the unique morphology of this animal species (Fig. 1). The formaline-preserved leeches that were transferred for further conservation into 70% ethanol had a body length of 30–45 mm and a maximum diameter of 3.0–3.5 mm. In the individual depicted here (Fig. 1a), the glandular clitellum covers annuli 26 to 40; the swollen clitellum of a sexually mature earthworm is shown in Fig. 3. In the head region of *Xerobdella*, the oral palps or 'tenacles' were apparent; these structures assist in foraging and feeding (Fig. 1b). Four pairs of dark-pigmented eyes were counted on all individuals investigated here. In the clitellar region, the male and first female gonopores are separated by three to four annuli. In addition, the accessory (second) female gonopore (bursa porus), a structure of unknown function, is also apparent in our photograph (Fig. 1c). Nesemann and Neubert (1999) have pointed out that specific radial furrows within the posterior sucker of *Xerobdella* are a characteristic feature of

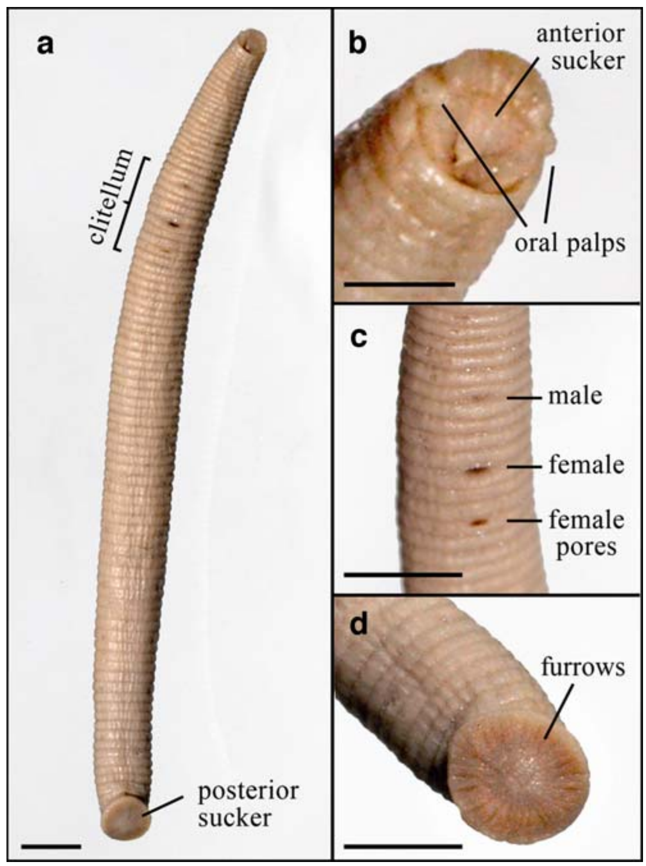

Fig. 1 Representative adult specimen of the European land leech (*Xerobdella lecomtei*), collected in Austria ca. 1960. Ventral view of entire animal (**a**); head region with oral palps, ventral view (**b**); clitellar region, showing the male and the two female gonopores, respectively (**c**), and posterior sucker with characteristic radial furrows (**d**). The leech was originally stored in formaline and since 2002 preserved in 70% ethanol. *Scale bars*=2 mm

this European annelid that appear to be identical with those of the tropical land leeches. In our adult specimens, these structures were detected (Fig. 1d), but the furrows are less pronounced than in the schematic drawings published by these earlier investigators.

Behaviour of the land leech

Our collection efforts into the beech forests around Graz yielded only one juvenile specimen of *X. lecomtei*, which was attached to a rotten leaf (Fig. 2a). The length of this individual was about 10 mm at rest (diameter approx. 1 mm); when fully extended, the leech reached a length of approximately 18 mm. During the day, the inactive leech coiled into a ball-like configuration with the head in the centre of the knot (Fig. 2b). At night (notably after midnight), the leech was active and, when hungry, regularly foraged for food (Fig. 2c).

Reisinger (1951) reported that adult hungry *Xerobdella* individuals, maintained in captivity, do not feed on amphibians such as *S. atra*, but rapidly attack and swallow small earthworms. However, foraging and feeding behaviour of a juvenile land leech has not yet been described. Nine feeding episodes of our individual (Fig. 2a) were recorded. A representative chain of events is shown in Fig. 3. The resting land leech in knotted posture (Fig. 3a) is alerted by the addition of an earthworm (adult *L. castaneus*

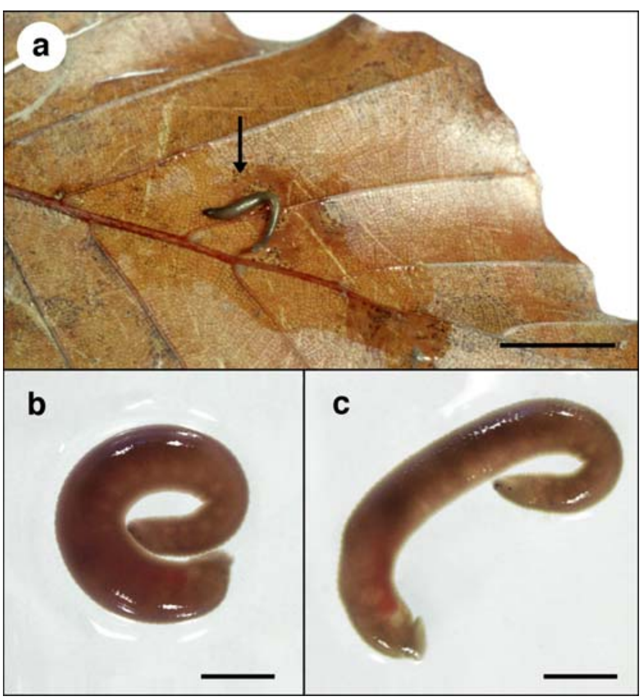

Fig. 2 Juvenile living individual of *Xerobdella lecomtei* (*arrow*), attached to a fallen leaf of birch (*Fagus sylvaticus*) from its natural habitat (**a**). The same leach on moist filter paper in resting position (**b**) and alerted by an earthworm (**c**). *Scale bars*=10 and 2 mm, respectively

or juvenile *Lumbricus terrestris*). The leech detects the slime trail of the nearby organism by means of the palp-like tentacles on either side of the mouth (Fig. 1b) and rapidly attaches to its prey (Fig. 3b). Within a few minutes, the leech cuts through the epidermis of the earthworm with the aid of the teeth on its three jaws and sucks body fluids from the wounds. This feeding episode, during which the juvenile leech is carried around by the mobile earthworm, lasts for 2 to 3 h. The thick, satiated leech then leaves its prey and returns to its knotted posture (Fig. 3c). The satiated leech remained in this characteristic resting position until the ingested body fluids were completely digested (ca. 1 week later).

Taxonomic status of *Xerobdella*

In accordance with earlier investigators, Reisinger (1951) interpreted *Xerobdella*, a European sanguivorous annelid, as a member of the Haemadipsidae (tropical land leeches). In this context, he regarded *Xerobdella* as a relict taxon from the Tertiary (Moosbrugger and Reisinger 1971). On the basis of nuclear 18 S ribosomal DNA (rDNA) sequence data, this hypothesis has been questioned (Borda and Siddall 2004). Because no mitochondrial DNA sequences were available for *Xerobdella*, we extracted DNA from our single specimen (Fig. 2) after its death and obtained a 648-bp mitochondrial COI gene sequence. In addition, new COI data were obtained for the following taxa: *Malagabdella fallax*, a common tropical land leech from Madagascar (Richardson 1978), *H. verbana*, a blood-sucking amphibious medicinal leech from Turkey (Kutschera 2006, 2007) and two relatively large terrestrial leech species from Germany, *T. pseudodina* (Pfeiffer et al. 2005) and the recently discovered taxon *H. elegans* (Grosser 2004). These five newly acquired COI sequences (GenBank accession nos. EF 125040–EF 125044) were supplemented by published COI data from the literature, for the following leech species: *Haemadipsa sylvestris* and *Chtonobdella bilineata* from Vietnam and Australia, respectively (Richardson 1968; Siddall and Burreson 1998), *Haemopis sanguisuga*, *Erpobdella octoculata* and *Trocheta haskonis* from Europe (Pfeiffer et al. 2004, 2005).

Our phylogenetic neighbour-joining tree (Fig. 4) yielded the following information. The three tropical land leeches (*Haemadipsa* from Asia, *Malagabdella* from Madagascar and *Chtonobdella* from Australia) form a clade that excludes the terrestrial *Xerobdella* from Europe. This rare annelid represents a separate line of descent, parallel to the haemopid/hirudinid clade (*Haemopis*, *Hirudo*). The amphibious predatory erpobdellid taxa of the genus *Trocheta*, supplemented by the aquatic type species *E. octoculata*, are not closely related to *Xerobdella* (outgroup). Hence, *X. lecomtei* is not a member of the tropical Haemadipsidae but may be a relative of the

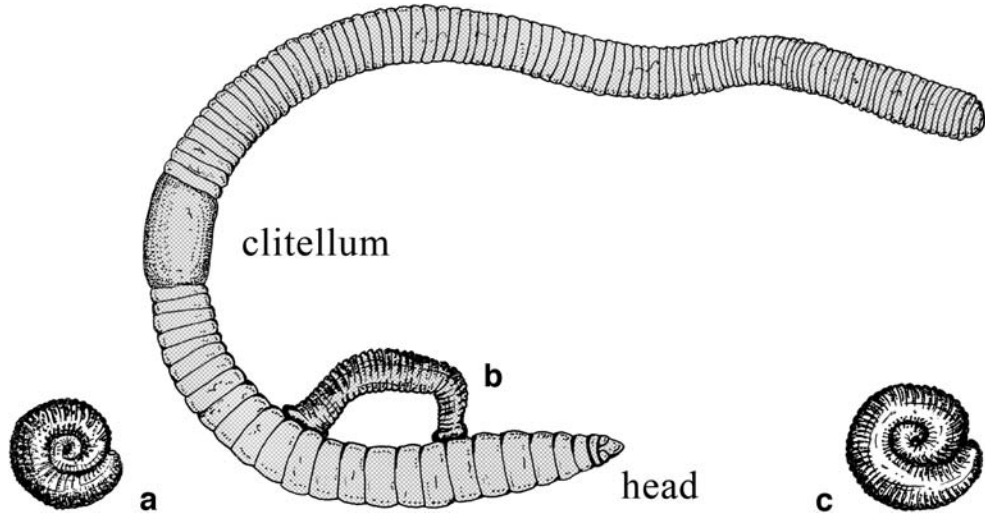

Fig. 3 Feeding behaviour of a juvenile land leech (*Xerobdella lecomtei*). The animal in knotted posture (**a**) is alerted by an adult earthworm (*Lumbricus castaneus*), rapidly attaches to its prey and sucks body fluids (**b**). Resting satiated leech (**c**) in characteristic ball-like configuration. *Scale bar*=10 mm

amphibious-terrestrial Haemopidae/Hirudinidae (Trontelj et al. 1999; Kutschera and Wirtz 2001).

Human-induced climate and habitat changes

Between 1960 and ca. 1971, Reisinger and the senior author of this report (Ebermann) encountered a number of adult *Xerobdella* individuals in the birch forests around Graz (Fig. 1a), although it should be noted that this species has always been rare. However, excursions to these localities carried out between 2001 and 2005 yielded only one living juvenile individual (Fig. 2), which suggests that this population of land leeches has been sharply declining in numbers. The climatologist Kabas (2005) compiled two Austrian temperature records spanning the past four decades (1961 to 2004). In two representative regions, the national park Hohe Tauern and a flat area in the south eastern part of the Steiermark, average air temperatures were recorded and analysed in detail. These data document that between 1961 and 2004, the mean annual air temperature increased in these regions by 2.00 and 2.41°C, respectively. In the southeastern part of the Steiermark, the increase in average summer temperature was +3.05°C (Table 1). All these recorded climate changes are statistically significant (Kabas 2005). In addition, we recognized that the moist soil, where *Xerobdella* individuals had been found until ca. 1971 under pieces of bark and rotten birch leaves, has become much dryer. In the hot summer of 2003, some of the original leech habitats around Graz had entirely dried up. However, we have no quantitative data (soil moisture contents) to further document these qualitative field observations.

Discussion

In this study, we provide information on the morphology, biology, feeding behaviour and DNA-taxonomy of *X. lecomtei*, the only supposed member of the ‘land leech family’ that inhabits relatively cool birch forests of some regions in Europe. Is this rare annelid in fact a close relative of these aggressive, blood-sucking haemadipsids?

Ninety years ago, Blanchard (1917) published a review article wherein he grouped together all blood-sucking leech species with a terrestrial habit, inclusive of *X. lecomtei*, and established the family Haemadipsidae. Most zoologists followed him, notably Reisinger, who described the European land leech as a relict taxon from the Tertiary (Moosbrugger

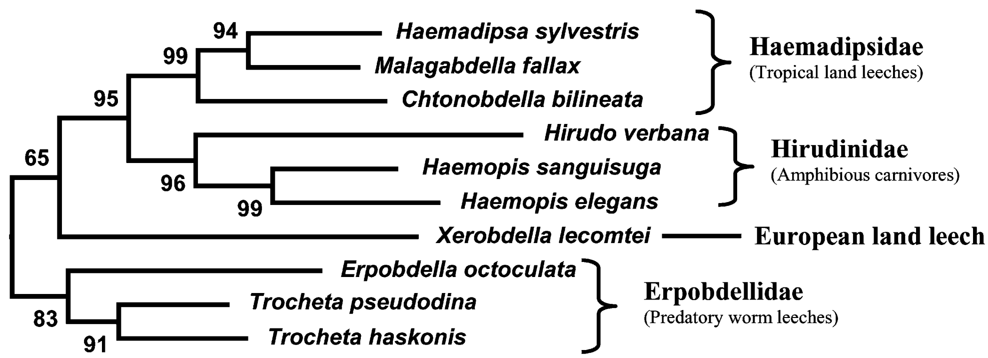

Fig. 4 Phylogenetic relationships of ten selected leech species with the Erpobdellidae as outgroup. The diagram shows a neighbour-joining tree obtained from newly acquired and published COI DNA sequence data, inclusive of the branch support values. Taxonomy of the leeches is adapted from Kutschera and Wirtz (2001)

Table 1 Mean increase in air temperature (°C) during the time period 1961–2004 in two regions of Austria

Region	Altitude above sea level (m)	Temperature increase (°C)
Hohe Tauern	500–3,106	2.00 (average), 2.34 (spring), 2.46 (summer)
Südoststeiermark	208–725	2.41 (average), 2.54 (spring), 3.05 (summer)

Data compiled from Kabas (2005).

and Reisinger 1971). This hypothesis has been accepted by Sawyer (1986); Nesemann and Neubert (1999) and others. It should be noted that Sawyer (1986) stressed that *Xerobdella* has only four pairs of eyes (instead of five in typical haemadipsids), but he nevertheless interpreted this European taxon as a member of the tropical land leech family. Although Reisinger's hypothesis has been questioned (see Soos 1966; Minelli 1979), only with the advent of molecular methods have new insights been obtained. Based on nuclear 18 S rDNA sequences, Trontelj et al. (1999) and other investigators (Borda and Siddall 2004) found that *Xerobdella* is more closely related to members of the genera *Haemopis* and *Hirudo* than to tropical *Haemadipsa* species.

In this study, we use a DNA-barcoding approach and show that on the basis of mitochondrial COI-sequence data, three genera of haemadipsids from Asia, Australia and Madagascar form a monophyletic clade, to the exclusion of the European *Xerobdella*. It should be noted that the genera *Haemadipsa* and *Chtonobdella* from Asia and Australia, respectively, are well-characterized taxa (Richardson 1968; Bhatia 1975; Sawyer 1986), but the biology and taxonomic status of haemadipsids from Madagascar are unknown. In the most recent monograph on the 'Natural History of Madagascar' (Goodman and Benstead 2003), leeches are not mentioned, although these aggressive ectoparasites are well-known pests to travellers (Bhatia 1975). In this study, we show that the common species *M. fallax* (Richardson 1978), collected in the centre of Madagascar for DNA extraction, is a close relative of its Asian and Australian counterparts. Our phylogenetic tree (Fig. 4) shows that *Xerobdella* is not a member of the Haemadipsidae; it may be more closely related to leeches of the genera *Haemopis* and *Hirudo*, as suggested by Trontelj et al. (1999). However, the branch of our tree leading to *X. lecomtei* has a very low support value; that is, in our analysis, the position of the European land leech towards other hirudineans is not conclusive. In accordance with Minelli (1979), we assign the taxon *X. lecomtei* to the family Xerobdellidae and to the suborder Hirudiniformes (Nesemann and Neubert 1999).

The suggested *Xerobdella–Haemopis* relationship is further corroborated by the facts that (1) both leech species are terrestrial earthworm feeders that forage in a similar way (Kutschera and Wirtz 2001), (2) they display an 'earthworm-like' resting position during periods of digestion (Sims and Gerard 1985; Fig. 2a) and (3) are characterized by a largely identical digestive tract and other anatomical features (Moosbrugger and Reisinger 1971). The similarities of *Xerobdella* to the recently discovered terrestrial taxon *H. elegans* from Europe (Grosser 2004) are especially striking (habitat preference and behaviour). However, more work is required to further explore the putative evolutionary relationship between members of the genera *Xerobdella* and *Haemopis* (Trontelj et al. 1999). It should be noted that our DNA-barcoding data indicate that the common species *H. sanguisuga* and its rare, morphologically similar relative *H. elegans* are different taxa, as suggested on the basis of field observations and microscopical studies (Grosser 2004).

In November 1867, Georg Ritter von Frauenfeld submitted his classical paper on *X. lecomtei* for publication. Only 140 years later, we have to describe the sad story of 'Lonesome George of the annelids' (Nicholls 2006)—a reminder that the impact of humans on the environment can be more rapid and subtle than previously thought. The birch forests around Graz still look like those where Reisinger had collected his *Xerobdella* individuals (Moosbrugger and Reisinger 1971). The data summarized in Table 1 document that a significant anthropogenic local warming had occurred that is not restricted to the habitat of the leech population investigated here. In the southeastern part of the Steiermark, where Reisinger had found most of his specimens, an increase in average summer temperature of +3.05°C is documented for the time period between 1961 and 2004. This local warming is in accordance with the global trend reported in the literature (Hughes 2000; Travis 2002; Schiermeier 2007). In the course of the hot summer of 2003, 'tropical temperatures' (higher than 30°C) were recorded on 41 days in the centre of Graz (Kabas 2005). As a consequence of this drastic warming, a spread of the European mantis (*Mantis religiosa*) occurred between 1970 and 1986 (Gepp and Kreissl 1988).This insect species prefers dry, sunny meadows and can only reproduce in warm regions.

The increase in air temperature led to a sharp decline in the moisture content of the soil of the birch forests where the land leeches live, notably in the hot summer of 2003 (Ebermann, unpublished observations). Because *X. lecomtei* belongs to those specialist species that have a low colonization ability and poor dispersal, this rare annelid may be prone to extinction as a result of climate change (Travis 2002). Reisinger reported that in the laboratory, the optimal temperature for the cultivation and maintenance of *Xerobdella* populations is around 12°C and that at 25°C these cold-adapted worms rapidly die (Reisinger 1951;

Moosbrugger and Reisinger 1971). Based on our climate data (Table 1) and field observations, we suggest that recent human-induced warming may have led over past decades to the almost complete extinction of a local population of this rare animal species. It should be noted, however, that the evidence for this hypothesis is only circumstantial. In colder alpine regions of Austria, other *Xerobdella* populations may still exist in moist local refugia, but currently, we have no proof for this assumption. Our 'Lonesome George' (Fig. 2) lives on as a COI GeneBank number (EF 125040) that can now be used by other scientists for further phylogenetic analyses (DNA barcoding initiative, see Pfeiffer et al. 2004, 2005; DeSalle et al. 2005; Bely and Weisblat 2006; Waugh 2007).

The general conclusions and recommendations that emerge from our study are threefold. First, human-induced warming without apparent habitat destruction may lead to subtle changes in biodiversity, notably the decline and extinction of populations that consist of cold-adapted species. Second, it is imperative to enhance research budgets in systematic biology, biodiversity research and taxonomy. We can much better protect organisms that specialists have collected, classified and described in the scientific literature than unknown biodiversity in regions unexplored by ecologists (Miller 1999). Finally, museums and biology departments should adequately preserve their specimens at low temperatures for future generations of scientists. The DNA-barcoding project (DeSalle et al. 2005; Bely and Weisblat 2006; Waugh 2007; Kutschera 2007) and other initiatives for the documentation and analysis of global biodiversity will depend on collections of ethanol-preserved specimens in this era of anthropogenic climate change and habitat destruction (Wilson 2003).

Acknowledgements This paper is dedicated to the naturalist Georg Ritter von Frauenfeld (1807–1873) on the occasion of his 200th birthday. We thank Mr. C. Grosser (Leipzig, Germany) and Dr. D. Rinke (Vogelpark Walsrode, Germany) for the provision of leech specimens. Financial support was provided by the Bundesministerium für Wirtschaft und Technologie (Förderkennzeichen 03 ESFHE 021).

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