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THE PRINCIPLE OF "FROZEN EVOLUTION" AND ITS MANIFESTATION IN THE FOSSIL RECORD: THE BRACHIOPOD GENUS *AEGIROMENA* HAVLÍČEK, 1961 (UPPER ORDOVICIAN, CZECH REPUBLIC)

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Introduction

The theory of frozen evolution (Flegr 1998, 2006, 2008) assumes that a sexually reproducing biological species loses relatively quickly (in terms of geologic time) the ability to respond to selection forces produced by the environment, because "centripetal" tendencies unifying the population became stronger than the tendencies increasing the population variability (e.g., natural selection). The "centripetal" effect is similar no matter whether we consider the (Darwinian) selection between individuals or the Neodarwinian (intra-allelic) competition. The theory of frozen evolution was found promising among some Czech palaeontologists after its more exoteric formulation and publication in the Czech language (Flegr 2006). The reasons are the following: First, the theory elaborates on the concept of Punctuated Equilibrium (Eldredge and Gould, 1972), which is generally well accepted in palaeontology; in addition, it adds a broader context (namely genetic data, effect of sexual reproduction, and concepts of evolutionary stable strategies) to a "bare" sequence of evolutionary events recorded in sedimentary rocks. Secondly, the theory does not exclude palaeontological data from the attempts to reconstruct the biological evolution and its controlling principles, as methodically (and rather mechanically) done by some of the competing attitudes. Thirdly, Flegr (2006, 2008) understood and accepted palaeontology as a historical science, producing the best results by suggesting plausible reconstructions of past events and processes based on multiple ways of reading the fossil record, not by a mechanical conversion of data to simple, "irrefutable" entities.

The aim of the present contribution is (besides the introduction of a case study) to initiate the discussion on how palaeontological data can be used to test the theory of frozen evolution: which requirements are to be applied to a set of entery (entered ?) data; which limitations are to be held in mind anyway, and which approach is to be adopted for testing the whole theory - not only its particular resources (e.g., the punctuated equilibrium).

Character of the fossil record

It is evident that not each presumed evolutionary line preserved (always *incompletely* preserved) in the fossil record is suitable for testing evolutionary theories. Moreover, a yet smaller proportion of evolutionary lines can yield information relevant to the theory of the frozen evolution. The restraints are as follows: 1, incompleteness of the fossil record, or, more precisely, excessive duration between well-recorded "windows to the past". For instance, if a set of strata representing a 20-million year time interval contains only four highly fossiliferous beds, the "sampling time" was too long for recording high-frequency changes of an evolutionary line; 2, a statistically insufficient number of specimens suitable for study; 3, the impossibility to substantiate convincingly the causation of the morphological change whose "plasticity" is to be tested. For instance, we may not be able to infer whether the reduction of eyes was caused by a shift of the populations to dysphotic zones, or by a turn to a chiefly infaunal (intra-sediment) habitat. In this case, we do not know which environmental changes are to be monitored to recognize "plastic" or "frozen" response of the population to these changes.

Thereby, the study material (1) should be obtained from non-condensed, richly fossiliferous sedimentary sequences, ideally from a palaeogeographically well-understood region, (2) should be abundant, and (3) should display a character whose presence/absence/variability can be assigned (by deduction or by a recent analogy) to a single parameter of the environment. (4) This parameter itself has to be well recorded and unequivocally recognizable in the set of strata.

Brachiopods of the genus *Aegiromena*; geological settings

Collections of the brachiopod genus *Aegiromena* Havlíček, 1961 from the Upper Ordovician of the Prague Basin (Barrandian area, Czech Republic) represent palaeontological material, which seems to meet the above outlined criteria. *Aegiromena* is a small strophomenid brachiopod; the width of adults reaches 8-20 mm; usual length is 5-10 mm. Pedicle valve is slightly convex and brachial valve is concave; therefore, the internal volume of the shell is very low. *Aegiromena* is known from the Upper Ordovician of the peri-Gondwanan region, with most representatives found in the Prague Basin (e.g., Havlíček 1967).

For the geological settings of the Upper Ordovician of the Prague Basin see, e.g., Havlíček (1999). The section shown in Fig. 1 herein (i.e. from the base of the Vinice Formation to the top of the Králův Dvůr Formation) is characterized by rather rapid, continuous sedimentation in a shallow sea, with no hiatuses and no recognizable omission surfaces. Most of the section is fossiliferous; the author found ca 1,100 specimens of *Aegiromena* spp. at various stratigraphic levels during his documentation of temporary outcrops in 1978-1986.

In the case of *Aegiromena*, the length/prolongation of the cardinal margin by sharp marginal "ears" can be regarded an "understandable character" which can be observed and interpreted in terms of evolutionary plasticity/rigidity. The prolonged cardinal margin was selectively advantageous on silty to carbonate/silty bottoms (classical softgrounds passing rather to firmgrounds than to "soupgrounds"), where it functioned as an anchor of the valve keeping it in an appropriate orientation towards waves and currents. On the contrary, on very soft (clayey) substrates, the prolonged cardinal margin could not work as an anchor; it probably even increased the probability that the specimen will appear at a wrong position in the sediment. The character of the bottom can be reconstructed from the petrographical composition of the rock.

The palaeogeographical aspect cannot be discussed herein at large. In brief, *Aegiromena* is rather a highly provincial form, and it cannot be expected that the changes of its populations during the geological time were highly influenced by faunal migrations or by palaeogeographic changes (e.g., the principle of geodispersal). For the classification of *Aegiromena* on a specific level (however complex and sometimes subjective) see Havlíček (1967) and Mikuláš (1996a).

The collection has already been studied by the author (Mikuláš 1996b), however, with a different purpose than the present study. Mikuláš (1996b) aimed to ascertain whether the shape of the shell was sensitive to the bottom composition *in any aspect*, which would support the idea of benthic life of *Aegiromena*. The relation between the substrate and the shape was demonstrated (Mikuláš 1996b); however, even this early study indicated a diminishing response to the substrate change during the geologic time.

Results

The results are summarized in Fig. 1; characteristic features of the studied brachiopod genus, as seen on real specimens, are shown in Fig. 2. A simplified geological section (Fig. 1 left) shows that during the time of existence of the studied evolutionary line the marine basin was filled chiefly with clay or silt material, with three incursions of carbonatic/ferritic oolites. Silts and oolites represented firmer bottoms, whereas the clayey bottoms may have been close to "soupgrounds".

In the study area, representatives of *Aegiromena* first appeared on silty or even silty/sandy substrates of the Letná Formation (underlying the Vinice Fm. shown in Fig. 1), already bearing a prolonged cardinal margin and sharp (but not "prominent", "long") ears. The material from the Letná Formation, however, is not involved in the present study, for the following reasons: 1, the collected material is not numerous; 2, it occurs in different rocks (chiefly sandstones) compared to the younger representatives of *Aegiromena*; therefore, the populations lived probably on sandy bottoms; effect of the enlarged cardinal margin on such substrates has not been considered yet; 3, no continuous fossil record is known form the Letná Formation; instead, rather isolated occurrences of fauna in otherwise non-fossiliferous rocks were ascertained; 4, considering the inner structures (namely, septa and muscular imprints), two different species of *Aegiromena* are probably concerned; one of them shows close relationships to the potential precursor of the whole evolutionary line, i.e. *Aegiromena mariana* Drot, occurring in early Middle Ordovician of the Mediterranean region. The above-mentioned points suppressed the uniform and "easily understandable" character of the fossil record required for the study (see above the paragraph "Character of the fossil record"). The precursor of the studied evolutionary line can be, anyway, identified among the representatives of *Aegiromena* in the Letná Formation; further collection of data and research is needed to clear this point.

The Vinice Formation is composed chiefly clayey shales with silty admixture; its degree of mixing by in-fauna is usually low, and, therefore, it can be understood as "average" substrate from the "point of view" of *Aegiromena*. Silts of the overlying Zahořany Formation hosted the best-developed "long-margin" populations. The first prominent incursion of fine clays (on top of the Zahořany Formation) corresponded to a shortening of the cardinal margin. The subsequent return to the relatively firm bottom (base of the Bohdalec Fm.) was marked by the return of rather long-margin, sharp-ear forms of *Aegiromena*. In the history of the evolutionary line, it was, however, the last return to this shell shape. Further incursions of firmer bottoms induced only a negligible prolongation of the cardinal line and sharpness of the ears. *Aegiromena* disappeared from the fossil record before the end of the Ordovician, prior to the dramatic palaeogeographical and climatic changes leading to the end-Ordovician mass extinction.

Conclusions

The presented study is in a good agreement with the idea of a "frozen evolution" of the genus *Aegiromena*, or, more precisely, it illustrates a gradual disappearance of the ability to respond to the environmental change by a selectively advantageous change in its morphology. Further evolution of *Aegiromena* (after its "freezing") brings very little news; only subtle changes in the size of adults, subtle and variable changes in the width/length ratio, and a changing variability of muscular imprints can be noted.

The presented result – both the form of its presentation and the (much reduced) discussion – should be considered preliminary. However, it was written with the aim to initiate discussion and criticism, and to specify the palaeontological attitude to testing evolutionary models, particularly the idea of frozen evolution.

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Fig. 1. Left: Simplified geological section of the mid-Upper Ordovician of the Prague Basin (modified after Havlíček 1977). Not to exact scale; the overall thickness of the section varies from few hundred metres to nearly 1,000 metres. Dashed area = siltstones; white area = claystones; black lenses: ferritic and carbonatic oolites; multiform bars = volcanic products. Right: "Average" outline of shells of *Aegiromena* sp. during their growth in various horizons. Scale in millimetres. The measured characters involve the valve width, length, the angle between the front margin and the cardinal margin, and (if appropriate) the length of the "ear". Except the youngest occurrence, the average outline was constructed form data obtained from dozens of individuals.

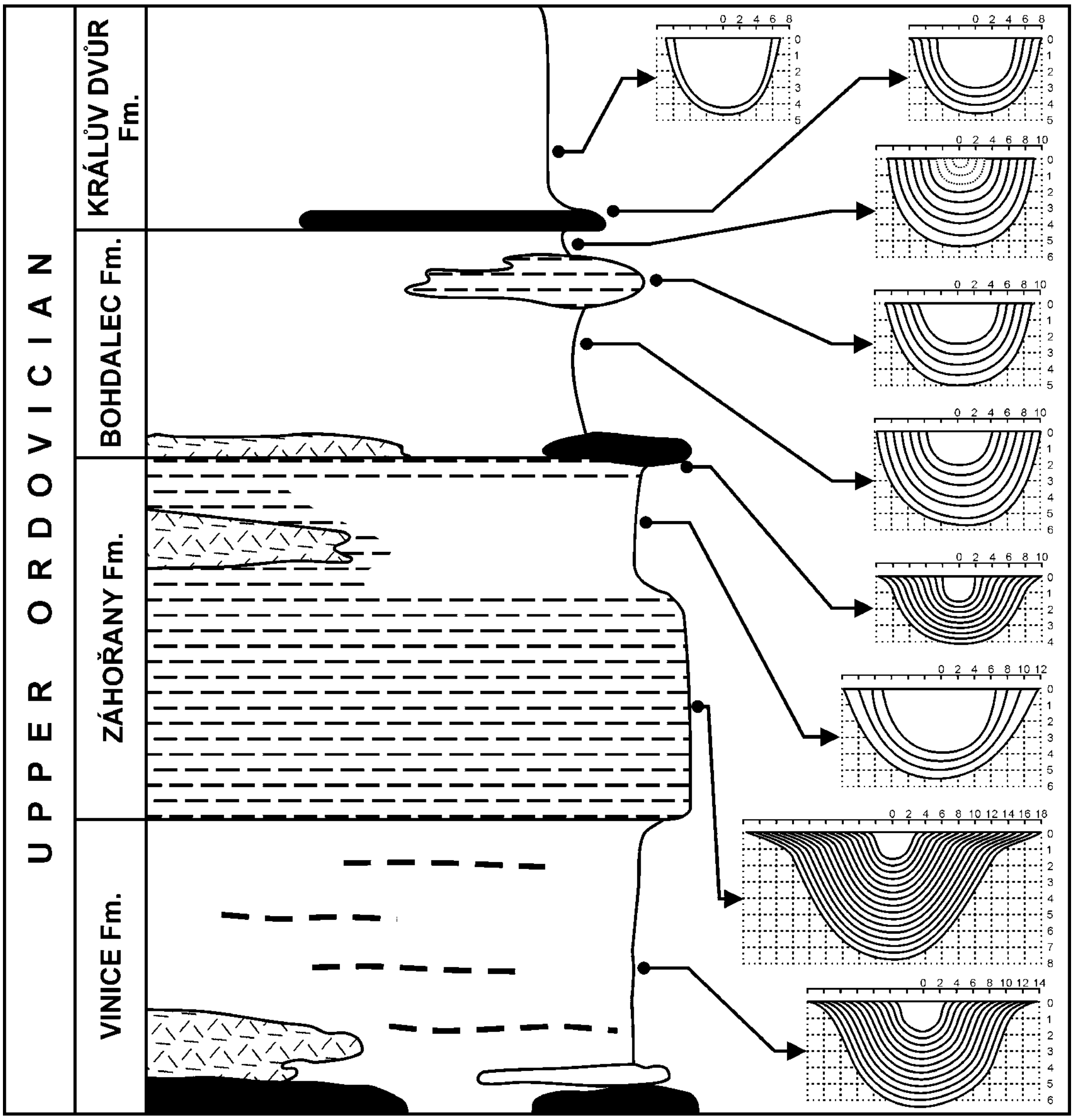

Fig. 2. 1-2: *Aegiromena praeultima* Mikuláš, 1982; base of the Kraálův Dvůr Formation, Podolí iron ore horizon; Vlnitá locality, Praha 4; enlarged x 12.0. 3-4: *Aegiromena descendens* (Havlíček, 1952); *Polyteichus* facies of the Bohdalec Formation; Na Strži locality, Praha 4; 3 – x 8.5; 4 – x 8.0. 5-6: *Aegiromena* aff. *descendens* (Havlíček, 1952); Karlík iron ore horizon at the base of the Bohdalec Formation; Praha-Spořilov; x 7.5. 7-8: *Aegiromena* aff. *descendens* (Havlíček, 1952); clayey shales of the top of the Zahořany Formation; Praha-Krč; 7 – x 6.5; 8 – x 8.5. 9-10: *Aegiromena aquila aquila* (Barrande, 1879); siltstones of the Zahořany Formation; Praha- Modřany; x 5.0. All photos by R. Mikuláš