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A bearer of population paleontology

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Ever since the early days of paleontology, invertebrate paleontologists have received important stimulation regarding the principles and methods of evolutionary study from eminent vertebrate paleontologists. The late Professor Björn Kurtén was clearly such a distinguished mammalian paleontologist, far ahead of his time. Although I am neither his pupil, nor a vertebrate investigator, he was, by a happy chance, so influential upon the formation of the concept and method of population paleontology in my youth, that it is my pleasure to contribute a short article to this memorial volume.

When I was a beginning graduate student in my present institute, Professor F. Takai, the head of the paleontological seminar at that time, asked me to read and introduce one of Björn's latest works. It was "Contribution to the history of a mutation during 1 000 000 years" (Kurtén, 1955), in which two forms of the first upper molar of *Ursus* were interpreted as being due to allelomorphism. Because I had no background knowledge on this subject, my introduction at the seminar must have been very incoherent. I felt, however, that there was something innovative and ambitious in this paper, and this experience still remains fresh in my memory, though I am not aware how Björn's interpretation has been accepted by subsequent investigators.

In spite of the establishment of the synthetic theory of evolution and the resultant revolution in systematics in the early 1940's, the population concept was still in the minority among paleontologists at that time. In Japan, the concepts of "new systematics" and "new paleontology" (e.g. Huxley 1940; Mayr et al. 1953; Sylvester-Bradley 1956) began to filter through to young paleontologists after 1957, when Professor T. Hanai presided over a reading circle in our institute.

Many years later, I encountered a significant sculpture dimorphism in the fossil and living populations of a Pliocene–Recent pectinid (scallop), *Cryptopecten vesiculosus* (Dunker) from south Japan. I realized the necessity of abandoning the concept of morphospecies and of distinguishing the concepts of phenon and a taxon. Though Pliocene and Early Pleistocene samples of this species are monomorphic, every Late Pleistocene–Recent sample contains mutant individuals, the relative frequency of which seems to have gradually increased over these 500 000 years. As a result of collecting living specimens, it became clear that the two phenotypes are strictly sympatric at every locality and have one and the same breeding season. The wild-type individuals show strong and quadrate radial costae, while the mutant ones are characterized by weak and rounded radial costae. No individual is morpho-

logically intermediate between the two phenotypes, and the evolutionary pattern can be recognized as currently ongoing phenotypic substitution (or transient polymorphism). The detailed genetic background of this dimorphism (i. e. dominant-recessive relation) and the cause of the phenotypic substitution (i. e. natural selection or random genetic drift) are not still clear, but I recognized that microevolution can be elucidated at least phenomenologically in paleontology (Hayami 1973, 1984). It is needless to say that my dim recollection of Björn's paper as well as subsequent reading in ecological genetics (Ford, 1964; etc.) triggered my exciting and long–term study on this subject.

Non-sexually determined sculpture dimorphisms may actually be widespread phenomena in fossil and extant pectinids. Sometimes different species-group names have been used for such a pair of phenotypes. As I have discussed in a preliminary manner (Hayami, 1985), *Volachlamys hirasei* (Pilsbry) and *V. awajiensis* (Pilsbry) from west Japan, East China Sea and Yellow Sea are morphologically discontinuous, but are nothing but an intrapopulational dimorphic pair. The former must be the mutant-type and has the nomenclatural priority.

The inferred pattern of evolution is quite similar to that of *Cryptopecten vesiculosus*. Though field evidence is still insufficient, the presence of sculpture dimorphism can be presumed also in the living populations of *Aequipecten commutatus* (Monterosato) from the western Mediterranean, *Pecten puncticulatus* Dunker from south Japan and East China Sea, and *Chlamys dieffenbachi* (Reeve) from New Zealand.

Björn's foresight in evolutionary paleontology can be found here and there in his works. Among other things, he was one of the pioneers in the study of evolutionary rates. We owe the concept of morphologic rate mainly to Haldane (1949) and the idea of taxonomic rate to Simpson (1944, 1953). Björn suggested a different type of evolutionary rate, called the index rate, which took into consideration the change in an allometric pattern (Kurtén 1958). Though the index rate did not become popular, he presented concrete figures for these various rates in many well established lineages of Quaternary mammals, discussing the patterns of evolution and their chronological change (Kurtén 1959a). I was especially deeply impressed by his study of a Pleistocene brown bear lineage, in which the length of the second lower molar was said to have increased during glacial ages and decreased during interglacial ages, because this oscillatory change is consistent with Bergmann's Rule.

Furthermore, Björn's "half-life concept", which assumes a constant rate of faunal turnover, is considered as valid method to estimate the mean longevity of species (Kurtén 1959b, 1972). This concept, though rarely cited in subsequent studies of this kind, was established much earlier than Stanley's (1975, 1977) comparative studies on the evolutionary rates of mammals and bivalves, which were founded on a similar premise. Van Valen's (1973) 'New evolutionary law" seems to demonstrate the adequacy of Björn's idea, because it was mainly derived from enormous empirical data of various taxonomic groups.

In the spring of 1975, I visited Helsinki with one of my colleagues to see Björn for the first time. The maestro, together with Dr. Ann Forstén, entertained us very warmly, and we had a pleasant time at his home around reindeer steaks. On that occasion I found that I shared with Björn not only many thoughts on population paleontology but also enthusiasm for the ecstatic music of Anton Bruckner, the romantic symphony composer. Björn's academic tradition, I think, can be expressed as a harmony of deductive and inductive approaches. His biometric studies were always developed on the basis of sound population concept. Finally, I pray his soul may rest in peace, thanking him sincerely for his kindness and the excellent stimulation thus bestowed on me.

References

Ford, E. B. 1964: Ecological genetics. — Methuen & Co., London. 410 pp.

Haldane, J. B. S. 1949: Suggestions as to quantitative measurement of rates of evolution. — Evolution 3:51–56.

Hayami, I. 1973: Discontinuous variation in an evolutionary species, Cryptopecten vesiculosus, from Japan. — J. Paleontol. 47:401–420.

— 1984: Natural history and evolution of Cryptopecten (a Cenozoic-Recent pectinid genus). — Bull. Univ. Mus. Univ. Tokyo 24:1–149.
— 1985: Systematics and evolution of Volachlamys from Japan (preliminary notes). — Venus (Jap. J. Malacol.) 44:3–13.
Huxley, J. S. 1940 (ed.): The new systematics. — Oxford Press. 583 pp.
Kurtén, B. 1955: Contribution to the history of a mutation during 1 000 000 years. — Evolution 9:107–118.
— 1958: A differentiation index, and a new measure of evolutionary rates. — Evolution 12:146–157.
— 1959a: Rates of evolution in fossil mammals. — Cold Spring Harbor Symp. Quant. Biol. 24:205–215.
— 1959b: On the longevity of mammalian species in the Tertiary. — Comment. Biol., Soc. Sci. Fennica 21:1–14.
— 1972: The 'half-life' concept in evolution illustrated from various mammalian groups. — In: Bishop, W. & Miller, J. A. (eds), Calibration of hominoid evolution: 187–194. Scottish Acad. Press.
Mayr, E., Linsley, E. G. & Usinger, R. L. 1953: Methods and principles of systematic zoology. — McGraw-Hill, New York. 336 pp.
Simpson, G. G. 1944: Tempo and mode in evolution. — Columbia Univ. Press. 237 pp.
— 1953: The major features of evolution. — Columbia Univ. Press. 434 pp.
Stanley, S. M. 1975: A theory of evolution above the species level. — Proc. Nat. Acad. Sci. U.S. 72:646–650.
— 1977: Trends, rates, and patterns of evolution in the Bivalvia. — In: Hallam, A. (ed.), Patterns of evolution: 209–250. Elsevier, Amsterdam.
Sylvester-Bradley, P. C. 1956 (ed.): The species concept in palaeontology. — System. Assoc. Publ. 2:1–145.
Van Valen, L. 1973: A new evolutionary law. — Evol. Theory 1:1–30.