

Steve Hopkin

Lithobius variegatus. Paul Sterry/Nature Photographers

entipedes are among the most widespread and common terrestrial arthropods (Eason 1964; Lewis 1981). Their name translates as 'hundred legs', although some species have fewer, and others more, than 50 pairs. All species are carnivorous and subdue their prey by injecting powerful venom through a pair of fangs, or poison claws, on the head. While there is little documented evidence for centipedes causing human fatalities, they can produce a particularly nasty 'bite'. The venom is rich in proteolytic (literally 'protein-breaking') enzymes that cause extensive inflammation and tissue breakdown around the wound, which is then prone to secondary infection by bacteria. If delivered by one of the large tropical species, such as Scolopendra gigantea, which can grow to 30cm or more in length, the bite is also extremely painful. British centipedes can occasionally bite humans, but the sensation is little more than that from a Stinging Nettle Urtica dioica. Centipedes are overwhelmingly beneficial as major predators of pests, such as slugs and insect larvae, and their presence in the garden is to be encouraged. Even the Ministry of Agriculture, Fisheries and Food (1984), in its advisory leaflet No. 150 for farmers on Millipedes and Centipedes, described centipedes as 'beneficial'.

Tropical centipedes are formidable animals. David Attenborough's recent BBC series Life in

the Undergrowth included some extraordinary footage of one of these monster centipedes dangling from the roof of a cave and grabbing a bat out of the air as it flew past (Molinari et al. 2005). British centipedes do not grow so large. The longest discovered was an 80mm specimen of Henia vesuviana. In the early 1990s, I managed to get this species included in the Guinness Book of Records as the 'longest British centipede', although it has not appeared in recent editions of

Ventral view of the head of *Henia vesuviana* showing the poison claws. The orange spot in the centre of each segment marks the openings of the glue-secreting glands. Steve Hopkin



Centipedes



Lithobius forficatus is an important natural enemy of garden pests such as slugs. Steve Hopkin

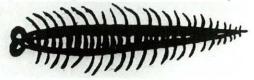
that book. The editors required evidence and, rather than send them a specimen, I took a photograph of one crawling across a sheet of graph paper and sent them that instead. The smallest species, *Lithobius lapidicola*, reaches only 8mm in length (Barber 2003).

The Subphylum Myriapoda comprises four classes of many-legged terrestrial arthropods. The Chilopoda (centipedes), and the less well-known Symphyla and Pauropoda, have only one pair of legs per segment, whereas the Diplopoda (millipedes) have two (Hopkin 2004). Centipedes always have an odd number of leg-bearing segments, and this has attracted the attention of molecular biologists interested in the role of *Hox* genes in development (Minelli 2000; Minelli & Fusco 2004). Thus, the mythical 'hundred legs' with an even 50 pairs of legs does not exist.

Centipedes in early literature

The earliest student of zoology whose work has survived was Aristotle (384-322BC). Several references to myriapods can be found in translations of his work. The distinction between polychaete worms, 'Sea Scolopendra', and centipedes, 'Land Scolopendra', was made, and became the source of much confusion in later centuries. There is one

Woodcut by a Byzantine artist in AD 512 to illustrate the Greek Herbal of Dioscorides. This could represent a polychaete worm or a littoral centipede.



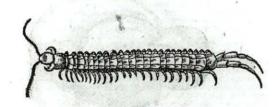
other pre-Renaissance reference to 'Skolopendra', in the form of a small woodcut made by a Byzantine artist in AD512 to illustrate the famous Greek Herbal compiled in the first century AD by Dioscorides. Skolopendra are included because of their supposed medicinal properties. However, here, as on numerous other occasions, it is difficult to decide whether centipedes or marine polychaete worms are being discussed and illustrated (Hopkin 1996).

The first definite illustration

of a centipede occurs in the herbal of Matthiolus (1500-1577), published in 1569. Although the animal is evidently a scolopendrid centipede drawn from a specimen rather than from memory, the artist clearly lost count, as 26 pairs of legs are shown instead of the 21 or 23 pairs possessed by this group. Indeed, the presence of the correct number of legs on a myriapod is a good indication of the scientific accuracy of the artist.

In Lib Secundum Dioscoridis.

SCOLOPENDRA.



A 'Scolopendra' from Matthiolus (1569).

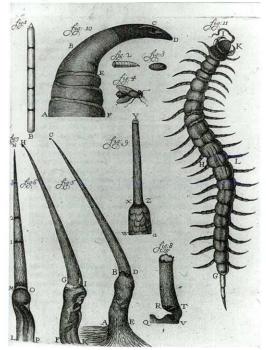
Edward Topsel (1572-1628), in his *History of Four-footed Beasts and Serpents* (1658), provided two pages of delightful prose 'concerning the Scolopendrae', including the following passage that vividly describes the effects of their bite:

'This Scolopender being provoked bites so sharply that Ludovicus Armarus who gave me one brought out of Africa could scarce endure him to bite his hand, though he had a good glove on, and a double linen cloth; for he struck his forked mouth deep into the cloth, and hung on a long time, and would hardly be shaken off. When the land Scolopender hath bitten, the

place is all black and blue, putrifies and swells, and looks like to the dregs of red wine, and is ulcerated with the first bite.'

Anthony van Leeuwenhoek (1632-1723), in his Werken, published between 1684 and 1718, made the first original observations on centipede anatomy. Leeuwenhoek discovered the aperture in the poison claws of centipedes. In his 'Letter 104', sent to the Royal Society on 17th October 1687 from Delft, he described features of giant centipedes collected by dockworkers unloading ships from the East Indies:

'The poisonous weapons of the Scolpendra, or centipes, are somewhat different from those of the spider. Its bite is so painful that it makes the patient almost mad. When the claws of its forceps are examined by a microscope, on the upper side of each of them, near the point, a small aperture appears, through which the venom is conveyed to the wound. By pressing the claw, a small drop of liquor issued out of this aperture.'



A plate from Leeuwenhoek's Werken (1684-1718). 'Fig. 10' shows the poison claws of a centipede ('Fig. 11') which has one of its rear-most legs missing. The other illustrations are of Stinging Nettle Urtica dioica.

Around 3,800 species of centipede have been described to date. Linnaeus, in the tenth edition of

Systema Natura, published in 1758, described only nine species in Genus 242 Scolopendra (centipedes were included in the section Aptera, devoted to wingless 'insects'). The names Scolopendra electrica (from elektron, 'a shining substance, amber or an alloy of gold and silver') and Scolopendra phosphorea clearly refer to properties of luminescence. Indeed, there are several well-documented cases of centipedes 'glowing in the dark'.

Lifestyle and classification

Centipedes have adopted two main lifestyles. 'Runners' are mostly surface-active and comprise four orders, namely the Scolopendromorpha (1,100 species worldwide), Lithobiomorpha (1,500 species), Scutigeromorpha (80 species), and Craterostigmomorpha (one species, confined to Tasmania and New Zealand).

The Scolopendromorpha (henceforth referred to as scolopendrids) and Lithobiomorpha (lithobids) are well represented in Britain, with three and 20 species respectively (Barber 2003). However, only one species of Scutigeromorpha (scutigerids) occurs here, namely the long-legged Scutigera coleoptera. This bizarre-looking animal is established in buildings on the Channel Islands, but turns up in houses from time to time on the British mainland.

The fifth order, Geophilomorpha (geophilids), is known as 'crawlers'. Geophilids are long 'worm-like' centipedes that dwell in the crevices between soil particles. Some 1,100 species are known worldwide and 30 occur in Britain, including three introduced species known only from heated glasshouses. All geophilids are blind, a reflection of their subterranean lifestyle.

Development

Male centipedes produce a spermatophore (packet of sperm) that is transferred to the female via a pair of gonopods at the posterior end. Females lay typically around 30 to 40 eggs, but the level of brood care varies greatly among the different orders.

The offspring of geophilids and scolopendrids are fairly helpless when they hatch from the egg, although they do at this stage possess the adult number of legs, represented by short stumpy appendages. The female wraps herself around her clutch of eggs and guards them aggressively. These

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Haplophilus subterraneus, a geophilid centipede. Steve Hopkin

'larvae' moult several times until they are able to fend for themselves and leave the care of their mother. Worldwide, different species of geophilid have between 27 and 191 pairs of legs. In the UK, the minimum number is 35 pairs, in *Chalandea pinguis*, and the maximum is 101 pairs, in the rare *Nesoporogaster brevior* known from a single locality in Cornwall. All scolopendrids have 21 or 23 pairs of legs, but the three species that occur in

Below Female *Henia vesuviana* wrapped around a clutch of eggs with the ventral surface exposed.

Bottom Second instar juvenile of *Lithobius forficatus* with eight pairs of legs. Steve Hopkin





the UK, all in the genus Cryptops, have 21 pairs each.

In contrast, the larvae of lithobids and scutigerids are active independent hunters from the moment when they emerge from the egg. However, they hatch with fewer pairs of legs than are possessed by the adult. First-instar lithobids have seven pairs of legs. Successive instars have eight, 10 and 12 pairs before the final larval moult to 15 pairs. The animal moults a further four times (or more moults in

some of the larger species) before it reaches maturity, increasing in size after each ecdysis, but not adding to the adult complement of 15 pairs of legs possessed by all lithobids. Similar development is observed in scutigerids. However, the larvae hatch with only four pairs of legs, increasing to five, seven, nine, 11, 13 and, finally, 15 pairs, the adult complement possessed by all scutigerids.

Biology

Centipedes are aggressive hunters and possess a range of sensory organs that provide them with information on their environment and prey. In lithobids, for example, the antennae are long and prehensile. A characteristic behaviour in the presence of food is to run each of the antennae between the poison claws in turn. Presumably there are taste receptors on the mouthparts which react to molecules that attach themselves to the antennae.

Centipede vision is probably quite poor. As already mentioned, all geophilids are blind. The eyes of lithobids usually have several ocelli, although they probably respond only to move-

ment, and to light and dark. The common *Lithobius variegatus*, for example, has around 15 ocelli in each eye. The maximum number of 40 ocelli occurs in *Lithobius pilicornis*, which, at 40mm in length, is the largest British lithobid. The most simple eyes, consisting of only one ocellus on each side of the head, are possessed by *Lamyctes emarginatus* (formerly known as



Lithobius forficatus, seen from below, passing its antenna through the mouthparts to 'taste' chemicals. Steve Hopkin

Lamyctes fulvicornis). This tiny species is only 10mm in length and was probably introduced to Britain from the southern hemisphere. It is found throughout the UK and is fairly common and widespread, with most records made between July and October (Barber & Keay 1988).

Behind the base of the antennae on each side of the head is a narrow slit in the cuticle. The slit leads to a complex sensory structure known as Tömösvary's Organ, after the Hungarian myriapodologist Ödön Tömösvary (1852-1884), who discovered it. All myriapods (and several other arthropod groups, such as Collembola) possess these post-antennal organs, which respond to changes in humidity and carbon dioxide concentrations (Yamana et al. 1986).

The coxal segments of the rearmost pair of legs bear coxal pores in a number of species. The number and arrangement of these pores is extremely important for identification (Barber 2003). However, their function is the source of much debate, some authors regarding them as osmoregulatory and others as the source of sexual pheromones (Minelli 1993).

Defence

In addition to providing formidable weapons for prey capture, a large pair of poison claws armed with powerful venom is an excellent form of defence. No one in his or her right mind would attempt to pick up a 30cm *Scolopendra gigantea* without wearing a thick pair of gloves. However, animals such as centipedes that are much longer than they are wide are vulnerable to attack from



The eye of *Lithobius variegatus* has between 13 and 18 simple ocelli. Steve Hopkin

the side or the rear. Thus, many species of centipede have evolved sophisticated methods of defence to deter or physically immobilise attackers and allow them to escape (Eisner *et al.* 2005).

Close examination of the posterior (15th) pair of legs of a lithobid centipede reveals numerous tiny pores in the cuticle. If the rear of the centipede is stimulated, a small amount of fluid is secreted from the pores. Ants that bite these legs step back and spend some time vigorously cleaning their antennae and mouthparts.

A much more spectacular defence mechanism is possessed by geophilids (Turcato et al. 1995). In response to attack from a predator, several species are able to secrete copious quantities of sticky glue from glands that open via pores positioned centrally on the ventral side of each segment. The

Lithobius forficatus, when stimulated at its posterior end, raises its rear legs and secretes a repellent chemical. Steve Hopkin



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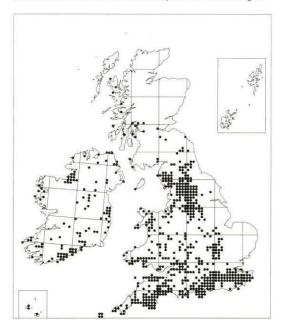
species that produces the most glue is *Henia vesuviana*, an uncommon geophilid found under surface debris in southern England. A specimen of *Henia vesuviana* 'milked dry' by stimulation of every segment loses about 15% of its body weight, a huge investment in resources. The glue consists predominantly of two types of protein with molecular weights of approximately 12,000 and 120,000; the former provides the sticky component and the latter the structural element of this peculiar natural 'superglue' (Hopkin & Anger 1992; Hopkin *et al.* 1990).

Experiments in a 'cardboard Coliseum', using the voracious predator the Devil's Coach-horse Beetle *Staphylinus olens*, have shown that the glue of *Henia vesuviana* is able to glue up the beetle's mouthparts for several hours, allowing the centipede to make good its escape. At rest, along with several other geophilids, this species curls into a ball with its soft underbelly exposed, enabling glue to be secreted onto the mouthparts of any predator foolish enough to bite it.

Distribution in Britain and Ireland

At least 54 species of centipede have been recorded from Britain and Ireland, including introductions to heated glasshouses (Barber 2003). The British

Figure 1 Records for *Lithobius variegatus* included in Barber & Keay (1988). More recent surveys have increased the coverage density (i.e. added more dots), but have failed to discover the species in East Anglia.



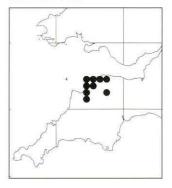
centipede fauna is probably better recorded than that of any other country in the world (Barber & Keay 1988) and new species turn up on a regular basis (not only from the Eden Project in Cornwall, the source of so many 'new to Britain' invertebrates!). Several species are ubiquitous in gardens (e.g. Lithobius forficatus, Haplophilus subterraneus), but others are rare and have been found in only one or very few hectads (10km squares). Only three species were included in the Red Data Book (Bratton 1991), namely Geophilus proximus (single specimen from Unst, Shetland), Lithobius lapidicola (Kent, Suffolk) and Lithobius tenebrosus (only one definite record, of a single specimen from Aberystwyth).

The distribution of some species is very intriguing. Lithobius variegatus (Fig. 1) occurs widely in Britain and Ireland but is apparently absent from East Anglia; a single published record in 1929 from Suffolk was included by Barber & Keay (1988) but is probably erroneous (Barber pers. comm.), and has been removed from the map shown here. Lithobius variegatus is found mainly in woodland sites, but tends not to occur in gardens where Lithobius forficatus dominates. Several experienced myriapodologists have searched for Lithobius variegatus in Norfolk and Suffolk but without success. The reasons for its absence are probably climatic (Eason & Serra 1986), and it will be interesting to see whether the 'stripy lithobid' spreads east during any future climate change.

Chalandea pinguis is the British geophilid centipede with the least number of legs (35 or 37 pairs), and perhaps the most peculiar distribution. It was first discovered in north Devon in 1970 and has since been found in only nine hectads close to the original local-

ity (Fig. 2). This distinctive 'stumpy' species (often referred to as being like 'half Haplophilus') been has searched for elsewhere but to no avail. It has all the signs of being introduction one of the north Devon

Figure 2 Chalandea pinguis is only known from nine hectads in north Devon.



ports (Bideford or Barnstable perhaps) and may be slowly expanding its range.

New discoveries are being made all the time. For example, *Geophilus carpophagus* has recently been split into two species (Arthur *et al.* 2001). These are now known as *Geophilus carpophagus* sensu stricto (the 'long form', with 51 to 57 pairs of legs) and *Geophilus easoni* (the 'short form', with 47 to 51 pairs of legs).

Identification

The book by Lewis (1981) is the best introductory text on centipedes. The classic *Centipedes of the British Isles* by Ted Eason (1964) has long been out of print, but has recently been made available on CDROM by Pisces Publications. A test version of an extremely user-friendly key to centipedes, by Tony Barber, was circulated in 2003.

Further information and current projects

The Centipede Recording Scheme is co-ordinated by the British Myriapod and Isopod Group (BMIG) (www.bmig.org.uk). The current Scheme Organiser is Tony Barber (tbarber@pcfe.ac.uk). BMIG also organises an annual field meeting, and keeps members updated with the latest centipede gossip via a regular free newsletter. Longer articles are published in the *Bulletin of the British Myriapod and Isopod Study Group*, available at modest cost (see the BMIG website for further details).

Internationally, the Centre International de Myriapodologie (CIM) co-ordinates myriapodological activity throughout the world. The CIM has an excellent website (www.mnhn.fr.assoc/myriapoda) and organises the International Symposia that are held every three years (the next gathering is at Görlitz, Germany, in July 2008).

Acknowledgements

I should like to thank Tony Barber for commenting on a draft of the text. The distribution map of *Chalandea pinguis* includes all records to date and was produced with DMAP (www.dmap.co.uk). The map for *Lithobius variegatus* was kindly supplied by the Biological Records Centre, Monks Wood, and is derived from that included in Barber & Keay (1988). This article is dedicated to Ted Eason (1915-2000), who first inspired me to take an interest in centipedes and was a constant source of advice and encouragement.

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We were very saddened to learn that Steve was tragically killed in a car accident shortly after completing most of the work on this article.

Steve Hopkin was a Senior Lecturer in Zoology at Reading University and Scientific Associate in Entomology at the Natural History Museum. He was also Chairman of the British Myriapod and Isopod Study Group. His main research interests were the ecology and taxonomy of soil arthropods, especially those of west Cornwall, to where he had recently moved with his wife, Ailsa. He had a rare ability to write lucidly about often neglected groups of invertebrates and was also an accomplished photographer. British natural history has sadly lost a first-rate communicator and advocate. We extend our sympathies to his family and friends.