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Amniotic Pore of a Silverfish, *Lepisma saccharina* Linnaeus (Hexapoda: Zygentoma, Lepismatidae)

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Introduction

Heymons (1897) long ago reported that the amniotic pore of *Lepisma saccharina* is not closed by the complete fusion of amnioserosal folds but filled by a cuticular substance or "cuticular plug," a concept with which Sharov (1953) later agreed. Heymons (1897) and Heymons and Heymons (1905) speculated that the amniotic pore as observed in *L. saccharina* represents a primitive form of that shown in pterygotes, which closes completely through a fusion of amnioserosal folds. This idea has since been followed by many authors (cf. Johannsen and Butt, 1941; Ando, 1962; Sharov, 1966). However, Larink (1983) reexamined the amniotic pore of *L. saccharina* and concluded that the amniotic pore in fact closed through a fusion of the amnioserosal folds as in pterygotes. Which observation is correct?

Materials and Methods

Adults of *Lepisma saccharina* collected at the laboratory of the Sugadaira Montane Research Center, University of Tsukuba, and in gravel under the Shinkoji Temple, Sanada, Nagano, were reared in the laboratory at room temperature (20–25℃). The eggs laid by these adults were kept at 20℃ in an incubator, before being fixed in Bouin's fluid, and processed into methacrylate resin sections 2 μm thick, in accordance with Machida *et al.* (1994). Sections were then stained with Delafield's hematoxylin, eosin and fast green FCF.

Results and Discussion

The invaginated embryo of *Lepisma saccharina* is initially situated at the periphery of the egg (Fig. 1A). As embryogenesis proceeds, the embryo sinks into the yolk, until it reaches the bottom of an extensive amniotic cavity (Fig. 2A). As a result of anatrepsis, the entire egg surface is covered by a serosa, and a serosal cuticle is secreted (Fig. 2A, B): in the egg in which anatrepsis has only just finished (Fig. 1A), the serosal cuticle is yet to be secreted (Fig. 1B). For a time, embryogenesis continues, with the embryo localized deep in the yolk. We processed *L. saccharina* eggs in these stages into sections. In 12 eggs, the amniotic pore was observed to be closed by a complete fusion of the amnioserosal folds (Fig. 2A, B), which would support Larink's findings (1983). In two eggs, however, the amnioserosal folds never fused, instead a cuticular substance, which was secreted by the serosa, plugged the amniotic pore (Fig. 3): this seems to support Heymons' observations (1897). In addition, in two examples, the serosal cuticle was thickened beneath the point of contact between the amnioserosal folds (Fig. 4).

The results of the present study are therefore consistent with both Heymons' (1897) and Larink's (1983) views. That is, in some cases the amniotic pore is closed by the fusion of the amnioserosal folds as in pterygotes (Fig. 2), but in others is filled by a cuticular plug (Fig. 3). It may be that the serosal cuticle is secreted prior to the complete fusion of the amnioserosal folds. We actually found examples of an intermediate condition: the amnioserosal folds had completely fused and a serosal cuticle had been heavily secreted beneath the point of contact (Fig. 4).

The elaborated amnioserosal fold–amniotic cavity system is one of the most important embryological features of Dicondylia (=Zygentoma+Pterygota) (cf. Machida and Ando, 1998). The closure of the amniotic pore, key aspect of the system, is fulfilled in the great majority of Dicondylia or Pterygota, by a fusion of the amnioserosal folds. The

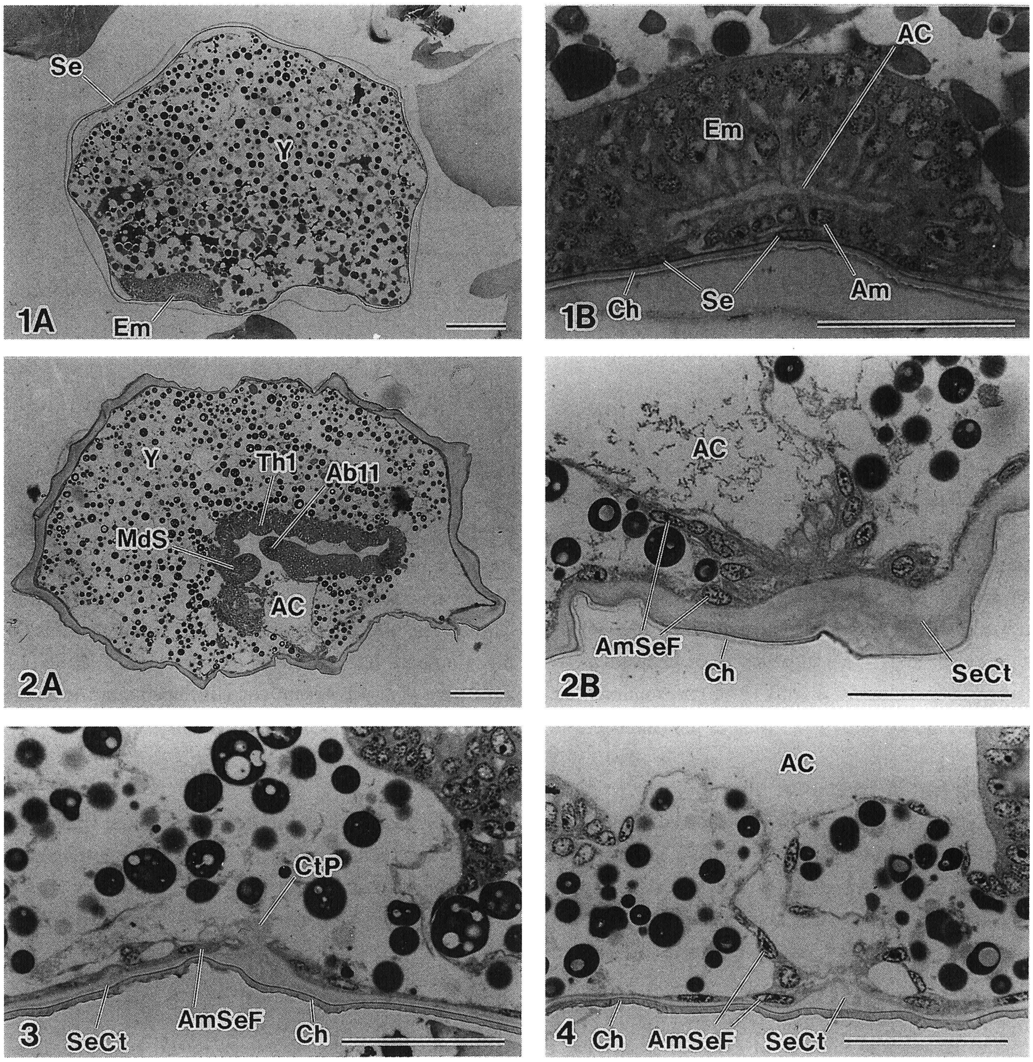

Fig. 1 A. Section of a *Lepisma saccharina* egg in which anatrepsis has just finished. B. Magnified view. The serosa is in direct contact with the chorion, and serosal cuticle is yet to be secreted.

Fig. 2 A. Section of a *Lepisma saccharina* egg in which the amniotic pore is closed by the complete fusion of amnioserosal folds. B. Close-up of the fused amnioserosal folds. The serosal cuticle has been secreted.

Fig. 3 Section of a *Lepisma saccharina* egg in which the amniotic pore is closed by a cuticular plug: close-up of the amniotic pore area.

Fig. 4 Section of a *Lepisma saccharina* egg in which the serosal cuticle is heavily secreted beneath the fused amnioserosal folds: close-up of the contact area of amnioserosal folds.

Ab11: 11th abdominal segment, AC: amniotic cavity, Am: amnion, AmSeF: amnioserosal fold, Ch: chorion, CtP: cuticular plug, Em: embryo, MdS: mandibular segment, Se: serosa, SeCt: serosal cuticle, Th1: prothoracic segment, Y: yolk. Bars =1A, 2A, 100 μm; 1B, 2B, 3, 4, 50 μm.

present study revealed that, in another dicondylian, primitive group, Zygentoma, the mechanism by which the amniotic pore closes is not fixed but flexible: that is, involving in some cases a complete fusion of the amnioserosal folds, and in others, the secretion of a cuticular plug, with intermediate forms thereof. Hence, in the ancestral forms of the dicondylian, the mechanism had yet to be established, as in the zygentomans. However, in Pterygota, the pore might have been closed in a fixed manner by fusion of the amnioserosal folds, leading to an embryological autapomorphy.

The amniotic pore of another zygentoman, *Thermobia domestica*, seemingly remains open (Wellhouse, 1953;

Woodland, 1957). Machida and Ando (1998) discussed the amnioserosal fold–amniotic cavity system in *T. domestica*, and concluded that the amniotic pore is closed in a novel fashion, which may be regarded as an autapomorphy of this species: an extensive "subchorionic cuticle" [nomenclature after Woodland (1957)] forms between widely separated amnioserosal folds. The closing of the amniotic pore in *T. domestica* resembles that by the cuticular plug in *L. saccharina*, in that a cuticular element is involved. This, however, is misleading, because the former element may be regarded as a specialized feature as Machida and Ando (1998) deduced, whereas the latter seems to represent an ancestral form present in "primitive dicondylians."

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