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CHARACTER SHIFT IN THE NATICID GASTROPODS FROM THE BADENIAN (MIOCENE) OF POLAND

Abstract. — *Natica millepunctata* from Korytnica is as elongate as *N. helicina* sympatric with it, whereas *N. millepunctata* from Nawodzice (the only naticid species at this locality) is significantly more globose than both the Korytnica naticids. It is here postulated that this intraspecific morphological differentiation resulted from either a convergent character displacement, or a divergent character release. Character shift has also been detected in shell size of *N. millepunctata*. The shifts were related to interspecific competition for food.

INTRODUCTION

Natica helicina Brocchi and *N. millepunctata* Lamarck occur very commonly in shallow-sublittoral deposits of the Polish and European Neogene. However, they show a significant intraspecific variation which prompted several authors to distinguish within each of these species some subspecies or varieties (Anderson 1960; Janssen 1969). In fact, the comparison of the Badenian (Miocene) populations of *N. millepunctata* from Korytnica and Nawodzice demonstrated that they distinctly differed in shell morphology. The present paper is just intended to analyse in some detail this intraspecific morphological differentiation and its relationship to the naticid paleoecology.

The geological setting of Korytnica and Nawodzice has been studied by Radwański (1969) and Szubzda (1973), respectively.

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PALEOECOLOGY

All the Naticidae are very active ubiquitous predators securing their food by boring shells of infaunal and semi-infaunal mollusks. One may claim that the Polish Badenian naticids bored each shell they found in

the sediment, which would account for the relatively high level of cannibalism and interspecific agression observed in their populations. Their feeding habits have recently been analysed (Hoffman *et al.* 1974; Hoffman and Szubzda 1976).

The Korytnica naticid populations displayed high constant mortality rates (figs 1 and 2) dependent mainly upon the abundance and distribution of food, and the level of both intra- and interspecific agression and

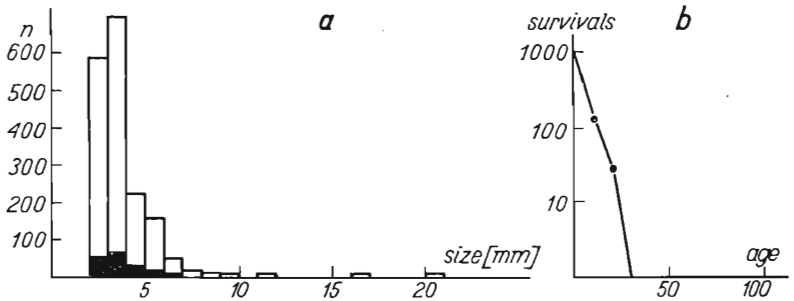

Fig. 1. Mortality pattern of *Natica millepunctata* Lamarck from Korytnica. Sample size n = 373, *a* size-frequency distribution (in each size-class the proportion of specimens drilled by the naticids is shown), *b* survivorship curve.

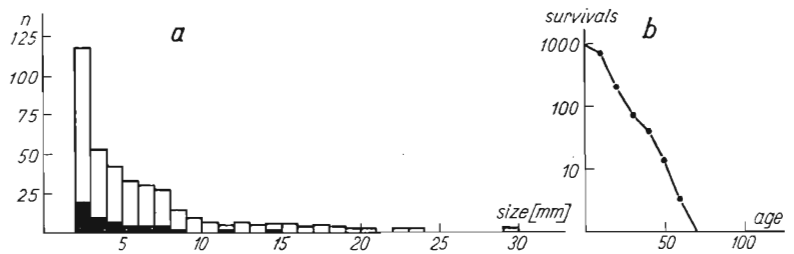

Fig. 2. Mortality pattern of *Natica helicina* Brocchi from Korytnica. Sample size n = 1766, *a* size-frequency distribution, *b* survivorship curve.

competition. This indicates that they were K-selected.

As judged by the criteria of Shuto (1974), the protoconch morphology of the Polish Badenian naticids suggests that their larvae were of lecithotrophic type.

APERTURE GROWTH

In the naticids, the foot plays an extremely important adaptive role since the stronger it is the larger and stronger prey the animal can capture and hold (Berg and Nishenko 1975), and the easier is the burrowing process (Trueman 1968). Size of the foot appears to be directly related

to the aperture area. The latter grows as a square of linear shell dimensions, whereas the body weight the foot should keep pace with, increases as a cube. Thus, their ratio must decline progressively with age if geometric similarity of the gastropod shell is retained. Therefore, growth modifications are required in order to maintain the functional similarity.

As it was shown by Gould (1968), there exist three strategies intended to prevent a collapse, that is drop of the gastropod-foot strength below the margin of safety. The foot can either grow with positive allometry, strengthen itself structurally without any external allometry, or exhibit preparatory growth. In *N. millepunctata*, the aperture area grows with a slight but statistically significant positive allometry relative to the shell height (fig. 3). However, the degree of this allometry appears to be inadequate to maintain the constancy of surface to volume ratio.

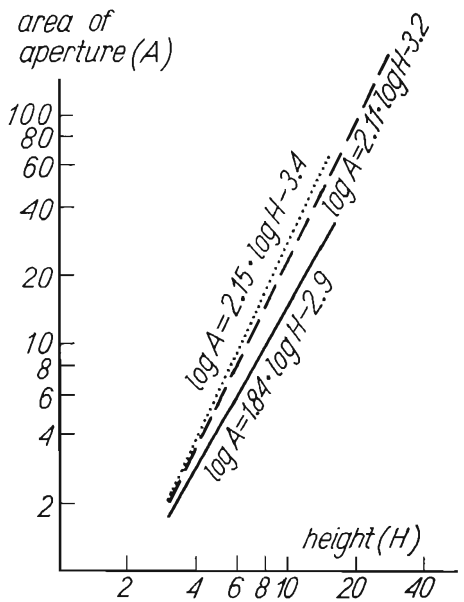

Fig. 3. Relative growth of the area of aperture with the height of shell solid line — *Natica helicina* Brocchi from Korytnica (sample size n = 142, dashed line — *Natica millepunctata* Lamarck from Korytnica (sample size n = 127), dotted line — *Natica millepunctata* Lamarck from Nawodzice (sample size n = 187).

N. helicina exhibits even a negatively allometric growth of the aperture area (fig. 3).

Hence, one may conclude that the Korytnica naticids chose either structural strengthening the foot, or its preparatory growth as the main strategy of overcoming the constraints of foot capacity on ontogenetic increase in body weight. They did so in common with many other gastropods (Gould 1968, 1969).

SHELL ELONGATION

The populations of *N. millepunctata* from Korytnica and Nawodzice were distinctly different in the shell elongation (fig. 4*b*-*c*). As indicated by the apparent similarity in the ontogeny of their aperture (fig. 3), this difference in shell elongation reflects variation in the rate of whorl movement from the coiling axis, all the other basic parameters of gastropod-shell growth (Raup 1966) remaining the same.

Because of this difference in shell elongation, the question could be raised whether or not these two populations do actually represent the

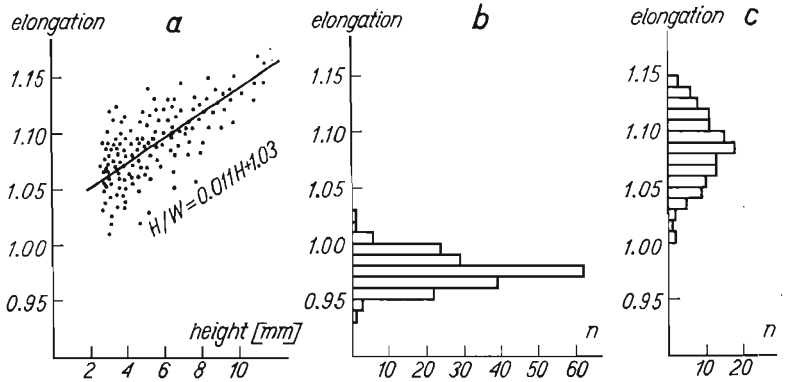

Fig. 4. Shell elongation *a* relative growth of the elongation of shell with the height of shell in *Natica helicina* Brocchi from Korytnica (sample size n = 142; correlation coefficient r = 0.72), *b* histogram of the elongation of shell in *Natica millepunctata* Lamarck from Nawodzice (sample size n = 187; correlation coefficient r = 0.11), *c* histogram of the elongation of shell in *Natica millepunctata* Lamarck from Korytnica (sample size n = 127; correlation coefficient r = 0.09).

same species. The present author is of the opinion that naticid species should be treated very widely, maybe as polytypical ones. Otherwise, the common co-occurrence of many similar phenotypes would be inexplicable. The naticid species are ecologically so similar one to another that such a co-occurrence of very large populations of these active but non-selective predators should result in an enormous interspecific competition and agression. This should in its turn cause significant fluctuations in population size or even a collapse of the ecological system. On the other hand, the co-occurring naticid phenotypes distinctly intergrade into one another (Janssen 1969); they appear so closely related genetically (as judged from the morphological relationships) that a significant hybridization might be expected. When reproductively independent populations of a widely defined species are considered, each one can contain various proportions of particular phenotypes. And, indeed, the associations of phenotypes of both *N. helicina* and *N.millepunctata* appear to be recurrent in the European Neogene although the particular phenotypes (i.e. subspecies or

varieties, or even related species) occur in somewhat different proportions (Kojumdgieva 1976; Venzo and Pelosio 1963; Janssen *l.c.*).

Hence, the populations of *N. millepunctata* from Korytnica and Nawodzice are to be regarded as truly conspecific. The difference in shell elongation may therefore be postulated to have arisen from a natural selection in reproductively independent populations. In fact, the independence of these populations is strongly substantiated by the lecithotrophic type of larvae, which restricted the migration ability.

The natural selection leading to this morphological difference might be postulated to have been induced by some physical environmental factors. When all paleogeographical and paleoclimatological data available on the Polish Badenian marine facies are taken into account, the substrate type and its derivatives appear to be the only environmental characteristics significantly different from Korytnica to Nawodzice. In fact, the Korytnica basin represents a clayey facies, while the Nawodzice outcrop represents a sandy facies. However, Friedberg (1911—1928) reported both the phenotypes of *N. millepunctata* from the Podolia sandy facies, which indicates that both were able to survive in a physical environment like that at Nawodzice. Therefore, this divergent natural selection in *N. millepunctata* may rather be postulated to have resulted from some biotic factors.

For *N. millepunctata*, the most important difference between the ecosystems of Korytnica and Nawodzice was probably the presence in the Korytnica basin of a very large population of another naticid species *N. helicina* which lacked at Nawodzice. One may expect that the ecological characteristics of the naticids resulted in the Korytnica basin in an intense interspecific competition and agression which could not be entirely overcome by increasing the intrinsic rate of reproduction since the mortality rates were, at least in part, density dependent. Hence, the morphological difference between the Korytnica and Nawodzice populations of *N. millepunctata* appears to represent an effect of character shift (*sensu* Grant 1972; Eldredge 1974).

Unfortunately, both the phylogeny of *N. millepunctata* and its relationship to *N. helicina* remain unclear. One cannot recognize whether the original character state was represented in allopatry or in sympatry. Therefore, it is impossible, at least for the moment, to decide whether the morphological difference between its populations from Korytnica and Nawodzice does actually represent the effect of character displacement or character release.

N. millepunctata from Korytnica is just as elongate as *N. helicina* sympatric with it, whereas *N. millepunctata* from Nawodzice is significantly more globose than both the Korytnica naticids (fig. 4). It is here postulated that this resulted from either a convergent character displacement, or a divergent character release.

Shell elongation appears to influence the naticid burrowing ability. One may expect a more elongate shell to be more easily pulled through the bottom sediment, the body weight and foot strength being equal; hence, the energy expense necessary to find a suitable prey would be lower. Therefore, in a zone of intense interspecific competition for food, the natural selection should tend to prefer the elongate phenotype of *N. millepunctata* over the globose one, just as it happened in the Korytnica basin. The dominance of the elongate phenotype of *N. millepunctata* has also been reported from other Miocene communities characterized by the co-occurrence of many large naticid population (Venzo and Pelosio 1963; Janssen 1969).

Shell elongation could, however, be genetically correlated also with some other ecological or physiological features which might cause a lower adaptedness of the elongate phenotype relative to the globose one under conditions of relaxed interspecific competition. This would explain dominance of the globose phenotype in areas where it represented the only naticid population.

SHELL SIZE

The variation in maximum size of *N. millepunctata* has not been studied quantitatively. However, purely qualitative analysis of the paleontological collections consisting of several hundreds of specimens indicates that *N. millepunctata* attained a considerably larger size at Korytnica than at Nawodzice. At Nawodzice, the maximum size of *N. millepunctata* was approximately 20 mm, i.e., it was just like that observed commonly in *N. helicina*. At Korytnica, the largest shells attained some 30 mm in size.

This difference in shell size (and by implication body size) between the populations sympatric and allopatric with *N. helicina* can also be postulated to reflect a character shift in *N. millepunctata*. The shift could actually represent either a divergent character displacement, or a convergent character release.

Increase in body size appears to be highly adaptive in the naticids since it allows to attack also a larger prey, that is to utilize food resources which would otherwise be unexploited. In other words, divergence in body size of two co-occurring naticid populations represents a simple mechanism of buffering the interspecific competition by focusing the feeding interests on different prey populations. Such divergent trends in body size are commonly observed in co-occurring closely related species (Grant 1965, 1968; Schoener 1970; Fenchel 1975).

Therefore, the natural selection arising from the intense competition with *N. helicina* tended in the Korytnica basin to prefer the larger-sized

phenotype of *N. millepunctata* over the smaller-sized one. At Nawodzice, the latter phenotype was preferred because all other remaining the same, the smaller-sized predators need less prey for survival than do the larger ones.

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MIKROEWOLUCYJNE PROCESY MORFOLOGICZNE WŚRÓD MIOCEŃSKICH ŚLIMAKÓW Z RODZINY NATICIDAE

Streszczenie

Natica millepunctata występująca w Korytnicy jest równie wysmukła jak sympatryczna z nią *N. helicina*. Natomiast *N. millepunctata* występująca w Nawodzicach, gdzie jest jedynym przedstawicielem rodziny Naticidae, jest znacznie bardziej pękata od obydwu populacji korytnickich. Przy dzisiejszym stanie wiedzy o filogenezie rodziny Naticidae nie można rozstrzygnąć, czy to zróżnicowanie kształtu muszli *N. millepunctata* to skutek konwergencji z *N. helicina*, czy też mikroewolucji dywergentnej. Efektem podobnego procesu mikroewolucyjnego jest zmienność maksymalnej wielkości muszli *N. millepunctata*. Obydwa procesy mikroewolucyjne to skutek międzygatunkowej konkurencji o pożywienie wśród naticidów współwystępujących w basenie korytnickim.

АНТОНИ ХОФФМАН

МОРФОЛОГИЧЕСКИЕ ПРОЦЕССЫ МИКРОЭВОЛЮЦИИ СРЕДИ МИОЦЕНОВЫХ БРЮХОНОГИХ СЕМЕЙСТВА NATICIDAE

Резюме

Natica millepunctata, встречающаяся в Корытнице, является также стройной, как и симпатричная с ней *N. helicina*. В то же время *N. millepunctata*, встречающаяся в Наводицах, является единственным представителем семейства Naticidae и имеет значительно более утолщённую форму по сравнению с обеими корытницкими популяциями. При современном уровне познания филогенеза семейства Naticidae невозможно установить, является ли это различие формы раковины *N. millepunctata* последствием конвергенции к *N. helicina* или же последствием дивергентной микроэволюции. Эффектом подобного микроэволюционного процесса является изменение максимальных размеров раковины *N. millepunctata*. Оба микроэволюционные процессы являются последствием межвидовой конкуренции в борьбе за пропитание среди натицидов, выступающих совместно в корытницком бассейне.