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Comparative spermatology and lower Lepidoptera phylogenesis*

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Lepidoptera appears to be a structurally homogeneous group due to the numerical dominance of the infraorder Ditrysia which comprises about 99% of the species of the order. To determine the evolutive pathway of this successful group of insects, however, it would be necessary to elucidate first the phylogenetic relatioships whthin non-Ditrysia lepidopterans. Only then, an inquiry on the phylogenetic relations between the two infraorders could be attempted. But the classification and phylogenetic position of the lower Lepidoptera groups is still unclear, notwithstanding the serious efforts invested hitherto in the study of this relatively small infraorder that comprises only 1% of the extant Lepidoptera (KRISTENSEN, 1984 ; NIELSEN, 1989). One of the factors contributing to the lack of solution on the question of phylygenetic and systematic relationships within the lower Lepidoptera is, most probably, that the morphological and behavioural characters that have been used until now in the related analyses, are insufficient for solving the problem. Consequently, it will be necessary resorting to additional unorthodox characters to complement the usual ones that have been already scrutinized.

Comparative spermatology can serve this aim. Spermatozoa morpholygy and spermatogenesis have been used as phylogenetic indexes for the study of several insect taxa (BACCETTI, 1979 ; JAMIESON, 1987). That is because spermatogenesis is a very accurate process showing a characteristic pattern which is distinctive among animal species. Deviations from the regular pattern of spermatogenesis lead to reduced fertility or even sterility. Very little, however, has been done in this field concerning classification and phylogenesis of lower Lepidoptera (FRIEDLÄNDER, 1983).

The normal spermatogenesis of higher Lepidoptera is dichotomous producing two kinds of concomitant spermatozoa : nucleate-fertilizing (eupyrene) and anucleate-sterile (apyrene) of unknown function but which reach the spermatheca of the inseminated female (FRIEDLÄNDER and GITAY, 1972). Dichotomous spermatogenesis appears to be an evolutionary novelty of Lepidoptera since it has been found in the lower lepidopteran *Hepialus sequoiolus* as well. It is lacking in the closely related orders Diptera and Siphonaptera and, most significantly, in

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the sister order Trichoptera (FRIEDLÄNDER, 1983). Therefore, the finding that dichotomous spermatogenesis is present in the micropterigid *Epimartyria pardella* strengthened the assertion that Zeugloptera belong to Lepidoptera rather than to a separated order (FRIEDLÄNDER, 1983). Recently, however, it has been reported that micropterigids of the genus *Micropterix* bear only one kind of spermatozoon (SONNENSCHEIN, 1990). If this report was confirmed, it would indicate either that Zeugloptera are paraphyletic or that apyrene (anucleate) spermatozoa have been secondarily lost in *Micropterix*.

The mature intratesticular eupyrene (nucleate) spermatozoon of the higher Lepidoptera (Fig. 1A) is coated by the most complicated surface structures so far known among insect male gametes: (a) the reticular appendage which is a rod of electron-opaque material connected by thin lamellae to the body of the cell and (b) the lacinate appendages which resemble, in transverse sections, sun rays radiating from the body of the cell. In contrast, the surface of the apyrene (anucleate) spermatozoon (Fig. 1B) is plain and free from any

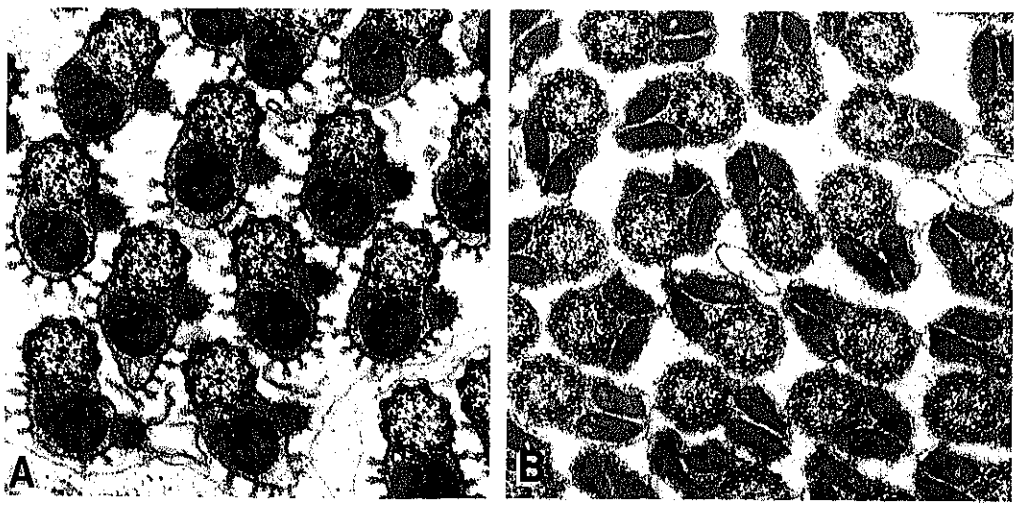

Fig. 1. Transverse sections through flagellae of the (A) nucleate (eupyrene) and (B) anucleate (apyrene) spermotozoa of the ditrysian codling moth *Cydia pomonella*.

appendages (PHILLIPS, 1970). Both kinds of appendages are absent from the spermtozoa surface of the Zeugloptera and Hepialidae so far studied (FRIEDLÄNDER, 1983; SONNENSCHEIN, 1990). If this phenomenon is generalized in the lower Lepidoptera, the appearance of appendage-like structures covering the spermatozoa of a systematic group belonging to the infraorder will indicate a very close phylogenetic relation between this taxon and the higher Lepidoptera. This approach, however, has not been exploited yet.

Additionally, there are several characters of spematogenesis that still have not been used

to this effect, such as the behaviour of the fragellar basal body, shape and distribution of mitochondrial derivatives, acrosome morphogenesis, etc. that could be turned to use to complement the customary characters already employed in phylogenetic studies of lower Lepidoptera.

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