# The weight of internal and external constraints on *Pupilla muscorum* L. (Gastropoda: Stylommatophora) during the Quaternary in Europe

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## INTRODUCTION

*Pupilla muscorum* L. is a terrestrial gastropod which is very common in European Quaternary deposits. It shows great morphological variability, mainly in shell size. To understand how this variability is expressed, a survey of modern and Quaternary European specimens of *Pupilla muscorum* was undertaken using multivariate analyses to characterize the morphology. This was followed by an ontogenic study of shell sections to determine the changes in the growth timing. The first step relates to intra-population variability which is mainly expressed in shape variation. The shape of the shell lies between two extremes: a fat shell with a slightly protruding aperture and a slim shell with a strongly protruding aperture. The second step describes inter-population variability, both temporal (for fossil populations) and spatial (for modern populations), which is mainly in size. During the Quaternary, the size variation parallels the climatic cycles: large shells during pleniglacial phases, small shells during interglacial ones. At present, N – S and E – W size gradients are present with the adult size varying between 2·5 and 4·7 mm. The final step addresses the occurrence of this growth variability by studying morphological indices, which

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characterise size and spire of the shell, against the number of whorls taken as age reference. The variations in these indices show that heterochronic processes (*sensu* McNamara 1986), acceleration and hypermorphosis, induce a supernumerary part-whorl of the spire in the juvenile phases of the growth. Because *P. muscorum* is in evolutionary stasis during the Quaternary, such morphological variations, channelled by external and internal constraints, are a good example of ecophenotypic iterative changes at the intraspecific level.

What does the ontogeny of a fossil organism represent? The study of the palaeontologist focuses on the effect of ontogeny on morphology which results from the interaction between internal (direct influences) and external (indirect influences) that express themselves by channelling phenotypic potentialities (Waddington 1974; Gould 1980; Alberch 1982).

An example of these constraints can be provided by the analysis of morphological variability in the terrestrial molluscs during the Quaternary in Europe. Quaternary deposits are frequently rich in malacofauna which permits precise reconstructions of past environments (Rousseau 1987). However, among the numerous terrestrial mollusc species, the pulmonate *Pupilla muscorum* L. is particularly common, especially in loess sections, and shows great morphological variability, mainly in shell size. The aim of this paper is to characterise both intra- and inter-population morphological variations and to explain this variability by studying changes in timing of the ontogeny of the shell.

## MATERIALS AND METHODS

*P. muscorum* is a small Holarctic species (2·5 to 4·7 mm high) living in open environments. The number of whorls, the size and the shape of the shell show a large variability. The species first appeared in the Early Pliocene (Wenz 1923).

Whatever the climatic conditions, *P. muscorum* is one of the more common species in Pleistocene malacofaunas. Generally, the populations have abundant individuals,

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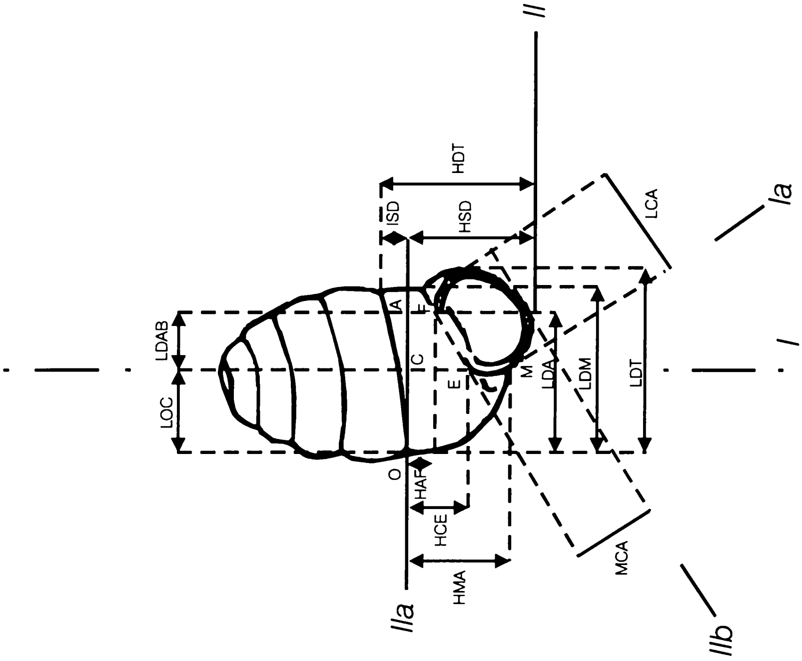
**Figure 1:** Morphometry of *Pupilla muscorum* used for the biometric study. The number of whorls is counted after the embyonic shell. All these parameters are studied by correspondence analysis.


II
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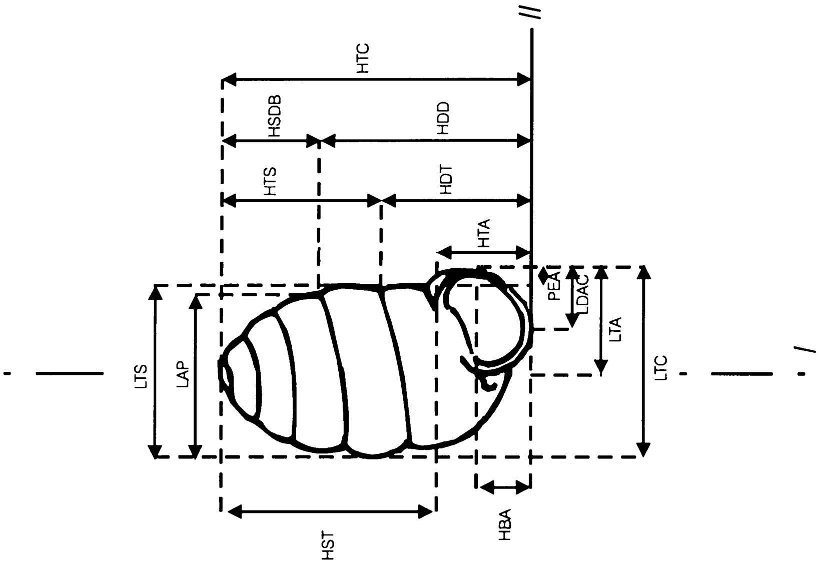
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I
LTS
LAP
HST
HBA

and show variations in the size of the shell. Among the Upper and Middle Pleistocene deposits analyzed in Achenheim (Alsace, France) there are more than 55 stratigraphic levels providing many fossil populations in which *P. muscorum* is abundant. From these populations, 709 individuals (up to 30 individuals per population, randomly selected from the total number) have been measured. Other fossil populations from French sites were added to those from Achenheim in order to improve the analysis of inter-population variations. The fossil variations were then compared to those in recent populations.

Measurements proceeded as indicated on Figure 1. In addition, in order to understand the morphological variations, the ontogeny was anaysed by studying indices characteristic of the spire (spire index SpL = H/L ,Cain 1977), the size (size index SI = H+L) and ß, the angle that each section of whorl spire makes with regard to the coiling axis.

## RESULTS

### *Morphological intra-population variation during the Pleistocene in Europe*

The spire fluctuations influence the morphology of the shell. They mainly affect the embryonic and infantile phases, which constitute the more sensitive growth stages of the animal to the environment. Certain shell size variations involve the shell dimensions and/or the whorl number within each population.

Shape variation of the shell is also evident within populations. It results from parallel tendencies between the spire and final whorl dimensions which establish two

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**Figure 2:** Size variations in *Pupilla muscorum.* **Recent populations:** 1. Cracow RA10 (HTC = 4·38 mm); 2. Arcy-sur-Cure YC16 (HTC = 3·53 mm); 3. La Rochepot RO17 (HTC = 2·41 mm); 4. Villers-la-Faye LF22 (HTC = 2·39 mm). **Fossil populations:** 5. Achenheim CL01 (HTC = 2·80 mm); 6 Schiltigheim SJ22 (HTC = 3·43 mm); 7, Biache-St Vaast (HTC = 4·10 mm) and for comparison 8. a recent individual of Cracow RE03 (HTC = 4·38 mm). Note the similarity of the size between the Polish (8) and fossil (7) individuals. **Extreme shapes of the morphology in *Pupilla muscorum*:** 9. slim shell with a high protusion of the aperture Individual AG29 (HTC = 3·35 mm); 10. fat shell with a low protusion of the aperture Individual CG08 (HTC = 3·61 mm); a = general view, b = detail of last whorl. 11. Difference in ornamentation between protoconch and the post-protoconch whorls.

1

2

3

4

5

6

7

8

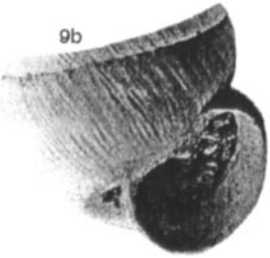
9a

11

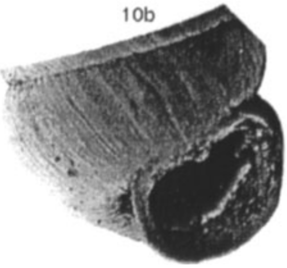
0.5 mm

10a

9b



10b



extreme morphologies: a fat shell and a slimmer shell. The fat shells present an aperture with a low protrusion and distant parietal crests (Figure 2). The slim shells have an aperture with a high protrusion and close parietal crests (Figure 2). On the other hand, analysis of the last whorl demonstrates the independence of the aperture dimensions. The shape of the aperture, rounded or ellipsoidal, does not correspond to a particular morphology of the rest of the shell.

No size–shape relation is observed, in spite of these two characters being both dependent upon the shell architecture. Intra-population variation depends on both size fluctuations and the expression of morphological tendencies.

### *Morphological inter-population variation during the Pleistocene in Europe*

Grouped by populations, the individuals determine overlapping ‘subclouds’ as indicated by the extreme populations AB and CI (Figure 3). The small morphologies of the former (AB) are plotted close to the ‘large ones’ of the latter (CI). This distribution shows an inter-population variation which is mainly due to shell size. Each population is plotted on the first factorial plane according to a size gradient represented by the first axis.

Analysis of the individuals from Achenheim reveals great intra- but also inter-population variability occurring during the Middle and Upper Pleistocene. Multivariate analyses of 496 individuals (Rousseau 1985) from other French deposits indicates a range of morphological variation that lies within the previously determined range of variability (Rousseau 1989). These results imply that morphological variations obtained for the Achenheim deposits are due neither to local environmental conditions, nor do they correspond to variations in isolated populations, but have to be generalized to European Quaternary deposits.

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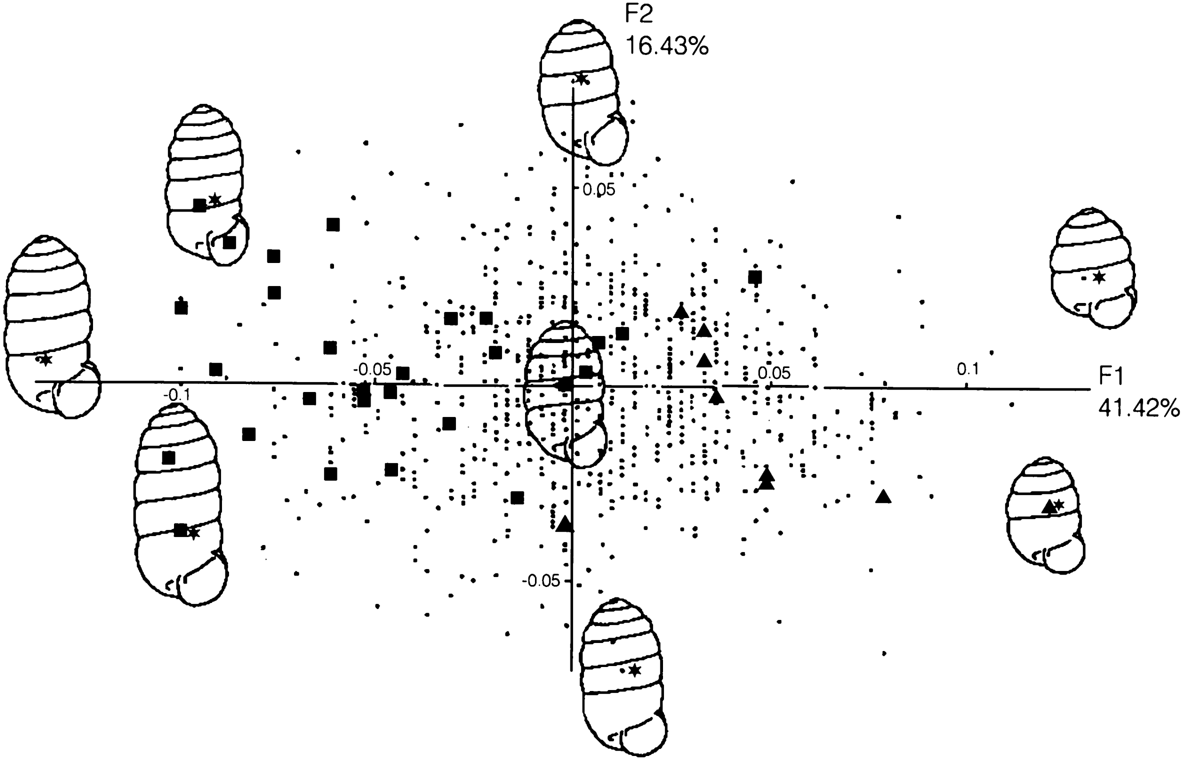
**Figure 3:** Correspondence analysis of Pleistocene samples (populations) using all the parameters. Distribution of the individuals from morphological criteria expressed by the first two axes. The triangles represent the individuals belonging to the populations CI (small shell), the squares those belonging to the population AB (tall shells); stars correspond to the drawn individuals.


F2
16.43%
0.05
-0.05
-0.1
-0.05
0.05
0.1
F1
41.42%

### ***Modern morphological variation in Europe***

In modern populations, as with fossil ones, the dimensions that describe the size (heights) of the shell discriminate the different morphologies more effectively. Among the parameters describing the aperture, those expressing the protrusion are dissociated from the other ones. As observed in fossil individuals, we see the contrast between fat shells, with slight protusion of the aperture, and slim shells, with high protrusion (Figure 2).

The local fluctuations lie within a more general biogeographic variation. In western and central Europe, *P. muscorum* is subject to very variable climatic and environmental conditions. Over the large area where a temperate climate prevails, the west is under an oceanic influence, whereas the climate becomes more and more continental towards the east. This continental trend of the climate induces a discrepancy in size variations, the small western shells having a morphology similar to the large eastern individuals.

There are great variations in shell size and this is observed in all Pleistocene localities studied. Several times during the Middle and Upper Pleistocene *P. muscorum* increased in shell size. After these increases there were always corresponding decreases. A parallelism has been demonstrated between climatic glacial–interglacial cycles and increasing–decreasing phases of shell size (Rousseau 1985, 1989).

By their reversibility, size variations do not express any evolutionary trends as classically defined. The rhythm over time is characteristic of iterative variations of increase and decrease of shell size during the Middle and Upper Pleistocene. Shape variations are independent of size fluctuations. Their link with time does not result from particular trends *a priori*. They seem to represent the random expressions of an architectural potential which has two poles:

- a fat shell with a small protrusion of the aperture;
- a slim shell with a large protrusion of the aperture.

If the size of the shell increases, all the other parts of the shell grow proportionally in order to conserve the architectural framework of *P. muscorum*. This conclusion demonstrates again the importance of the first stages of ontogeny and also emphasizes the subtle inter-relationships of the various characters.

The fossil variability expressed in the Pleistocene deposits is, for this period, similar to that recognized in the recent populations. The dimensions of the aperture indicate the same variations in fossil as in recent individuals. An identical interpretation concerning the cephalopodium of individuals must be proposed. According to Gould (1968), two strategies are available for changing in shell size, from one population to another:

- an increase or a decrease of the shell size correlative to a proportional variation of the size of the organism,
- an internal structural strengthening without any size modification of the organism.

Such a correlation between recent and fossil populations implies certain consequences for the evolution of *P. muscorum.* During the Middle and Upper Pleistocene, *P. muscorum* was the subject of morphological variations identical to those recently observed, demonstrating the lack of any evolutionary change. Nevertheless, the species present a stable global morphological equilibrium, as a result of internal and external (i.e. climatic) constraints, which the analysis of the shell ontogeny can help us to characterise.

### ***Ontogeny of* Pupilla muscorum**

Two main points must be recalled:

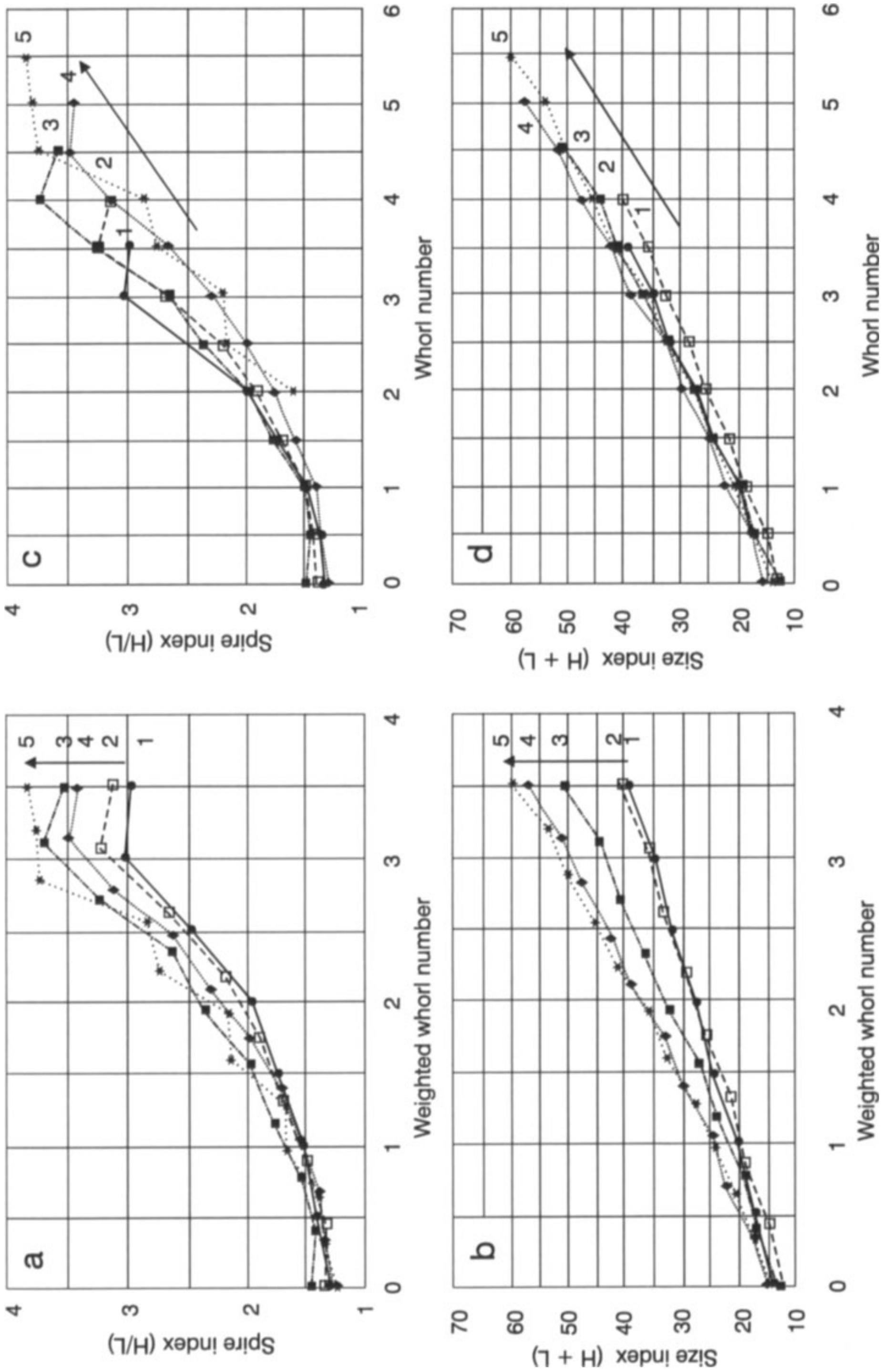
1. an individual has its own trajectory corresponding to changes in the growth rate during ontogeny with the acquisition of the pupiform morphology;
2. differences appear in ontogenic trajectories of individuals from the same population.

These two conditions determine the limits in the global timing of growth for *P. muscorum.*

Size has to be disregarded initially in order to characterise the (heterochronic) process(es) (*sensu* Gould 1977; McNamara 1986) responsible for these morphological variations. The shells studied were at the adult stage (see above for adult criteria). The number of whorls was taken as a standard reference for age because they are more representative of the growth pattern, and adult characters are expressed on the shell at the end of the growth. In order to provide reliable and valuable comparisons between the different morphologies, a reference value is necessary. 3·5 whorls is the lower limit of the adult morphological variability and this value was therefore chosen as the standard value for the 'age character'.

If we consider the spire index (SpL) variations with weighted whorl number (Figure 4a), we note that the values, from common or relatively close origins and through the adult stage, are clearly different. This illustrates a morphological acceleration: compared to the standard trajectory; that studied shows an accelerated rate of morphological development during the juvenile stages of the growth. A similar result is obtained for size index (SI) vs. weighted whorl number (Figure 4b). If we consider the Spire (SpL) and the size indexes (SI) variation with unweighted whorl number, we note that an acceleration is linked with a hypermorphosis: extension of the juvenile growth period caused by a delay in maturation. This provides the size variation (as a consequence of the acceleration, Figure 4). Acceleration-hypermorphosis is one of the possibilities for hyperamorphosis *sensu* Dommergues *et al.* (1986). At this stage of the analysis, it is tempting to be satisfied with these results. One may argue the importance of the role of two heterochronic processes. Nevertheless when variations of angle ß are examined with respect to weighted whorl number (Figure 5), clear differences exist at the end of the protoconch with similar magnitude to those occurring in the adult stage. This result implies that with a relatively equal height, the protoconchs have a comparable width. Angle ß is not the same in one morphology as another. Consequently, the shape of the aperture of the protoconch is not the same in the different cases, which has an immediate repercussion on the following whorls. These initial variations of angle ß permit understanding of how the shell shape is channelled, leading to fat or slim morphologies. If the angle is high, according to the pupiform schema, the value of the angle will become progressively reduced and the shell will be slimmer. On the

**Figure 4:** Reference ontogenetic trajectories established. 1. with weighted whorl number: a) variation in spire index SpL; b) variation in size index SI. 2. with non-weighted whorl number: c) variation in spire index Spl, d) variation in size index SI. (1 = 3·5, 2 = 4, 3 = 4·5, 4 = 5 and 5 = 5·5 whorls.)


a
b
c
d
Spire index (H/L)
Size index (H + L)
Weighted whorl number
Whorl number
1
2
3
4
5
0
1
2
3
4
5
6
10
20
30
40
50
60
70

other hand, if the angle is proportionally low, the value of the angle will become progressively larger and consequently, the shape morphology will be fat. There are no heterochronic processes involved to explain the shape variations. All are determined by the protoconch morphology.

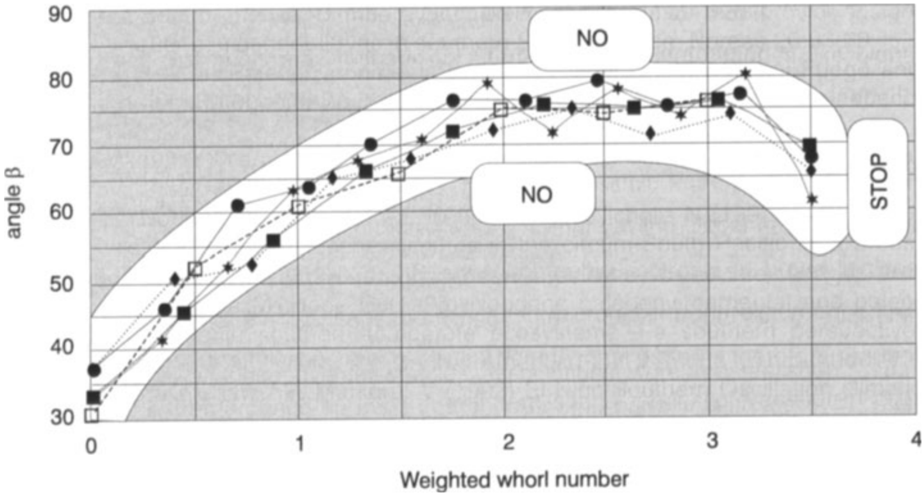


**Figure 5:** Channelling of the morphology as expressed by angle β in its variations versus the weighted whorl number. (Same conventions as in Figure 4)

DISCUSSION

Size variations between individuals or between populations seem to be the result of the combined interplay (more or less pronounced) of acceleration and hypermorphosis, if a shell with 3·5 whorls of spire is considered as a standard reference. Also, this variation will be more evident in an inter-population than in an intra-population context because of environmental contraints. The shape variation (slim–fat) is directly induced right from the protoconch by the angle ß which contrains the coiling of the rest of the shell. Variations of ß with regard to the weighted whorl number demonstrate that ß also has an impact on the size of the shell and that it characterises the internal constraints that act on the shell of *P. muscorum*. The smallest shells have 3·5 whorl spires, the largest 5·5. Considering the mean values at the end of the protoconch, we note that these two limits correspond to the lowest values for the ß variations. Intermediate morphologies show higher ß values. All of them determine the structural limits imposed by the pupiform scheme of growth. This explains why recent morphological variations of *P. muscorum* are identical to those observed during the glacial–interglacial cycles, although a pleniglacial climate cannot be attributed to present-day central Europe. It appears that in the two types of situation, the organism approaches the two limits of its morphological variation, which it cannot overstep. Based on these results, although it does not appear in the literature, the intra-population variation may also be interpreted as the result of the occurrence of heterochronic processes.

After eliminating the problem of the standard reference of age, absolute age correlations must be attempted by choosing the biological age (represented by the weighted whorl number) rather than the size of the shell. The real duration of post-embryonic growth in *P. muscorum* can be expected to be annual, based on observations made on living individuals in the laboratory (DD Rousseau, unpublished data). How can the modifications of the growth rate be explained? The existence of modifications in the growth cycle have been confirmed at different latitudes and altitudes in pulmonate gastropods (Tompa 1984). In *Arianta arbustorum*, a taller snail (HTC = 10–22 mm and LTC = 14–28 mm) than *P. muscorum*, individuals in central Europe, for example, are sexually mature at 3 or 4 years. Populations from France and western Germany, however, are adult at the first or second year of life (Terhivuo 1978). Uminski (1975) has demonstrated that *Vitrina pellucida* and *Semilimax kotulai* in Poland have two different growth cycles depending on the altitude at which they are found on the same slope. Below 1200 m, the growth cycle is annual, whereas above 1200 m it is bi-annual. These facts confirm the dependence of maturation and growth of pulmonates on temperature (Raven 1975). Logically, a gradient, both N–S and E–W, seems to appear where the age of the organisms at maturity is doubled. The same rule can plausibly be applied to *P. muscorum.* The non-weighted number of whorls is thus the most representative characteristic of the absolute age of the organism rather than its size. In these conditions, if we refer to the previously defined trajectories, it is evident that morphological acceleration during the juvenile stage becomes dominant. However, there is a paradox, because this acceleration actually corresponds to a graphic morphological prolongation of growth in response to environmental stress. This acceleration characterises the modification of the rate of calcium carbonate secretion during the infant stage. The final hypermorphosis is only the apparent consequence of the modification of the growth cycle initiated by temperature.

Intra-population variation is reflected in both size and shape fluctuations of the shell. Numerous intermediate morphologies exist between a fat shell (low protrusion of the aperture) and a slim shell (high protrusion of the aperture). These morphologies are due to differences occurring right from the protoconch in terms of the aperture angle, without any indication of heterochrony. The inter-population variation is mainly characterised by important fluctuations in shell size due to the combined interplay of acceleration and hypermorphosis, or of neoteny and progenesis, in accordance with the morphological type taken as reference. This variation is identical to that demonstrated among recent populations for *P. muscorum* and is related to the environment.

From a temporal point of view, identical variations have been recorded during the Quaternary, in parallel with climatic variations corresponding to successions of cooling and warming. In such conditions, a 'mutation–selection' mechanism, as described in the literature, is not necessarily the explanation of these temporal variations. Simply an alteration of the ontogenic sequence in response to environmental stress can be proposed. During the infant phase, which corresponds to the more stenoecious stages of the animal, important structural variations occur which consequently lead to a larger or smaller size with the presence or absence of a supplementary part of a whorl. We remain in the intraspecific realm, and on the basis of results obtained for modern shells, these morphological oscillations have to be described as ecophenotypic (Rousseau 1985, 1989; Rousseau and Laurin 1984; Solem 1986).

## CONCLUSIONS

Based on previous results, we can characterise the constraints acting on *P. muscorum* morphology. In the morphological space of *Pupilla*, *P. muscorum* morphology is channelled by a pupiform framework (fat or slim), which represents the phylogenetic background. Organisation and stimulation of the mantle cells (structural constraints) permits the elaboration of a supernumerary portion of a whorl (functional constraints) in response to climatic stress (environmental constraints). Morphological variation of *P. muscorum* must be understood in a dynamic way as the result of heterochronic processes (acceleration–hypermorphosis or neoteny–progenesis) regulating and channelling the internal and external constraints.

Such morphological stability reinforces the adaptative potential of this species with regard to its environment. Variations in recent *P. muscorum* have been related to environmental parameters. Two complementary data sets confirm this interpretation in fossil populations. In this way the morphological variations in *P. muscorum* during the Middle and Upper Pleistocene do not express any evolutionary trend. The species is in a global morphological and evolutionary stasis. Nevertheless, the phenotypic expression presents important intra- and inter-population variations which, analysed using ontogenic trajectories, define the potential morphological landscape.

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