

WATER RELATIONS, HABITAT AND SIZE IN LITHOBIOMORPH AND GEOPHILOMORPH CENTIPEDES (MYRIAPODA; CHILOPODA)

J G E Lewis

Somerset County Museum, Taunton Castle, Castle Green, Taunton, Somerset TA1 4AA, UK
Address for correspondence: Manor Mill Farm, Halse, Taunton, Somerset TA4 3AQ, UK.

ABSTRACT

Centipedes show considerable variation in their resistance to desiccation and the permeability of the integument as indicated by survival on immersion in water. Geophilomorphs are generally more resistant than lithobiomorphs. The advantages of a relatively permeable cuticle may be that it allows respiratory gas exchange, excretion of nitrogen as ammonia and/or the uptake of soluble nutrients.

Although lithobiomorphs are mainly found in superficial habitats and geophilomorphs below the surface, some small lithobiomorphs are soil inhabitants and some geophilomorphs inhabitants of superficial habitats. The advantages of soil-dwelling are discussed.

The great range in segment number in geophilomorphs suggests a varied mode of life: the long forms are efficient burrowers but nothing is known of the burrowing ability of short species, and they may have undergone a secondary reduction in segment number. In most Geophilomorpha there is a correlation between size and segment number but this is not the case in the family Mecistocephalidae. The excessive length of some geophilomorphs is puzzling. It may be to provide a long gut for digestion, a long ovary for high fecundity or a large surface area for absorption of nutrients.

INTRODUCTION

The water relations and habitats of centipedes and millipedes were discussed by Blower (1955). These matters are re-examined here but only in respect to lithobiomorph and geophilomorph centipedes. Subsequent work is reviewed and the possible reasons for variation in permeability in centipedes and the great range in segment number in geophilomorphs are discussed.

WATER RELATIONS

Desiccation experiments

Blower (1955) stated that geophilomorphs, although better waterproofed, did not show an appreciably greater resistance to desiccation than lithobiomorphs notwithstanding the marked difference in the permeability of their cuticles. This, he considered, was due to the imperfect spiracle closing devices of both orders. A subsequent review of the literature (Lewis, 1981) indicated, however, that there are considerable differences between both lithobiomorph and geophilomorph species. For example Roberts (1956) showed that *Lithobius forficatus* (L.) and *L. variegatus* Leach have much greater survival times than the much smaller *L. duboscqui* (= *L. microps* Meinert). Geophilomorphs vary a great deal in their resistance to desiccation and the most desiccation resistant species are found in this order.

Immersion experiments

Blower (1955) found that geophilomorphs were able to survive immersion in water for much longer than 24 h (exact times depending on species and the amount of air in solution). Lithobiid centipedes were, however, only able to survive immersion for a few hours. There is, nevertheless, considerable variation in the survival time of species of both groups (Lewis 1981). Of particular interest in this respect are Vaitilingham's (1960) results which showed that the small lithobiids *L. microps* and *L. curtipes* C. L. Koch have a much greater survival time than large *L. variegatus* and *L. forficatus*, the reverse of Roberts (1956) findings for resistance to desiccation.

SIGNIFICANCE OF DIFFERENCES IN PERMEABILITY

The fact that large *Lithobius* spp. show greater resistance to desiccation but have lower survival times in immersion experiments than small species may be explained in terms of surface area/volume ratios. Large animals may owe their resistance to a low SA/V ratio and if cutaneous respiration were important this would account for low survival times under water. Small species with a higher SA/V ratio would desiccate more rapidly but have a relatively larger surface available for gas exchange (Lewis, 1981).

As might be expected, centipedes that live in more superficial habitats are generally more resistant to desiccation than those from below the surface (Auerbach, 1951, Roberts, 1956) but there may be advantages for those species that have a relatively permeable integument.

A relatively permeable cuticle allows an exchange of respiratory gases across the integument. This may be important during flooding and is suggested by Blower's (1955) finding that the survival time of immersed geophilomorphs was dependent on the amount of air in solution. A relatively permeable cuticle would also allow waste nitrogen to be excreted as ammonia. This is the case in woodlice and the subject was reviewed by Sutton (1972). *Porcellio scaber* Latreille and *Oniscus asellus* L. produce ammonia as a gas and this is lost (with water) through the cuticle. Hartenstein (1968) suggested that this saved energy because ammonia need not be converted into urea or uric acid. This may be true for some centipedes. In *Lithobius forficatus* and *L. variegatus* 50-60% of total soluble nitrogen is excreted as ammonia, 1-8% as uric acid (Bennett and Manton 1963). Another possibility is that in some geophilomorphs, the cuticle is involved in the uptake of soluble organic compounds (see below). Permeability may, of course, be of little importance in soil-dwelling species and a waterproof epicuticle may have been lost with little effect ecologically.

HABITAT

Eason (1964) noted that details of habitat had been largely ignored by both British and European workers but with the introduction of the British Myriapod Group recording scheme, which was started in 1970, a great deal of data accumulated. The information was presented and analysed in Barber and Keay's (1988) *Provisional Atlas of the Centipedes of the British Isles*. Barber (1992) gave a further analysis of some of the data. He pointed out that the nature of most collecting tends to favour large and conspicuous species and those from superficial microsites so that smaller and soil dwelling species tend to be under-recorded.

Geophilomorpha

Barber (1992) stated that geophilomorphs are mostly below surface dwellers, but the three reddish brown geophilomorphs *Strigamia crassipes* (C. L. Koch), *S. acuminata* and *Geophilus carpophagus* and the commonly sub-cortical *Brachygeophilus truncorum* are relatively less common in the deeper layers. Eason's (1979) two 'forms' of *Geophilus carpophagus* are in fact two species, the smaller *G. easoni* Arthur et al., the larger: *G. carpophagus* (Arthur et al, 2000). Poser (1990), working in Germany, reported that *Strigamia acuminata* increased significantly in plots with augmented litter and Fründ et al (1996) collected 10 *Strigamia acuminata* from pitfall traps and only one from soil cores as compared to two and 37 respectively for *Schendyla nemorensis* (C. L. Koch). *Strigamia chionophila* (Wood) in Michigan (USA) was commonly observed on topmost leaves of litter basking in subdued sunlight and being one of the last species to migrate down into the deeper layers of the soil as winter approaches (Johnson, 1952). It would appear that members of the genus *Strigamia* are litter rather than humus or soil inhabitants. An exception is the littoral *Strigamia maritima* (Leach) most commonly found on shingle beaches.

Lithobiomorpha

Blower's (1955) generalisation that lithobiids are neither mechanically nor physiologically adapted to life in the soil and are thus mainly confined to the litter or suitable surface retreats (under stones, beneath moss and bark etc.) appears to be true for most but not all species. All but two of the seven species of *Lithobius* studied by Roberts (1956) were restricted to the litter layer. The exceptions were *L. melanops* (confined to rotten logs) and *L. microps* which penetrates the lower litter/humus layers. He pointed out that the body width of *L. microps* was less than 1 mm and the larval stadia much smaller (0.2 mm) which explained the abundance of these stadia in the upper humus. The body width 2-3 mm and large poison claws must contribute to the limitation of *Lithobius variegatus* to the litter layers of the forest floor. Poser (1990) found that *L. crassipes* L. Koch was able to live in plots without litter and Tuf (2000) found large numbers of *L.*

mutabilis in the top 10 cm of soil in three flood plain forests in the Czech Republic. Fründ et al (1997) collected 119 *L. forficatus* from pitfall traps in German woodlands, but none from soil cores. By contrast only seven juvenile lithobiomorphs were taken in pitfall traps, whereas 44 were extracted from soil cores.

The advantages of the soil as a habitat

The advantages of being able to retreat into the soil at times of drought or low temperature are obvious but there are other possible advantages. The microclimate in the soil, with its reduction in climatic extremes, may well extend the season of growth and reproduction. An example of the latter may be Leach’s (1817) observation, probably in the West of England, of a female *Haplophilus subterraneus* (Shaw) with 26 young in garden soil in January

Soil-dwelling also reduces predation. Fründ (1992) has recorded the frequency of scars in nearly 6000 centipedes as an indicator of predation intensity. He found that there is a decrease in scar frequency in Lithobiomorpha between the F- and H-horizon. In Geophilomorpha there is no difference between F- and H-layer but the proportion of scarred individuals was higher from the uppermost L-horizon. Fründ suggested that the higher mobility of adult and subadult developmental stages of centipedes might partly explain why they exhibit higher scar frequencies than the younger stages. Moving around implies that the centipedes leave their usual shelter in the soil and are at a higher risk of encountering an ambush predator. There are clearly major differences in food sources on the surface, in litter and in the soil but there appear to be no data on this or on the chances of +infection by parasites as between surface and soil dwellers.

SEGMENT NUMBER, SIZE AND HABIT IN GEOPHILOMORPHA

Geophilomorphs are invariably described as burrowing animals and this habit is associated with the high segment number. It seems surprising, therefore that geophilomorphs show such a great range in the number of pediferous segments, namely 27 to 191 (Minelli et al 2000). This seven-fold difference between the least and the most must be reflecting differences in mode of life. In British species the range is much less: Eason (1964) gives 35 to 83. A plot of number of pediferous segments against maximum body length (Figure 1) shows that there is a reasonable correlation between the two, the smallest species having the lowest segment number. The correlation is even more obvious when the data for the much richer French fauna (Brolemann, 1930) are plotted (Figure 2).

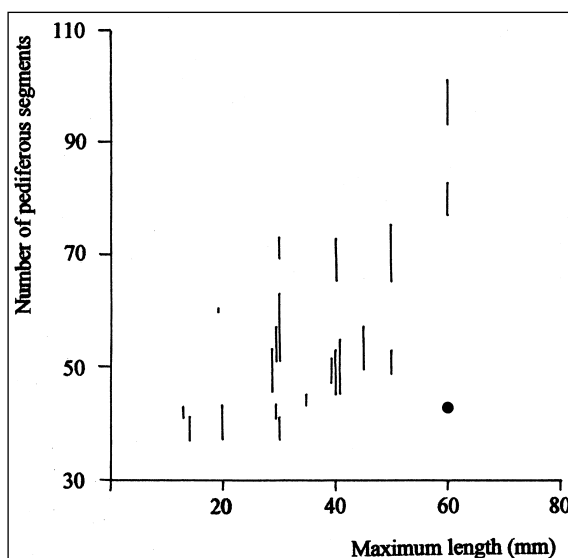


Figure 1. The relationship between the number of pediferous segments and maximum length in British geophilomorphs (data from Eason, 1964). Closed circle: *Dicelophilus carniolensis*.

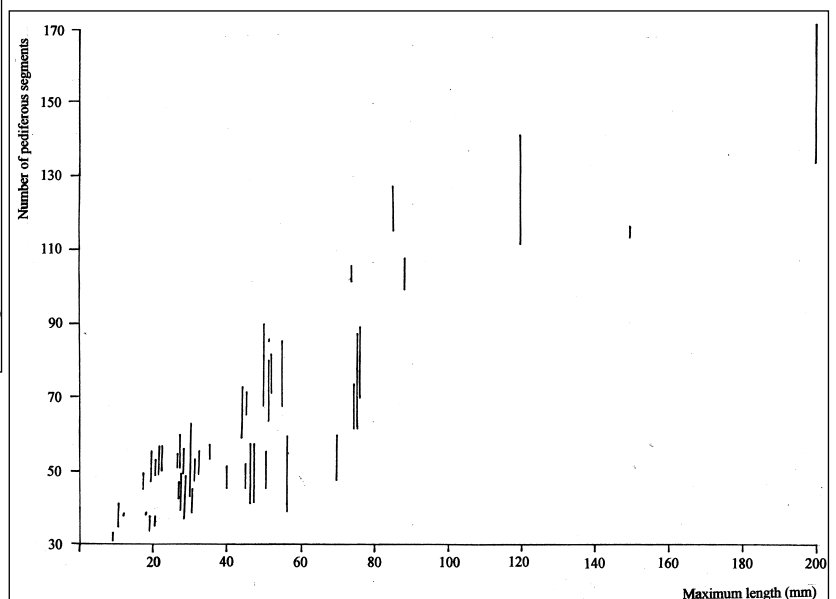


Figure 2. The relationship between the number of pediferous segments and maximum length in French geophilomorphs (data from Brolemann, 1930).

One British species, *Dicellogophilus carniolensis* (C. L. Koch), however, has a noticeably low number of pediferous segments for its length. This species is one of the two of the family Mecistocephalidae in the British Isles, both have been introduced. A plot of the number of pediferous segments against body length in the Mecistocephalidae (data from Attems, 1929) shows little correlation between leg number and maximum body length and a very considerable range in size in species with the same segment number (Figure 3).

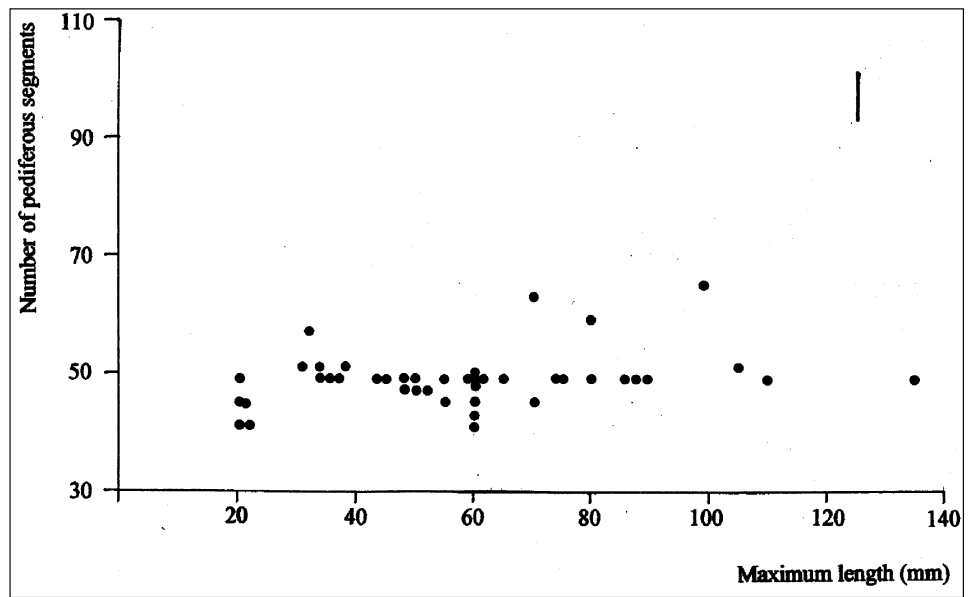


Figure 3. The relationship between the number of pediferous segments and maximum length in mecistocephalids (data from Attems, 1929). Vertical bar: range of pediferous segments in *Mecistocephalus microporus* (data from Bonato et al, 2001).

For example the maximum size of species with 49 leg-bearing segments varies from 20 mm to 135 mm. This suggests a mode of life in mecistocephalids different from that of other geophilomorphs. The Mecistocephalidae, Verhoeff's (1905-25) Placodesmata, are a sister group to all other geophilomorphs (Adesmata) (see Foddai & Minelli, 2000, Edgecombe and Giribet, 2002). Unlike other geophilomorphs, each species of mecistocephalid, with one exception, has a fixed number of pediferous segments (41-65). The exception is *Mecistocephalus micropus* Haase 1887 from the Philippines, which has an exceptionally number of pediferous, segments (93–101) (Bonato et al, 2001) which the authors' suggest is due to recent quasi-duplication.

According to Manton (1952) an animal roughly resembling a geophilomorph but with a small number of segments (about 30 to 35) and feeble powers of telescoping the sclerites and stretching the pleural region would have the possibility of developing into either a geophilomorph or a scolopendromorph. The conspicuous characteristics of the Geophilomorpha, such as the strong longitudinal musculature, well-developed intercalary tergites and sternites, the several isolated sclerites of the tergal region, and the short legs, Manton (1958) suggested, were correlated with the ability to burrow. She argued that species with high segment numbers (to some 130) would be more efficient burrowers as an increase in the number of body segments together with a decrease in their length must result in more joints being present per unit length leading to greater telescoping ability. The head and anterior third of the trunk segments (the anterior 35 segments in *Orya*) do most of the work of burrowing.

Geophilomorphs with a low number of pediferous segments ('short forms') may not be efficient burrowers and their ability to move through the soil may be due to their small size as appears to be the case with small lithobiids. There appear to be no data on locomotion in these forms. Indeed, Manton (1965) noted that "It is not easy to observe burrowing in the small British Geophilomorpha, because bright light stimulated them to shelter by running over firm soil or by pushing themselves into light soil, shifting soil particles by the force of each leg, but not burrowing by earthworm-like body movements". It may be that short forms are too short to burrow efficiently, or too small to need to. Nevertheless they show the conspicuous characteristics that Manton (1958) suggested were correlated with the ability to burrow in geophilomorphs. This may suggest two evolutionary trends in the Geophilomorpha, an initial increase in the number of pediferous segments accompanied by an increased efficiency in burrowing, followed by a secondary reduction in size and segment number in some groups.

Some geophilomorphs have a very high number of pediferous segments and it is difficult to see, in the light of Manton's (1958) findings, how this would increase burrowing efficiency. If excessively high segment number is not associated with burrowing efficiency then it may have some other function. One possibility is that it provides a very long gut to allow time/space for digestion. This seems unlikely as geophilomorph intestine contains little in the way of solid food (Lewis 1961). Increase in length would also

allow a higher fecundity providing more space for developing ova (they are arranged linearly). Alternatively, the length and strap-shaped trunk of species such as the Mediterranean *Himantarium gabrielis* (L.) and the Western European *Haplophilus subterraneus* Shaw give a large surface area which could be used for the absorption of nutrients from organically rich soil. This method of nutrition has not been suggested hitherto for centipedes but the small head and poison claws but a long body suggest a reduced importance of the mouthparts in nutrition.

POSTSCRIPT

Gordon Blower and Ted Eason's early work on British centipedes has provided a firm foundation for further investigations and the two men had a seminal influence on the development of the British Myriapod and Isopod Group. The Group has produced a great deal of data on the geographical distribution and habitat preferences of centipedes but there is still much to be learnt about them. In particular detailed investigations of the habitat of individual species, especially of small geophilomorphs are required. Also seasonal investigations of the species of a specific habitat would be very rewarding, not to mention behavioural and physiological investigations such as those of Blower on water relations.

ACKNOWLEDGEMENTS

My thanks are due to Tony Barber and Helen Read provided helpful advice and discussion and to Dennis Parsons and the staff of the Somerset County Museum, Taunton for providing assistance in the preparation of this paper

REFERENCES

- Attems, C. (1929) Myriapoda 1. Geophilomorpha. *Das Tierreich* **54**: 1-308. Berlin: Walter de Gruyter.
- Arthur, W., Foddai, D., Kettle, C., Lewis, J. G. E., Luczynski, M. & Minelli, A. (2001) Analysis of segment number and enzyme variation in a centipede reveals a cryptic species *Geophilus easoni* sp. nov., and raises questions about speciation. *Biol J. Linn. Soc.* **74**: 489-499.
- Auerbach, S. I., (1951) The centipedes of the Chicago area with special reference to their ecology. *Ecol. Monogr.* **21**: 97-124.
- Barber, A. D. (1992) Distribution and habitat in British centipedes. *Ber. Nat.-med. Verein Innsbruck*. Suppl. 1: 339-352.
- Barber, A. D. & Keay, A. N. (1988) *Provisional Atlas of the centipedes of the British Isles*. pp1-127. Biological Records Centre, Natural Environmental Research Council, Huntingdon.
- Bennett, D. & Manton, S. M. (1963) Arthropod segmental organs and Malpighian tubules with particular reference to their function in Chilopoda. *Ann. Mag. nat. Hist.* ser. 13, **5**: 545-556.
- Blower, G. (1955) Millipedes and centipedes as soil animals. In: D. K. M. Kevan (ed.) *Soil Zoology* London, Butterworth, pp 138-151
- Bonato, L., Foddai, D. & Minelli, A. (2001) Increase by duplication and loss of invariance in segment number in the centipede *Mecistocephalus microporus* (Chilopoda, Geophilomorpha, Mecistocephalidae). *Ital. J. Zool.* **68**: 345-352.
- Brolemann, H-W. (1930) Myriapodes Chilopodes. *Faune de France* **25**. Paris: Imprimerie Toulousaine, 405 pp.
- Eason, E. H. (1964) *Centipedes of the British Isles*. London: Warne and Co., 294 pp.
- Eason, E. H. (1979) The effect of the environment on the number of trunk-segments in the Geophilomorpha with special reference to *Geophilus carpophagus* Leach. In: M. Camatini (ed.) *Myriapod Biology* London: Academic Press, pp 233-240.

- Edgecombe, G. D. & Giribet, G. (2002) Myriapod phylogeny and the relationships of Chilopoda. In: Lorente Bousquets, J. & Morrone, J. J. (eds.), *Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México: Hacia una Síntesis de su Conocimiento*. **3** México Pressas de Ciencias, UNAM, pp143-168
- Foddai, D. & Minelli, A. (2000) Phylogeny of geophilomorph centipedes: old wisdom and new insights from Morphology. In Wytwer, J. & Golovatch, S. (Eds.) *Progress in Studies on Myriapoda and Onychophora. Fragm. Faun.* **43**, Suppl.: 61-71.
- Fründ, H.-C. (1992) The occurrence and frequency of scars in centipedes. *Ber. Nat.-med. Verein Innsbruck Suppl.* 1: 269-275.
- Fründ, H.-C., Balkenhol, B. & Ruszkowski, B. (1997) Chilopoda in forest habitat-islands in north-west Westphalia, Germany. *Ent. Scand. Suppl.* 51: 107-114.
- Hartenstein, R. (1968). Nitrogen metabolism in the terrestrial isopod *Oniscus asellus*. *Am. Zool.* **8**: 507-519.
- Johnson, B. M. (1952) The centipeds and millipeds of Michigan. Ph.D. thesis University of Michigan. pp. xvi + 472.
- Leach, W. E. (1817) The characters of the genera of the class Myriapoda, with descriptions of some species. *Zoological Miscellany* **3**: 31-45.
- Lewis, J. G. E. (1981) *The Biology of Centipedes*. Cambridge: Cambridge University Press, 476 pp.
- Manton, S.M, (1952) The evolution of arthropod locomotory mechanisms. Part 3. The locomotion of Chilopoda and Pauropoda. *J. Linn. Soc. (Zool.)* **42**: 118-166
- Manton, S. M. (1958) Habits of life and evolution of body design in Arthropoda. *J. Linn. Soc. (Zool.)* **44**: 58-72.
- Manton, S. M. (1965) The evolution of arthropod locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeletomuscular systems and an appendix on the comparison between burrowing forces in annelids and chilopods and its bearing upon the evolution of the arthropod haemocoel. *J. Linn. Soc. (Zool.)* **46**: 251-483
- Minelli, A. Foddai, D., Pereira, L. A. & Lewis, J. G. E. (2000) The evolution of segmentation of centipede trunk and appendages. *J. Zool. Syst. Evol. Research* **38**: 103-117.
- Poser, T. (1990) The influence of litter manipulation on the centipedes of a beech wood. Minelli, A. (Ed.) *Proceedings of the 7th International Congress of Myriapodology*. E. J. Brill, Leiden. 235-245
- Roberts, H. (1956) An ecological study of the arthropods of a mixed beech-oak woodland, with particular reference to Lithobiidae. Ph.D. thesis, University of Southampton.
- Sutton, S. L. (1972) *Woodlice*. Ginn & Co Ltd, London. 143 pp.
- Tuf, I. H. (2000) Communities of centipedes (Chilopoda) in three floodplain forests of various age in Litovelské Pomoraví (Czech Republic). Wytwer, J. & Golovatch, S. (Eds.) *Progress in Studies in Myriapoda and Onychophora. Fragm. Faun.* **43**, Suppl.: 327-332.
- Verhoeff, K. W. (1905-25) Chilopoda. In: Bronn, H. G. (ed.) *Klassen und Ordnungen des Tierreichs*, **5** abt. 2, Buch 1. Akademische Verlagsgesellschaft, Leipzig. pp 1-725.
- Vaitilingham, S. (1960) The ecology of the centipedes of some Hampshire woodlands. M.Sc. thesis, University of Southampton.