

Relationship between intraspecific variation in segment number and geographic distribution of *Himantarium gabrielis* (Linné, 1767) (Chilopoda: Geophilomorpha) in Southern Europe

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Abstract

Arthropods have mainly an invariant number of trunk segments. However, segment number increases with growth and post-embryonic development in certain arthropod groups. As concerns centipedes, most of geophilomorph species present intraspecific variation in the number of trunk segments that is not age-related. Previous studies have shown that species of geophilomorphs from cold and temperate regions tend to have fewer segments than those from warmer regions. Here, we study the geographic pattern of variation at the phenotypic level in *Himantarium gabrielis* (Linné). To better understand the geographic patterning, we compared 436 specimens from the Balkan and the Apennine peninsulas. Data are provided, all of which reveal evidence of a difference between the peninsulas, towards an increased number of segments in the Balkan region in both sexes. Our results indicate that in males, the variation between the Apennine and the Balkan specimens approaches 32 segments, whereas in females the difference is even higher, reaching 48 segments. We also observed a bimodal distribution of segment numbers in Apennine samples but not in those from the Balkan region. We investigated possible relations of this bimodality with environmental and historical characteristics of the region.

Keywords: Apennine, Balkans, bimodality, contingency tables, leg-bearing segments, Mediterranean region

1. Introduction

Although there is considerable variation in segment number among arthropod groups, the vast majority of arthropod species have a fixed number of segments, thereby providing no variation for natural selection to act upon the character (Arthur & Chipman 2005a). However, most geophilomorph species exhibit an intraspecific variability in segment number (Kettle et al. 2003), both between and within sexes, the main exception being represented by the species of the family Mecistocephalidae (Minelli & Bortoletto 1988). Particularly for some species of the chilopod order Geophilomorpha, specimens from cold and temperate regions tend to be smaller and with fewer trunk segments than those from warmer regions (Arthur 1999, Arthur & Kettle 2001). In the Geophilomorpha, leg-bearing segments (LBS) are always odd and range from 27 to 191 (Minelli & Bortoletto 1988, Minelli et al. 2000). There are numerous

studies revealing the geographic patterns of variation at the phenotypic level (Arthur & Kettle 2001) dealing with several geophilomorph species, such as *Strigamia acuminata* (Leach, 1815) (Prunescu & Capuse 1971, Arthur 1999), *Pachymerium ferrugineum* (C. L. Koch, 1835) (Prunescu & Capuse 1971, Arthur 1999, Simaiakis & Mylonas 2006), *Strigamia maritima* (Leach, 1817) (Kettle & Arthur 2000, Kettle et al. 2003, Arthur & Chipman 2005a, 2005b), *Geophilus carpophagus* Leach, 1815 (Eason 1979, Lewis 1985, Arthur & Kettle 2001, Arthur et al. 2001), *Henia illyrica* (Meinert, 1870) (Prunescu & Capuse 1971), as well as *Haplophilus subterraneus* (Shaw, 1789), *Brachygeophilus truncorum* (Bergsoe & Meinert, 1886) and *Necrophloeophagus flavus* (De Geer, 1778) (Arthur & Kettle 2001). Among these works, Arthur et al. (2001) presented the best documented case concerning the identification of a cryptic species in Britain, namely *Geophilus easoni* Arthur et al., 2001. Moreover, there have been significant studies on body segmentation in centipedes, especially segmentation processes (Minelli & Bortoletto 1988, Arthur & Farrow 1999, Kettle et al. 1999, Minelli 2000, Minelli et al. 2000, Minelli 2001, Hughes & Kaufman 2002, Minelli & Fusco 2004). For example, *Strigamia maritima* has been used as model organism in several studies which investigate the evolutionary significance, and the origins, of its intraspecific variation in segment number (Kettle et al. 2003), and how this developmental process operates (Chipman et al. 2004, Arthur & Chipman 2005a, 2005b).

In our case, *Himantarium gabrielis* (Linné) is widely distributed in the Mediterranean region (Albania, Algeria, Bosnia and Herzegovina, Bulgaria, Corsica, Croatia, FYR Macedonia, Greece, Italy, Morocco, Montenegro, Portugal, Sardinia, Sicily, Slovenia, southern France, southern Romania, Tunisia and western Turkey) (Zapparoli 1990, 2002, 2006). Despite the Mediterranean character of the species, it is unexpectedly absent from several areas (Spain, Middle East and Cyprus, southern Aegean Islands and Crete, Libya, Egypt and Sinai Peninsula). Leg-bearing segments vary from 87 to 171 in males and from 95 to 179 in females (Minelli et al. 1984, Berto et al. 1997). Among many centipede species, sexual dimorphism often takes the form of females having two additional segments (Arthur 1999), but in *H. gabrielis*, where the number of leg-bearing segments is larger, the differences between male and females may amount to 8 LBS (Minelli & Bortoletto 1988). According to Minelli & Bortoletto (1988, 1990), in males of *H. gabrielis*, a significant set of frequency maxima occurs at 85, 101, 117, 133, 149 and 165 LBS, whereas in females LBS shift by eight segments towards higher numbers (93, 109, 125, 141, 157 and 173). Moreover, in both sexes, the maximum intraspecific variation is about 90 segments (Minelli et al. 1984). Arthur & Chipman (2005b) have already identified that there is a pressing need for experimental work on the genetic and environmental factors that cause variation in segment number within geophilomorph species.

In this study we examine the geographic patterning of variation in *H. gabrielis* by comparing specimens from Southern Europe. Our results indicate that there is clear intraspecific variation in specimens of *H. gabrielis* between the Apennine and the Balkan peninsulas, with increased numbers of segments in the Balkan region. There is also a bimodal distribution of segments in Italy, which is absent from the Balkan area. We explore the possible relationship of this variation with environmental and historical characteristics of the region.

2. Materials and methods

Data collection

For our study of *H. gabrielis* we used old and recent data from museum collections as well bibliographic references. Most of the specimens were collected by hand and were preserved in 75 % alcohol.

As regards the museum collections, we examined the centipede collection of the Natural History Museum of Crete – NHMC (33 specimens collected from 1999 to 2006 and derived mainly from the Aegean archipelago, such as Andros, Chios, Karpathos, Kythira, Salamina and Skyros islands and a region in the central continental Greece), as well as that of the Natural History Museum of Vienna, NHMW (186 specimens derived mainly from Croatia, Montenegro, and Bosnia and Herzegovina) (Tab. 1). Additionally, we used the published Apennine records for *H. gabrielis* along the Apennine Peninsula and its satellite islands (217 specimens derived mainly from the mainland and the islands of Sardinia and Sicily) (Minelli et al. 1984) (see Tab. 1).

Tab. 1: The pool of data used to analyse the geographical pattern of *H. gabrielis* segment numbers, females (F) and males (M). N: Total number of individuals, NHMC: Natural History Museum of Crete, NHMW: Natural History Museum of Vienna, IR: Italian Records. *: Total number of individuals per sex in continental Italy, Sardinia and Sicily (females and males are not recorded for each Italian compartment) (Minelli et al. 1984).

Locality	NHMC (N = 33)		NHMW (N = 186)		IR (N = 217)	
	M	F	M	F	M	F
Continental Greece	5	3	9	8		
Aegean Islands	13	12				
Ionian Islands			19	11		
Continental Italy			20	11	99*	118*
Sardinia			7	13		
Sicily			3	4		
Croatia			22	26		
Montenegro			7	13		
Bosnia & Herzegovina			8	5		

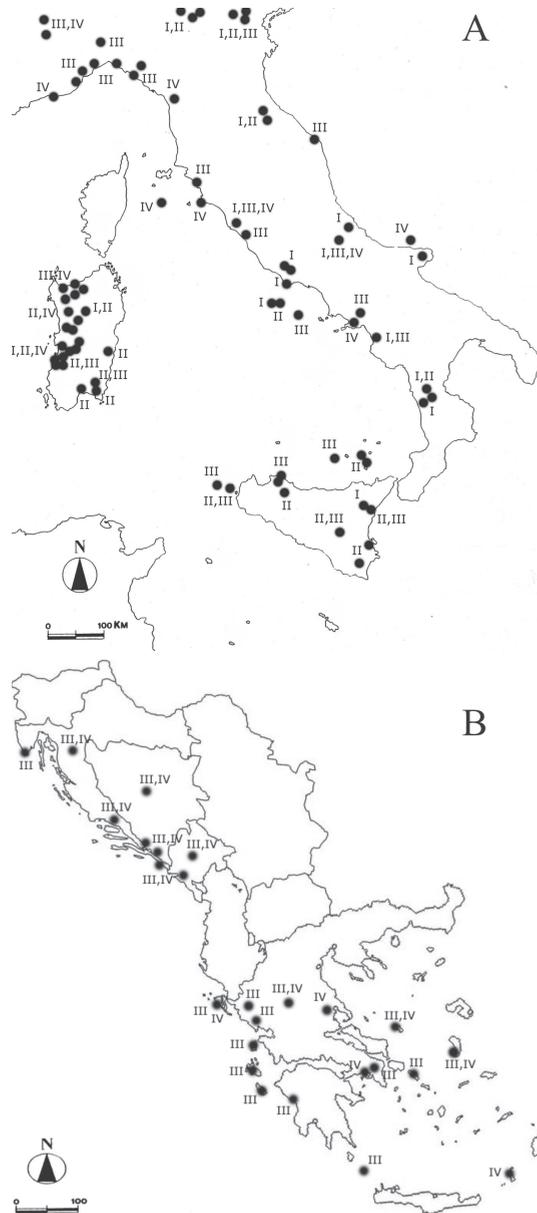


Fig. 1 A: Geographic variation in leg-pairs of *Himantarium gabrielis* in the Apennine Peninsula (including Sicily, Sardinia and the surrounding islets), as constructed by Minelli et al. (1984); B: Geographic variation in leg-pairs of *H. gabrielis* in the Balkan Peninsula (Croatia, Montenegro, Bosnia and Herzegovina, mainland Greece) and the adjacent islands of Greece; I: up to 103 segments in males, up to 117 in females; II: 105–123 segments in males, 119–137 in females; III: 125–145 segments in males, 139–159 in females; IV: at least 147 segments in males and 161 in females.

Statistical analysis

Comparisons between the peninsulas were made using both chi-square (χ^2 -test) and the log-likelihood ratio (G-test) for contingency tables (Zar 1996). In a chi-square analysis of contingency tables it is recommended that no expected frequency can be less than 1; otherwise, the resulting chi-square value will be biased and may not be compared legitimately with the critical values of the chi-square distribution (Zar 1996). Therefore, primitive data have been pooled (combining adjacent segment numbers) forming groups of 8 and 16 pairs of legs. The observed (obs) and the expected (exp) number of samples were examined to decide which group segment or even better which modal value is associated with which geographical region (Italy or Balkan). The highest χ^2 value ($\chi^2 = (\text{obs}-\text{exp})^2$) among the different group segments is considered to be the modal value for each geographical region and sex.

Two maps were constructed showing the geographic variation of LBS for the Apennine and the Balkan peninsulas (Figs 1A, 1B). In order to easily draw the pattern of segment variation along the two peninsulas we used four classes of segments (I: up to 103 LBS in males and 117 in females, II: 105–123 LBS in males and 119–137 in females, III: 125–145 LBS in males and 139–159 in females, IV: at least 147 LBS in males and 161 in females). The classes of segments presented on the maps are in accordance with the geographic variation of pairs of legs of *Himantarium gabrielis* in the Apennine Peninsula (including Sicily, Sardinia and the surrounding islets), as described by Minelli et al. (1984) and Minelli & Bortoletto (1988, 1990).

3. Results

The frequency distribution of the number of leg-bearing segments in both sexes of the Balkan and Apennine specimens of *H. gabrielis* is presented in Figs 2A & 2B, respectively. In Apennine, the lowest LBS values are 87 in males and 95 in females, with the maximum values at 171 in males and 179 in females. In the Balkan Peninsula, the lowest LBS values are 131 in males and 139 in females, with the highest LBS values at 171 in males and 177 in females. In Apennine, total variation in both sexes is almost 90 LBS, whereas in the Balkan region the variation in segments is more restricted, reaching 40 LBS. Therefore, a substantial cluster of LBS, varying between 87 and 123 segments in males and 95 and 137 in females, is absent from Balkan material (see also Figs 2A, 2B).

Contingency tables of segment number (observed and expected values) for the Apennine and the Balkan samples of *H. gabrielis* for both sexes are presented below (Tabs 2A, 2B). The results of chi-square (χ^2) and log-likelihood (G) tests comparing the segment number distribution between Apennine and Balkan samples are given in Tab. 3. The two grouping categories (A: 8, B: 16) significantly support the same general pattern, towards more segments in Balkan the region in both sexes (see Tab. 3).

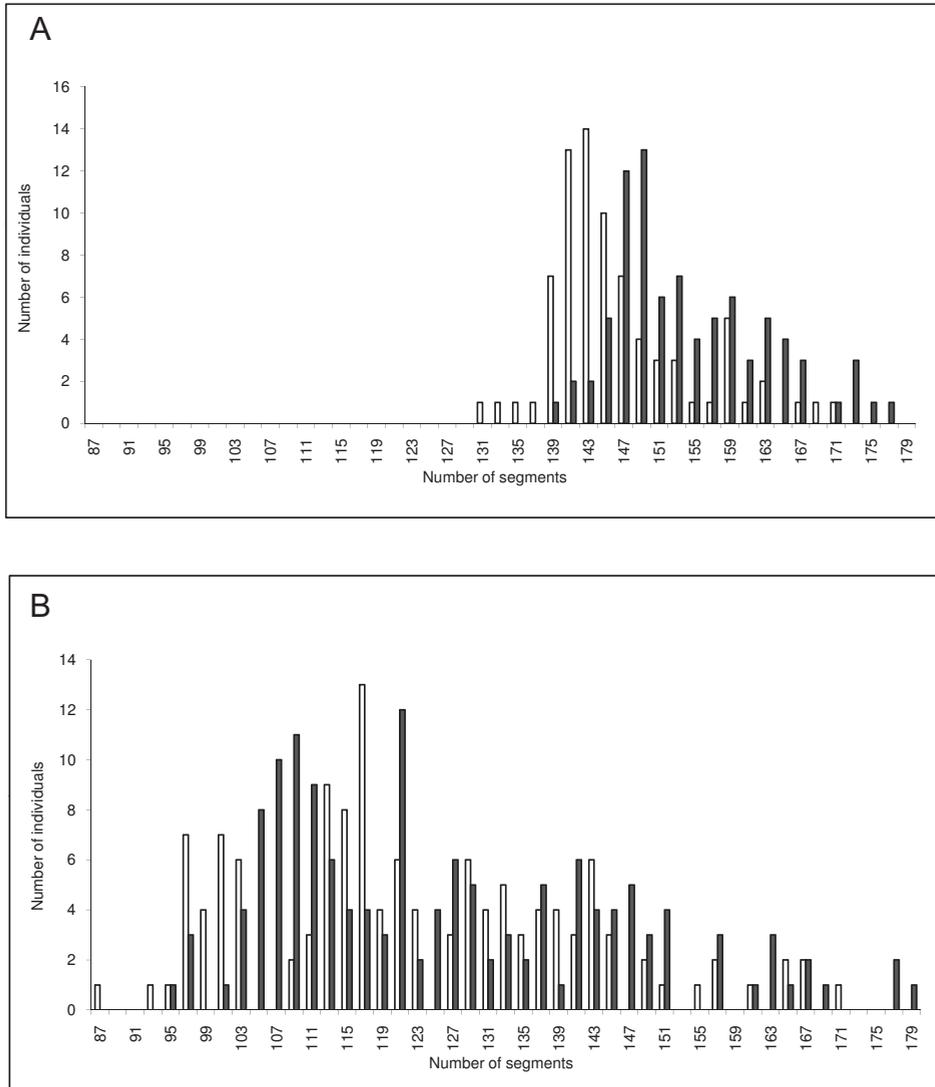


Fig. 2 Frequency distribution of the number of LBS in *Himantarium gabrielis* in males (black bars) and females (white bars). A: Balkan (data derived from NHMC and NHMW); B: Apennine Peninsula (redrawn after Minelli et al. 1984 with additional data derived from material stored in NHMW).

Tab. 2 (A-B). Contingency tables of segment number for Southern European populations of *H. gabrielis* females and males (obs: observed, exp: expected). A: 8-segment group, B: 16-segment group. Modal values are presented in bold, group of segments associated with a certain geographical region (Apennine or Balkans) are presented in grey boxes.

A. Females	≤ 101	≤ 109	≤ 117	≤ 125	≤ 133	≤ 141	≤ 149	≤ 157	≤ 165	≤ 173	> 173
LBS											
Apennine (obs/exp)	3/5/2017	33 / 20.90	23 / 14.56	21 / 13.30	10/16/2013	10/14/1976	16 / 30.39	7 / 18.36	5 / 14.56	6/3/1933	2/2/1953
Balkans (obs/exp)	0 / 1.83	0 / 12.10	0 / 8.44	0 / 7.70	0 / 5.87	6/3/2024	32 / 17.61	10/22/1964	8/18/1944	3/7/1967	1/2/1947
A. Males											
LBS											
Apennine (obs/exp)	21 / 13.09	4/8/1999	33 / 20.57	8/14/1972	12/18/1946	14 / 22.43	11 / 28.67	7/4/1948	6/3/1986	3/3/1974	
Balkans (obs/exp)	0 / 7.91	0 / 3.01	0 / 12.43	0 / 5.28	7/2/1954	22 / 13.57	35 / 17.33	4/8/1952	4/8/2014	2/3/2026	

B. Females	≤ 109	≤ 125	≤ 141	≤ 157	≤ 173	> 173
LBS						
Apennine (obs/exp)	38 / 24.06	44 / 27.86	30 / 20.90	23 / 48.76	8 / 20.90	2/2/1953
Balkans (obs/exp)	0 / 13.94	0 / 16.14	12/3/2010	54 / 28.24	12/25/2010	1/2/1947
B. Males						
LBS						
Apennine (obs/exp)	21 / 13.09	41 / 25.55	32 / 21.19	25 / 51.10	7 / 14.33	3/3/1974
Balkans (obs/exp)	0 / 7.91	0 / 15.45	12/2/1981	57 / 30.90	8/16/1967	2/3/2026

Tab. 3 Summary of χ^2 and G tests for differences in segment number between the Balkan and the Apennine Peninsula in *Himantarium gabrielis*, classified by sex (M: Males, F: Females). df: degree of freedom, P: P values.

	Sex	df	χ^2	P	G	P
8-group	M	9	100.22	< 0.001	126.06	< 0.001
	F	10	119.38	< 0.001	150.16	< 0.001
16-group	M	5	97.86	< 0.001	121.62	< 0.001
	F	5	117.41	< 0.001	144.91	< 0.001

The pooled data from the 8-segment grouping category (Tab. 2A) show that, in males, there is a difference approaching 32 segments between the modal number of the Apennine (≤ 117) and the Balkan specimens (≤ 149). For females, the difference is higher, reaching 48 segments respectively (≤ 109 and ≤ 157). It is remarkable to note that along the Apennine Peninsula females modal value (≤ 109) is lower than that of males (≤ 117), which is only an artefact of the chi-square contingency results. Consequently, in the 8-segment grouping category there is a unique modal number for each region and each sex (see Tab. 2A). However, the analysis of the 16-grouping category and the distribution of segment numbers for *H. gabrielis* (see Fig. 3: A) indicate a distinct pattern for Apennine material. In particular, females and males are strongly associated with two modal segment numbers, ≤ 125 and ≤ 157 , as well ≤ 117 and ≤ 149 , respectively, a phenomenon known as bimodality (see Tab. 2B). In contrast, in the Balkan Peninsula, there is only one modal value for females and males (≤ 157 and ≤ 149 respectively) (see also Tab. 2B).

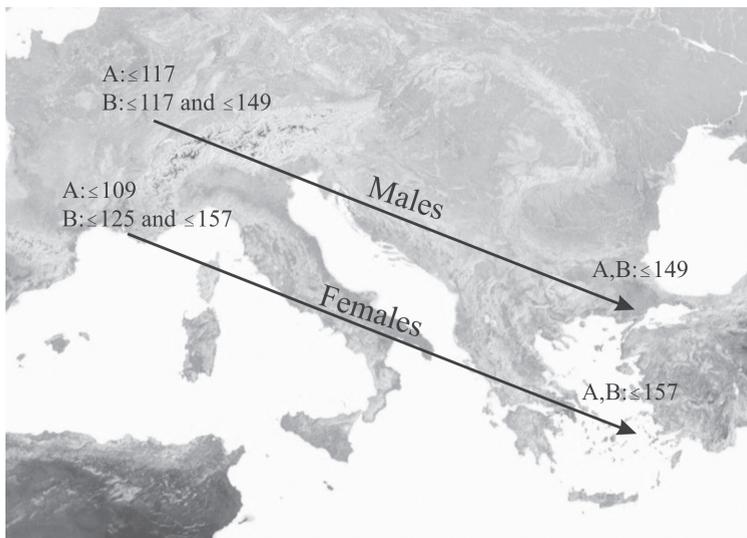


Fig. 3 Geographic pattern of leg-bearing segment frequencies in *Himantarium gabrielis* (males and females) along the Apennine and the Balkan peninsulas. A, B represent the two grouping categories (A: 8-, B: 16-group) as defined in material and methods. The numbers (pairs of legs) are showing the modal value for each grouping category. Lines represent geographic patterning between the two peninsulas.

4. Discussion

It is commonly accepted that on a sufficiently extensive geographical scale, a latitudinal cline in segment number becomes clear, with trunk segments increasing in number towards the south (Kettle et al. 2003). Arthur & Kettle (2001) have carried out the only study of a north to south cline along a wide geographical zone (comparison between British and Canarian populations in *Geophilus carpophagus*), awaiting more data from continental European areas for other geophilomorph species. However, a latitudinal cline is known to exist in *Strigamia maritima* along a narrower geographical area (Kettle & Arthur 2000). A rather tentative suggestion of a geographical cline is also known for *Pachymerium ferrugineum* between Finland and North African populations (Meinert 1870, Palmén 1949, Eason 1979). However, some exceptions dealing with data derived from a restricted geographical area show erratic geographical patterns, such as *Pachymerium ferrugineum* in the Aegean archipelago (Simaiakis & Mylonas 2006) or British populations of *Geophilus carpophagus* (short form) (Arthur & Kettle 2001).

With the above examples in mind, material of *H. gabrielis* was examined. Along the geographic gradient of the Apennine and Balkan peninsulas, our data make a strong case for the existence of significantly different number of segments within this species. However, we refrain from using the term 'cline' to describe this pattern. Due to the northwest-southeast orientation of the two peninsulas several collecting sites in southern Italy were further east than some of the northernmost parts of the Balkan Peninsula. Thus, evidence for a cline, either longitudinal or latitudinal, between the two peninsulas could be compromised. It was also impractical to investigate a possible wider geographical trend (e.g. by comparing Mediterranean with northern European populations), because of the strictly Mediterranean range of *H. gabrielis* (Zapparoli 2002, Simaiakis et al. 2005).

It is interesting to note that Minelli et al. (1984) referred to two forms within *H. gabrielis*, called '*oligopodi*' and '*polipodi*' respectively. These possible forms can be related to our data which show that the segment numbers of males and females in Apennine are strongly bimodal (see Tab. 2B). To further support this convergence, it would be reasonable to study more characteristics (morphological and/or molecular), in the same way that Minelli et al. (1984) and Arthur et al. (2001) did in previous works. However, since most of the 436 specimens were preserved in 75 % ethanol for many decades and some for more than a century, it was not possible to count and evaluate further morphological characters, such as the number of coxal pores and the pigmentation. Nor was it possible to extract proteins and genetic material for molecular analyses. Thus, quantification of variation in leg-pairs reveals patterns that appear to be intraspecific, but not directly informative concerning speciation (Arthur et al. 2001).

The identity of the forms of *H. gabrielis* has been much debated and refined over the years, albeit without supporting experimental data. Meinert (1870), Attems (1929) and Verhoeff (1943) suggested that there were two sympatric species distributed in Italy, *Himantarium rugulosum* C. L. Koch, 1841 and the widespread *H. gabrielis*. Other studies (Chalande & Ribaut 1909, Brolemann 1930, Matic 1972) and in-depth phenotypic examination of these two species (Minelli et al. 1984) resulted in the conclusion that *H. rugulosum* was merely a synonym of *H. gabrielis*. Our data strongly support the occurrence of two distinct geographic curves (modal values) along the Apennine Peninsula.

Previous papers have demonstrated the importance of temperature on intraspecific variation, supporting the view that species of geophilomorphs from cold and temperate regions tend to have fewer segments than those from warmer regions. Here, temperature seems to only slightly affect the present geographical template. Based on the land surface temperature over the Mediterranean, temperature seems to increase from north to south but not from west to east (El-Kharraz et al. 2003). Therefore, any conclusion relating the temperature gradient and the geographic patterning of variation in LBS between the Apennine and Balkan regions would be uncertain.

When considering the complex palaeogeography of the Mediterranean region, there is a possible scenario which describes the existed geographical difference and the possible migration routes for the dispersal of *H. gabrielis* all over the Mediterranean basin. In particular, the late upper Miocene (5.5–6 Ma), could help to explain the unexpected absence of *H. gabrielis* from Crete and Cyprus. During the Messinian period (dry with high salinity), despite the low sea-level, Crete remained separated from continental Greece and the Anatolian area (Dermitzakis 1990), as was Cyprus from the Middle East and Turkey, whereas Italy was joined with the northern coast of Africa in the region of what is now Tunisia (Roegl & Steininger 1983, Hsü et al. 1977). This evidence could be used to suggest that *H. gabrielis* might have reached the eastern Mediterranean (Balkan region and western Turkey) during that period.

The critical question that now arises is whence this species could have invaded the Mediterranean region. It might have moved into the Apennine Peninsula via two geographical pathways, southwards through the central Europe or northwards through the Sicilian Land Bridge between the Tunisian and the Apennine mainland. The presence of remnant populations of *H. gabrielis* in central Europe (Attems 1929, Brölemann 1930) reinforces the first assumption. Thus, the ancestral population could have originated in central Europe, moving southwards to the Balkan and the Apennine peninsulas. Due to unknown reasons, the ‘oligopodi’ populations colonised mountainous places along Apennine but not along the Balkan Peninsula. The ‘short’ form was also distributed in coastal areas in both regions. The usage of different habitats along a broad altitudinal range creates genetically distinct populations either within the Apennine Peninsula or between the two peninsulas. This could explain Apennine populations showing higher segment variation than Balkan ones, which are significantly related to two modal group segment numbers (≤ 125 and ≤ 157 in females and ≤ 117 and ≤ 149 in males).

In both cases, Italy and the Balkans have been well separated for a period of at least 5 million years ago, providing strong evidence for the existence of intraspecific variation of leg-bearing segments. In the future, many more data are required in order to decide whether this geographical pattern concerns other Mediterranean regions, such as the Iberian and the Anatolian peninsulas, as well as the Middle East and North African countries (Algeria, Tunisia, Morocco). Furthermore, detailed ecological information on species (altitudinal records, habitat preferences) will be required to produce more secure inferences.

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