*Ann. Zool. Fennici* 50: 247–255 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 31 October 2013 

# Influence of climate on segment number in *Geophilus flavus*, a centipede species inhabiting Sognefjord in western Norway

Stylianos M. Simaiakis[1,2,*], Per Djursvoll[3] & Robert Bergersen[4]

[1)] *Department of Biological Sciences, University of Cyprus, P.O. Box 20537, CY-1678 Nicosia, Cyprus (*corresponding author's e-mails: ssimaiakis@yahoo.com & simaiakis@biology.uoc.gr)*
[2)] *Natural History Museum of Crete, University of Crete, Knossos Av., P.O. Box 2208, GR-71409 Heraklion, Greece*
[3)] *University Museum of Bergen, Realfagbygget, NO-5020 Bergen, Norway*
[4)] *Tromsø Museum, University of Tromsø, NO-9037 Tromsø, Norway*

*Received 12 Oct. 2012, final version received 2 Feb. 2013, accepted 1 Mar. 2013*

Simaiakis, S. M., Djursvoll, P. & Bergersen, R. 2013: Influence of climate on segment number in *Geophilus flavus*, a centipede species inhabiting Sognefjord in western Norway. — *Ann. Zool. Fennici* 50: 247–255.

Since in laboratory experiments a relationship between segment number and temperature in geophilomorph centipedes has been proven, we suggest that climatic variation in nature could have a direct effect on segment number. To address this hypothesis we examine the way in which local climatic factors in Sognefjord — air temperature and precipitation both changing along a longitudinal gradient — exert their effect on segment number in *Geophilus flavus*. Changes in *G. flavus* segment number along the climatic gradient are similar to that found in previous laboratory experiments with *Strigamia maritima*, but are even more pronounced. In *G. flavus*, a 1.5 difference in the mean segment number is found in populations that occur in Sognefjord along a temperature gradient of only about 1.4 °C. In contrast, several degrees centigrade were required to produce a similar increase in the mean segment number in laboratory experiments involving *S. maritima*.

## Introduction

There are five extant orders of centipedes: Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha with 15 leg pairs, Scolopendromorpha with 21 or 23 leg pairs (although in *Scolopendropsis duplicata* also other numbers have been found, *see* Minelli *et al*. 2009), and Geophilomorpha whose numbers of leg pairs vary widely: from 27 to 191 (Minelli & Bortoletto 1988, Minelli *et al*. 2000). All adult centipedes have an odd number of leg-bearing segments (LBS). There have been numerous studies presenting segment numbers in geophilomorphs (Bergsoe & Meinert 1866, Stuxberg 1871, Attems 1929, Hammer 1931), while some others focused on the geographic variation in segment numbers (Lewis 1985, Horneland & Meidell 1986, Arthur 1999, Arthur & Kettle 2001, Simaiakis & Mylonas 2006). Only recently, scientists have started to seek the mechanism of segmentation in geophilomorphs (Arthur & Farrow 1999, Minelli 2000, 2001, Kettle *et al*. 2003, Chipman *et al*. 2004a, Chipman & Akam 2008, Brena & Akam 2012) and study the evolution of body patterns (Minelli *et al*. 2010) to show that a double-segment periodicity was involved in segment generation (Chipman *et al*. 2004b). Kettle and Arthur (2000) were the first to find out that number of leg pairs varies with latitude across the east coast of Britain, in accordance with the proposal that body size increases with decreasing latitude (specimens from colder regions tend to be smaller and with fewer trunk segments than those from warmer regions, *see* Eason 1979, Hayden *et al*. 2012).

Up to now, *Strigamia maritima* is the main model species for studies of segmentation and segment number variation (Kettle *et al*. 2003, Vedel *et al*. 2010, Brena & Akam 2012, Hayden *et al*. 2012). Previous works have shown that this variation has both environmental and genetic bases (for further discussion *see* Vedel *et al*. 2008, 2009). Moreover, the results of laboratory experiments presented to date demonstrate that in *S. maritima*, temperature affects the number of LBS that develop during embryogenesis (Vedel *et al*. 2010). Therefore, we hypotesize that in geophilomorphs in nature, temperature variation — not necessarily resulting from a latitudinal cline — during early embryogenesis, could have a significant effect on segment number (*see* also Vedel *et al*. 2010). To proove this hypothesis, adequate climatic data from a particular area would be necessary. There are several reasons why Sognefjord — located in Sogn og Fjordane county (61°N, 5°–8°E) — was selected to be a region to study geographic variation in *S. maritima* segment number: (i) rich network of permanent and temporary meteorological stations across the fjord (Norwegian Meteorological Institute, Utaaker & Skaar 1970), (ii) long west–east profile from the open Norwegian Sea to the central parts of southern Norway (Utaaker & Skaar 1970), and (iii) topography causing significant differences in local climate (e.g., temperature, precipitation) over short distances (Utaaker 1980).

Previous studies mainly dealt with segment number variation along a wide or narrow geographical gradient either in the northwestern Europe (Kettle & Arthur 2000, Arthur & Kettle 2001, Simaiakis *et al*. 2010) or in the north-eastern Mediterranean area (Simaiakis & Mylonas 2006, Simaiakis 2009). However, none of these studies attempted to correlate local meteorological variables with segment numbers to support the case for the existence of temperature-dependent plasticity and related geographic clines within geophilomorph species. Since we now have strong laboratory evidence for the effect of temperature on the number of leg pairs in *S. maritima* (Kettle *et al*. 2003, Vedel *et al*. 2008, 2009, 2010) we decided to carry out a study in a geographical region (Sognefjord) where climatic data are available to find the effect of temperature and precipitation on LBS numbers in a geophilomorph species. Since in embryos LBS numbers increase lineary with increasing temperature (for more details *see* Vedel *et al*. 2008), we may expect changes in climate parameters towards the inner part of the fjord to explain, at least partially, the variation in LBS number in *G. flavus*.

## Material and methods

### Sample collection in Sognefjord

Individuals of *Geophilus flavus* can be easily found in Sognefjord at low altitudes along certain parts of the fjord (e.g., narrow valleys at the heads of its branches, close to the sea shore, and along river banks). For the purpose of this study, 421 adult specimens were collected between 31 May and 25 August 2009 from eight location in the fjord (*see* Fig. 1). All the specimens were collected by hand, preserved in 75% ethanol, identified according to the descriptive key in Andersson *et al*. (2005), and deposited in the University Museum of Bergen. While collecting the animals between 31 May and 20 June, we observed many brood cavities with females coiled around their eggs (Fig. 2).

The total number of specimens collected as well as other data used in this study are presented in Table 1.

### Climate data

To obtain the climate data for the study sites

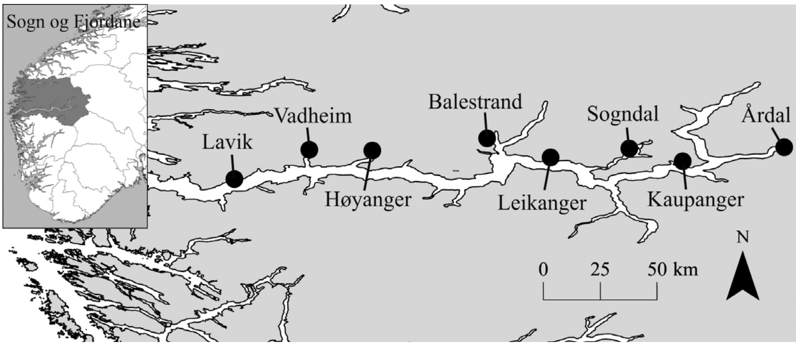


**Fig. 1.** Sampling sites in Sognefjord (Sogn og Fjordane district) in western Norway. Lavik (La), Vadheim (Va), Høyanger (Ho), Balestrand (Ba), Leikanger (Le), Sogndal (So), Kaupanger (Ka) and Årdal (Ar).

we used the climate database of the Norwegian Meteorological Institute accessible via the free web portal "eKlima". The database contains climate data from numerous weather stations in Sognefjord since 1931 to present. In addition, detailed climatic tables for the years 1964–1966 were obtained from Utaaker and Skaar (1970). In this study, we used mean monthly normal values of temperature (°C) and sum monthly normal values of precipitation (mm) for the period 1931–1990 from meteorological stations located close to the sampling sites (*see* Appendix). Since the climate data for Kaupanger (site 7, *see* Appendix) were insufficient, we used the data from the Gaupne meteorological station (Norwegian Meteorological Institute), and temporary meteorological stations which operated between 1964 and 1966 (Utaaker & Skaar 1970) close to Kaupanger and almost at the same longitudinal coordinate.

**Fig. 2.** Female *Geophilus flavus* with eggs in a brood cavity *in situ*. This photo was taken at the collection site near Vadheim, on 20 June 2009.

The long-term meteorological data indicate that the climate in the fjord changes from strictly oceanic in its outer part (6.9 °C mean annual air

**Table 1.** Numbers (*n*) of female and male *Geophilus flavus* collected from each site in Sognefjord, numbers of specimens with particular leg-bearing-segment (LBS) numbers (49 to 57), and mean LBS in females and males. The sites are arranged from west (Lavik) to east (Årdal).

| Site in Sognefjord | Sampling date | Lat. (°N) | Long. (°E) | Females | | | | | Males | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | LBS | | | | | LBS | | | | |
| | | | | *n* | 53 | 55 | 57 | mean | *n* | 49 | 51 | 53 | 55 | mean |
| 1. Lavik (La) | 31 May 2009 | 61.105 | 5.505 | 36 | 15 | 18 | 3 | 54.33 | 48 | 2 | 25 | 21 | 0 | 51.79 |
| 2. Vadheim (Va) | 20 June 2009 | 61.212 | 5.838 | 32 | 16 | 16 | 0 | 54.00 | 33 | 0 | 26 | 7 | 0 | 51.42 |
| 3. Høyanger (Ho) | 20 June 2009 | 61.219 | 6.074 | 21 | 5 | 15 | 1 | 54.62 | 16 | 1 | 3 | 12 | 0 | 52.38 |
| 4. Balestrand (Ba) | 25 Aug. 2009 | 61.226 | 6.485 | 11 | 1 | 7 | 3 | 55.36 | 14 | 0 | 0 | 14 | 0 | 53.00 |
| 5. Leikanger (Le) | 25 Aug. 2009 | 61.185 | 6.808 | 24 | 1 | 19 | 4 | 55.25 | 28 | 0 | 7 | 20 | 1 | 52.57 |
| 6. Sogndal (So) | 20 Aug. 2009 | 61.231 | 7.086 | 17 | 2 | 12 | 3 | 55.12 | 37 | 0 | 13 | 21 | 3 | 52.46 |
| 7. Kaupanger (Ka) | 20 Aug. 2009 | 61.177 | 7.266 | 26 | 3 | 15 | 8 | 55.38 | 22 | 0 | 1 | 19 | 2 | 53.09 |
| 8. Årdal (Ar) | 20 Aug. 2009 | 61.238 | 7.698 | 22 | 0 | 17 | 5 | 55.45 | 34 | 0 | 1 | 30 | 3 | 53.12 |

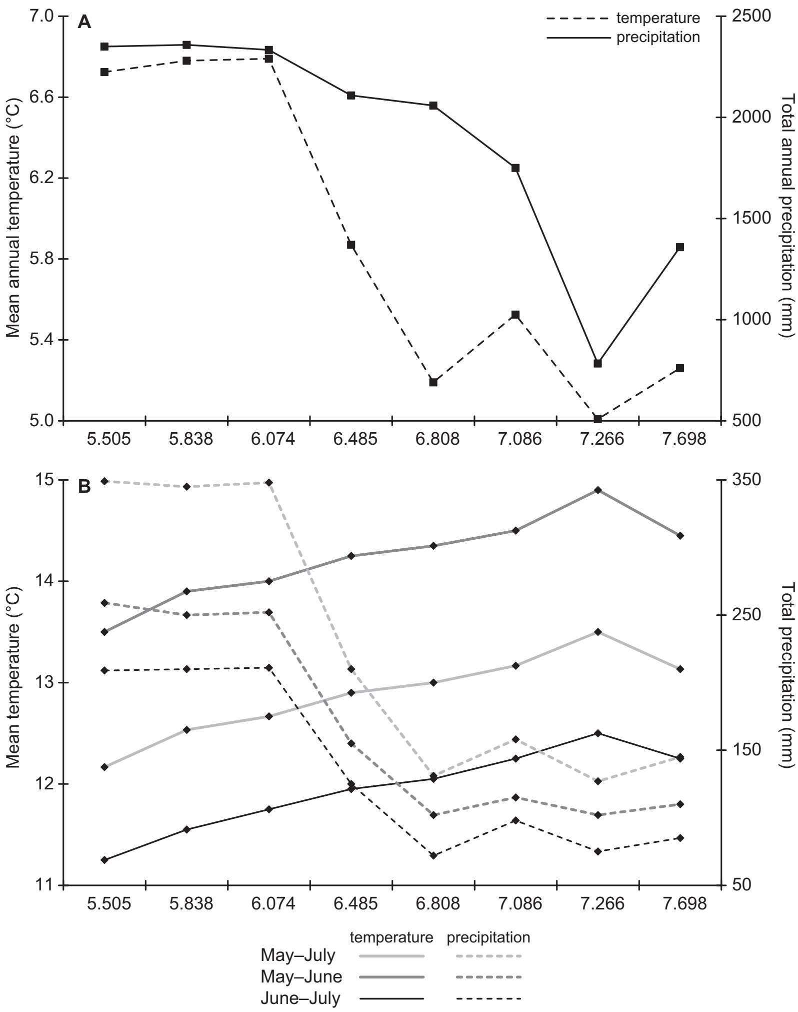


**Fig. 3.** Climate data from eight meteorological stations close to the sampling sites (source Norwegian Meteorological Institute) for 1931–1990. (**A**) Mean annual temperature (Tm) and total annual precipitation (Pr), and (**B**) mean temperature and total precipitation for selected periods.

temperature and about 2000 mm mean annual rainfall) to relatively continental in its innermost part (5.8 °C mean annual air temperature and almost 300 mm mean yearly rainfall) (Wielgolaski 1973, Norwegian Meteorological Institute). However, the west–east temperature gradient is not annually stable (Fig. 3A), that is, although there is a west–east decrease in mean annual temperature across Sognefjord, a reverse west–east gradient is observed during the period between late spring (May) and early summer (June, July) (Fig. 3B, *see* also Appendix). It has been found that *S. maritima* breeds from late May to early June (Lewis 1961, Kettle *et al.* 2003) or late June (Chipman *et al.* 2004) is the. According to our *in situ* observations *G. flavus* breeds during the same period. Thus, to study the effect of temperature and precipitation on LBS number, we also used temperature and precipitation data for May–July or May–June (e.g., Kettle *et al.* 2003, Vedel *et al.* 2008, 2010) (*see* Fig. 3B and Appendix).

## Statistical analysis

Regression analysis was used to test the effects of geographical location (longitude), mean temperature and total precipitation on LBS number of *G. flavus*. To test the differences in LBS numbers among *G. flavus* from the eight sampling sites we used a $\chi^2$-test (Zar 2009) for contingency tables (Table 2). To avoid biased results, when the frequencies were < 1 (here only in case of males) (*see* Sokal & Rohlf 1995), we pooled the numbers of contiguous leg pairs (*see* Table 2). LBS number variation at all sampling sites in Sognefjord and for each sex, was summarised with correspondence analysis (CA).

## Results

LBS numbers in *G. flavus* from Sognefjord decreased significantly from east to west regardless of sex (Fig. 4). The mean segment number for females in the westernmost population was 54.33 whereas the respective value for the easternmost population was 55.45 (difference of 1.12). In males, the mean segment number was 51.79 in the westernmost sample and 53.12 in the most eastern population (difference of 1.33). Both mean temperature (positively) and total precipitation (negatively) during the breeding period of May–July or May–June, affected the LBS number (*see* Fig. 4).

The $\chi^2$-test and the log-likelihood ratio ($G$) showed that modal segment numbers differed significantly among the eight populations studied, and that the variation between the main localities was significant in both sexes (Table 3). In females, the relative frequency values that could be reconstructed from a single dimension reproduced more than 88% of the total $\chi^2$ value for the two-dimensional scatter plot (Fig. 5). In males, more than 83% of the total $\chi^2$ value could be explained (Fig. 5). Females with 53 LBS were positively associated with the western fjord populations (Lavik, Vadheim and Høyanger), whereas females with 55 and 57 LBS were positively correlated with the eastern fjord populations (Balestrand, Leikanger, Sogndal, Kaupanger and Årdal) (Fig. 5). In males, the main dimension distinguished mostly between 49 and 51 LBS, which were positively associated with western fjord populations (Lavik and Vadheim), and 53 and 55 LBS, which were positively correlated with eastern fjord populations (Høyanger, Balestrand, Leikanger, Kaupanger and Årdal) (*see* also Fig. 4).

**Table 2.** Numbers of male *Geophilus flavus* collected from each site in Sognefjord whose leg-bearing-segment (LBS) numbers were 49 and 51 or 53 and 55.

| | *n* | 49/51 | 53/55 |
|---|---|---|---|
| 1. Lavik (La) | 48 | 27 | 21 |
| 2. Vadheim (Va) | 33 | 26 | 7 |
| 3. Høyanger (Ho) | 16 | 4 | 12 |
| 4. Balestrand (Ba) | 14 | 0 | 14 |
| 5. Leikanger (Le) | 28 | 7 | 21 |
| 6. Sogndal (So) | 37 | 13 | 24 |
| 7. Kaupanger (Ka) | 22 | 1 | 21 |
| 8. Årdal (Ar) | 34 | 1 | 33 |

## Discussion

In geophilomorphs, there is a significant breeding synchrony between populations and even at smaller scales. Embryogenesis in *S. maritima* and *G. flavus* generally takes place between late May and late June (*see* Chipman *et al*. 2004, Vedel *et al*. 2008). Each female forms a brood cavity in the ground and lays a number of eggs into it (for details on *S. maritima see* Vedel *et al*. 2008, *see* also Fig. 2). Soil surface temperature may, therefore, affect embryonic development, and in particular determin segment numbers in geophilomorphs. Although information on ground temperature would be ideal to study this phenomenon, measurements of soil temperature are often lacking. Since air temperature and precipitation affect soil surface temperature (Geiger *et al*. 2003), we chose these two parameters to study thier effects on LBS number in *G. flavus* populations from Sognefjord.

Previous laboratory experiments showed that temperature has a pronounced effect on segment number. Indeed, *S. maritima* embryos grown at 18 °C hatched with a higher mean segment number than their siblings grown at 10 °C (the mean segment numbers differed by about 1.5, *see* Vedel *et al*. 2008, 2010). However, in our study,

**Table 3.** Summary of tests for differences in segment number in *G. flavus* grouped by sex. Comparison of segment number variation between the eight different localities in Sognefjord. *** $p < 0.001$.

| *Geophilus flavus* | df | $\chi^2$ | $G$ |
|---|---|---|---|
| Females | 14 | 46.42*** | 53.78*** |
| Males | 7 | 71.98*** | 83.09*** |

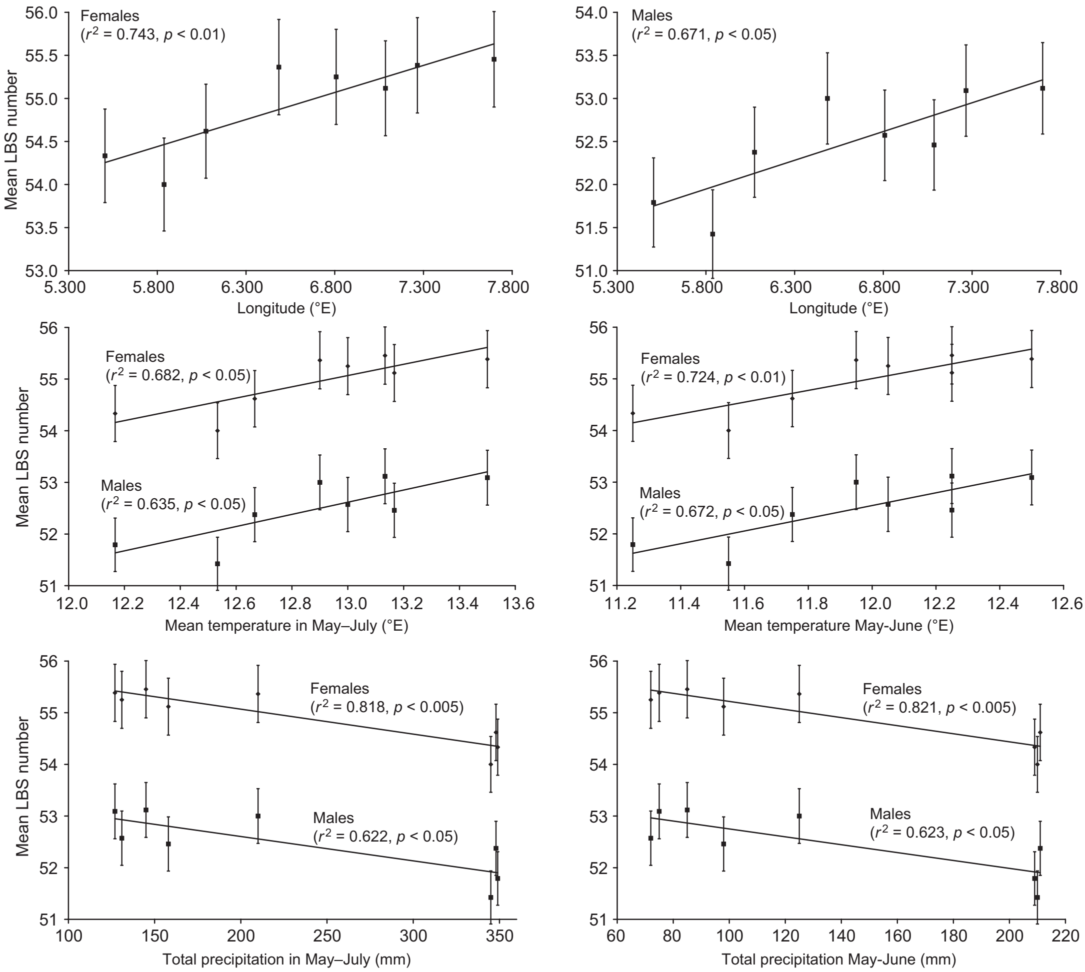


**Fig. 4.** Regressions of *G. flavus* mean leg-bearing-segment (LBS) numbers against longitude, mean temperature and total precipitation in Sognefjord. Bars represent standard errors.

a difference of this magnitude in mean LBS numbers for *G. flavus*, (54 and 55.5 in females, or 51.5 to 53 in males) was found in populations that occur in a fjord, where differences in mean temperature and total precipitation during the breeding period (May–July or May–June) were ~1.4 °C (13.4 and 12 °C, eastern and western fjord, respectively) and ~315 mm (430 and 115 mm, western and eastern fjord, respectively), respectively.

While most of the variability in LSB number in *G. flavus* across the fjord is likely due to a plastic response to climate during embryogenesis (similar to *S. maritima*, *see* Vedel *et al.* 2008, 2010), it is quite probable that genetic differences between populations may also be responsible (*see* Vedel *et al.* 2009). In their laboratory experiment with *S. maritima*, Vedel *et al.* (2008) controled for genetic variation, hence rearing temperature was the only possible factor affecting segment number. Due to the nature of our experiment, however, we could not exclude the possible effect of genetic variation between populations on LBS number.

Based on our results, its may seem that there is a difference between *S. maritima* and *G. flavus* in the degree of temperature sensitivity depending whether the species are studied in the laboratory or filed conditions. This may, however, be due to differences between species rather than between lab and field environments. *Geophilus-flavus*, as a generalist species, is able to occur in

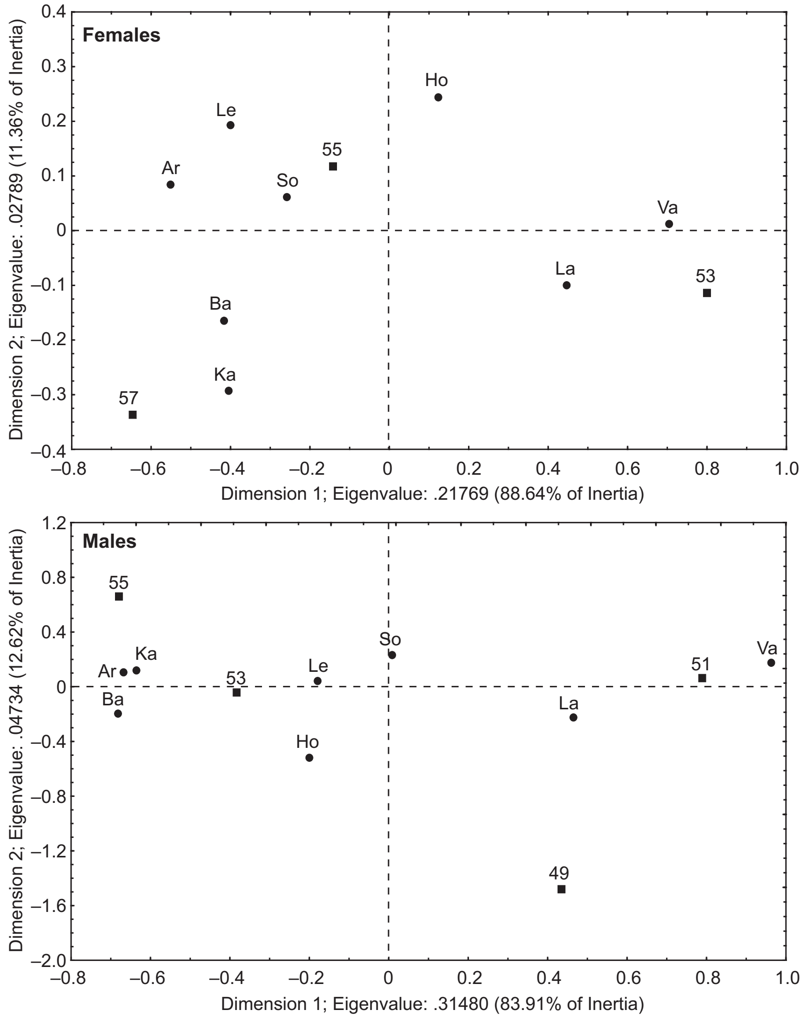


**Fig. 5.** Two-dimensional correspondence analysis plots of variation in leg-bearing-segment (LBS) number for females and males from eight populations studied. La: Lavik, Va: Vadheim, Ho: Høyanger, Ba: Balestrand, Le: Leikanger, So: Sogndal, Ka: Kaupanger, Ar: Årdal.

a wider variety of environmental conditions than *S. maritima* which is highly specialized and prefers sea-shore habitats.

As per relationships between LBS number, body length and temperature (Vedel *et al*. 2008, 2009, 2010, Hayden *et al*. 2012, Brena & Akam 2012), more work should to be carried out to investigate the pattern itself both in laboratory- and in nature.

## Acknowledgements

This research project has been funded mainly by the Research Council of Norway (International Scholarship Section - IS) and partly by the University Museum of Bergen. We thank Wallace Arthur for his remarks on the manuscript.

## References

Andersson, G., Meidell, B. A., Scheller, U., Winqvist, J.-Å., Osterkamp, M., Djursvoll, P., Budd, G. & Gärdenfors, U. 2005: *Nationalnyckeln till Sveriges flora och fauna. Mångfotingar. Myriapoda*. — ArtDatabanken, SLU, Uppsala.

Arthur, W. 1999: Variable segment number in centipedes: population genetics meets evolutionary biology. — *Evolution & Development* 1: 62–69.

Arthur, W. & Farrow, M. 1999: The pattern of variation in centipede segment number as an example of developmental constraint in evolution. — *Journal of Theoretical Biology* 200: 183–191.

Arthur, W. & Kettle, C. 2001: Geographic patterning of variation in segment number in geophilomorph centipedes: clines and speciation. — *Evolution & Development* 3: 34–40.

Attems, C. G. 1929: *Geophilomorpha*. — Das Tierreich 52,

W. de Gruyter and C., Berlin and Leipzig.

Bergsoe, V. & Meinert, F. 1866: Danemarks Geophiler. — *Naturhistorisk Tidsskrift* 3(4): 81–103.

Brena, C. & Akam, M. 2012: The embryonic development of the centipede *Strigamia maritima*. *Developmental Biology* 363: 290–307.

Chipman, A. D., Arthur, W. & Akam, M. 2004a: Early development and segment formation in the centipede *Strigamia maritima* (Geophilomorpha). — *Evolution & Development* 6: 78–89.

Chipman, A. D., Arthur, W. & Akam, M. 2004b: A double segment periodicity underlies segment generation in centipede development. — *Current Biology* 14: 1250–1255.

Chipman, A. D. & Akam, M. 2008: The segmentation cascade in the centipede *Strigamia maritima*: Involvement of the Notch pathway and pair-rule gene homologues. — *Developmental Biology* 319: 160–169.

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: Camatini, M. (ed.), *Myriapod biology*: 233–240. Academic Press, New York.

Geiger, R., Aron, R. H. & Todhunter, P. 2003: *The climate near the ground*. — Rowman and Little field Publishers, New York.

Hammer, P. 1931: *Tusindben*. — Danmarks Fauna 35, Gads Forlag, Kjøbenhavn.

Hayden, L., Parkes, G. & Arthur, W. 2012: Segment number, body length, and latitude in geophilomorph centipedes: a 'converse-Bergmann' pattern. — *Biological Journal of the Linnean Society* 107: 166–174.

Horneland, E. O. & Meidell, B. A. 1986: The epimorphosis of *Strigamia maritima* (Leach, 1817) (Chilopoda: Geophilidae). — *Entomologica Scandinavica* 17: 127–129.

Kettle, C. & Arthur, W. 2000: Latitudinal cline in segment number in an arthropod species, *Strigamia maritima*. — *Proceedings of the Royal Society of London B* 267: 1393–1397.

Kettle, C., Johnstone, J., Jowett, T., Arthur, H. & Arthur, W. 2003: The pattern of segment formation, as revealed by engrailed expression, in a centipede with a variable number of segments. — *Evolution & Development* 5: 198–207.

Lewis, J. G. E. 1961: The life history and ecology of the littoral centipede *Strigamia* (= *Scolioplanes*) *maritima* (Leach). — *Proceedings of the Zoological Society of London* 137: 221–248.

Lewis, J. G. E. 1985: Centipedes entering houses with particular reference to *Geophilus carpophagus* Leach. — *Entomologist's Monthly Magazine* 121: 257–259.

Lundberg, A. 1996: Environmental change and nature management in Norway. — *Norsk Geografisk Tidsskrift* 50: 143–156.

Minelli, A. 2000: Holomeric vs. meromeric segmentation: a tale of centipedes, leeches, and rhombomeres. — *Evolution & Development* 2: 35–48.

Minelli, A. 2001: A three-phase model of arthropod segmentation. — *Development Genes and Evolution* 211: 509–521.

Minelli, A. & Bortoletto, S. 1988: Myriapod metamerism and the arthropod segmentation. — *Biological Journal of the Linnean Society* 33: 323–343.

Minelli, A., Foddai, D., Pereira, L. A. & Lewis, J. G. E. 2000: The evolution of segmentation of centipede trunk and appendages. — *Journal of Zoological Systematics and Evolutionary Research* 38: 103–117.

Minelli, A., Chagas-Júnior, A. & Edgecombe, G. 2009: Saltational evolution of trunk segment number in centipedes — *Evolution & Development* 11: 318–322.

Minelli, A., Maruzzo, D. & Fusco, G. 2010: Multi-scale relationships between numbers and size in the evolution of arthropod body features. *Arthropod Structure & Development* 39: 468–477.

Nesje, A. & Sulebak, J. R. 1994: Quantification of late Cenozoic erosion and denudation in the Sognefjord drainage basin, Norway. — *Norsk geografisk Tidsskrift* 48: 85–92.

Nesje, A. & Whillans, I. M. 1994: Erosion of Sognefjord, western Norway. — *Geomorphology* 9: 33–45.

Ramstad, H., Hovgaard, P., Yasumoto, T., Larsen, S. & Aune, T. 2001: Monthly variations in diarrhetic toxins and yessotoxin in shellfish from coast to the inner part of the Sognefjord, Norway. — *Toxicon* 39: 1035–1043

Simaiakis, S. 2009: Variation in geophilomorph segment number among south European populations – the case of *Himantarium gabrielis* (Linné, 1767) (Chilopoda, Geophilomorpha, Himantariidae). — *Soil Organism* 81: 359–371.

Simaiakis, S. & Mylonas, M. 2006: Intraspecific variation in segment number in *Pachymerium ferrugineum* (C. L. Koch, 1835) (Chilopoda: Geophilomorpha) in the south Aegean Archipelago (north-east Mediterranean, Greece). — *Biological Journal of the Linnean Society* 88: 533–539.

Simaiakis, S., Iorio, E., Djursvoll, P., Meidell, B. A., Andersson, G. & Kirkendall, L. 2010: Study of diversity and geographic variation of leg pairs in geophilomorphs (Chilopoda, Geophilomorpha) in northwestern Europe. — *Biological Journal of the Linnaean Society* 100: 899–909.

Sokal, R. R. & Rohlf, F. J. 1995: *Biometry: the principles and practice of statistics in biological research*. — W. H. Freeman, New York.

Stuxberg, A. 1871: Bidrag till Skandinaviens Myriopodologi. II. Sveriges Chilopoder. — *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* 4: 493–512.

Utaaker, K. 1980: Local climates and growth climates of the Sognefjord region. — *International Journal of Biometeorology* 24: 13–22.

Utaaker, K. & Skaar, E. 1970: Local climates and growth climates of the Sognefjord region. — *Acta Agriculturae Scandinavica* 1: 1–218.

Vedel, V., Chipman, A. D., Akam, M. & Arthur, W. 2008: Temperature-dependent plasticity of segment number in an arthropod species: the centipede *Strigamia maritima*. — *Evolution & Development* 10(4): 487–492.

Vedel, V., Brena, C. & Arthur, W. 2009: Demonstration of a heritable component of the variation in segment number in the centipede *Strigamia maritima*. — *Evolution &*

*Development* 11: 434–440.

Vedel, V., Apostolou, Z., Arthur, W., Akam, M. & Brena, C. 2010: An early temperature-sensitive period for the plasticity of segment number in the centipede *Strigamia maritima*. — *Evolution and Development* 12: 347–352.

Wielgolaski, F. E. 1973: Influence of climate on primary production in a northern mountain area. — *International Journal of Biometeorology* 17: 355–357.

Zar, J. H. 2009: *Biostatistical analysis*. — Pearson Prentice-Hall, Upper Saddle River, NJ.

**Appendix**. Climate data from the Sognefjord (1961–1990; Meteorological Institute of Norway). Temperatures (mean monthly normal values), and precipitations (sum monthly normal values) for 8 meteorological stations next to the sampling sites. Long: longitude, MJJt: mean May–July temperature, MJJp: sum May–July precipitation, MJt: mean May–June temperature, MJp: sum May–June precipitation, Pr: sum annual precipitation, Tm: mean annual temperature.

| **Temperature** (°C) | Long. | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Tm | MJJt | MJt |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. Lavik | 5.550 | 0.7 | 0.5 | 2.2 | 4.8 | 9.5 | 13.0 | 14.0 | 13.8 | 10.3 | 7.7 | 3.8 | 1.9 | 6.9 | 12.2 | 11.3 |
| 2. Vadheim | 5.830 | 0.2 | 0.3 | 2.1 | 4.9 | 9.8 | 13.3 | 14.5 | 14.0 | 10.3 | 7.6 | 3.6 | 1.7 | 6.9 | 12.5 | 11.6 |
| 3. Høyanger | 6.070 | 0.0 | 0.2 | 2.0 | 5.0 | 10.0 | 13.5 | 14.5 | 14.0 | 10.3 | 7.5 | 3.5 | 1.5 | 6.8 | 12.7 | 11.8 |
| 4. Balestrand | 6.530 | –0.6 | –0.3 | 1.7 | 5.0 | 10.2 | 13.7 | 14.8 | 14.2 | 10.3 | 7.0 | 2.8 | 0.5 | 6.6 | 12.9 | 12.0 |
| 5. Leikanger | 6.867 | –0.8 | –0.5 | 1.6 | 5.0 | 10.3 | 13.8 | 14.9 | 14.2 | 10.3 | 7.0 | 2.6 | 0.3 | 6.6 | 13.0 | 12.1 |
| 6. Sogndal | 7.100 | –1.5 | –1.0 | 1.0 | 5.0 | 10.5 | 14.0 | 15.0 | 14.0 | 10.0 | 6.5 | 2.0 | –0.5 | 6.3 | 13.2 | 12.3 |
| 7. Kaupanger | 7.289 | –4.0 | –3.8 | –0.1 | 4.2 | 10.7 | 14.3 | 15.5 | 13.4 | 9.5 | 5.5 | 0.7 | –2.5 | 5.3 | 13.5 | 12.5 |
| 8. Årdal | 7.720 | –2.0 | –1.8 | 1.0 | 5.0 | 10.5 | 14.0 | 14.9 | 13.7 | 9.5 | 5.5 | 1.5 | –1.5 | 5.8 | 12.7 | 11.8 |
| **Precipitation** (mm) | Long. | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Pr | MJJp | MJp |
| 1. Lavik | 5.547 | 193 | 151 | 173 | 102 | 90 | 119 | 140 | 169 | 293 | 284 | 258 | 252 | 2224 | 349 | 209 |
| 2. Vadheim | 5.830 | 225 | 160 | 185 | 100 | 95 | 115 | 135 | 160 | 290 | 285 | 255 | 275 | 2280 | 345 | 210 |
| 3. Høyanger | 6.065 | 229 | 160 | 188 | 97 | 96 | 115 | 137 | 159 | 293 | 286 | 255 | 275 | 2290 | 348 | 211 |
| 4. Balestrand | 6.530 | 133 | 90 | 105 | 57 | 55 | 70 | 85 | 103 | 179 | 175 | 158 | 160 | 1370 | 210 | 125 |
| 5. Leikanger | 6.867 | 64 | 39 | 50 | 21 | 29 | 43 | 59 | 65 | 81 | 88 | 73 | 78 | 690 | 131 | 72 |
| 6. Sogndal | 7.100 | 105 | 68 | 79 | 38 | 43 | 55 | 60 | 76 | 125 | 131 | 120 | 125 | 1025 | 158 | 98 |
| 7. Kaupanger | 7.289 | 37 | 25 | 34 | 19 | 25 | 50 | 52 | 55 | 73 | 41 | 48 | 49 | 508 | 127 | 75 |
| 8. Årdal | 7.720 | 75 | 45 | 55 | 25 | 35 | 50 | 60 | 65 | 90 | 100 | 80 | 80 | 760 | 145 | 85 |