Amnioserosal Fold of the Jumping Bristletail *Pedetontus unimaculatus* Machida (Hexapoda, Microcoryphia, Machilidae)

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Introduction

Heymons and Heymons (1905) reported the development of amnion without the proceeding amnioserosal fold formation in a jumping bristletail *Machilis alternata*. They assumed this to be the prologue to the appearance in evolution of the amnioserosal fold, which may be acceptable as a synapomorphy of Thysanura-Pterygota. Furthermore, they extended this assumption to propose an evolutional lineage of embryonic membrane formation and blastokinesis, Microcoryphia-Thysanura-Pterygota. Their assumption has been widely accepted (Johannsen and Butt, 1941; Sharov, 1966; Jura, 1972; *etc.*).

Larink (1969), however, demonstrated that a structure identical to the amnioserosal fold of Thysanura-Pterygota is formed also in the Microcoryphia, in his detailed embryological study on another machilid species *Petrobius brevistylis*. Here, in order to bestow sound bases to the phylogenetical discussion on insects, we examine the amnioserosal fold of a machilid *Pedetontus unimaculatus*, aiming at obtaining a characteristic morphological state of the amnioserosal fold in Microcoryphia. The methods employed are as described in Machida *et al.* (1990), and the staging in the description is after Machida (1981).

Results and Discussion

A germ disc is formed at the posterior pole of egg from the initially formed broad embryonic area through concentration and proliferation of the cells in this area (Figs. 1a, 2a) (Stage 1E). Cells are arranged in the germ disc as converging to a point at the posterior pole. This causes the germ disc being fan-shape in section. The serosal cells neighboring on the embryonic area move over the ventral surface of the germ disc during concentration of the embryonic area. The movement of the serosal cells along the ventral surface of the embryo continues to cause the serosal cells rolling up to form the serosal fold (Figs. 1b, 2b). The formation of serosal cuticle has already commenced at the time of germ disc formation (Stage 1E), and cells of serosal fold secrete cuticles into a mushroom-form to the ventral of the embryo (cuticular plug, Cup in Figs. 1c, d, 2b-d; see also Machida and Ando, 1985). The space bordered by serosal fold and embryo is here named the serosal cavity, and the opening of the cavity is closed by the cuticular plug.

As the embryo grows, its margins (presumptive amnion) spread out mid-ventrally to form the amnion between the embryo and the serosal fold (Figs. 1c, d, 2c) (Stage 1L). After this stage, the embryonic membrane fold beneath the embryo contains amnion in addition to serosa. Thus this fold can be called an amnioserosal fold, and the space between the embryo and the fold an "amnioserosal cavity".

Soon after, however, the amnioserosal fold withdraws so that the ventral surface of the embryo is exposed (Fig. 2d). Withdrawal of the amnioserosal fold generally occurs sometime in the period between Stage 2L and 3, in which the embryo becomes pear-shaped and its segmentation commences, but this occasionally shifts to earlier or later stages. The earliest observed was at the germ disc stage in which the production of amnion has not yet taken place. In this case the embryonic membrane fold should be purely serosal. In most delayed cases, we observed embryos with ventral flexture (Stage 4) whose ventral surface is still covered with the amnioserosal fold.

As described above, the amnioserosal fold of the Microcoryphia is formed through sequential steps: formation of serosal fold and additional participation of amnion to the fold. Our observation suggests that the manner of formation of amnioserosal fold in the Microcoryphia is unique in the Hexapoda, and is apparently diffe-

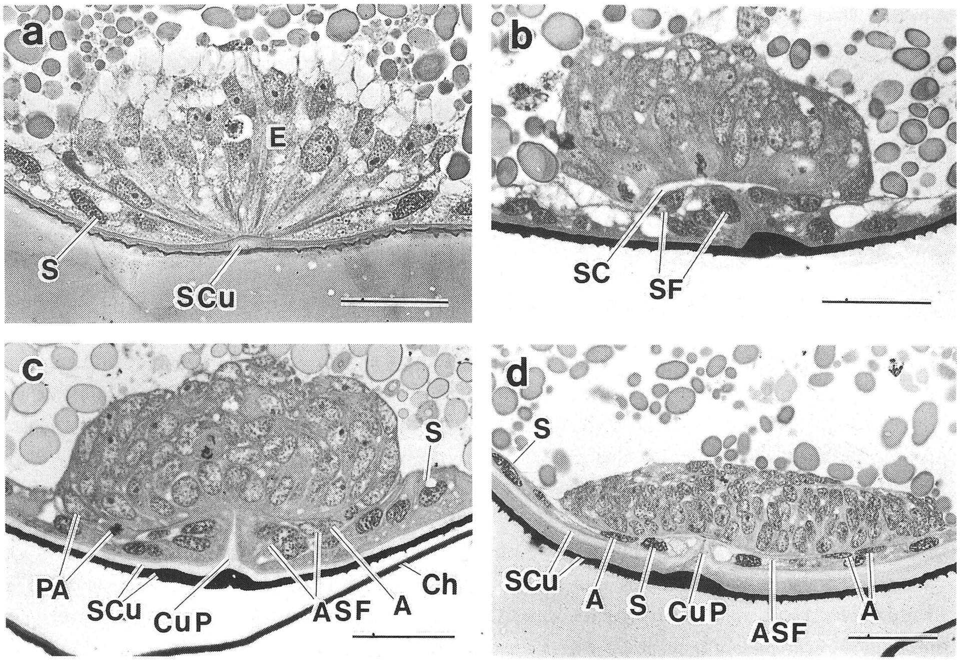

Fig. 1 Sections of embryos of *Pedetontus unimaculatus* in formation of amnioserosal fold at Stages 1E and 2 (a-d). Scales $= 50 \mu m$. A:amnion, ASF:amnioserosal fold, Ch:chorion, CuP:cuticular plug, E:embryo, PA:presumptive or developing amnion, S:serosa, SC:serosal cavity, SCu:serosal cuticle, SF:serosal fold.

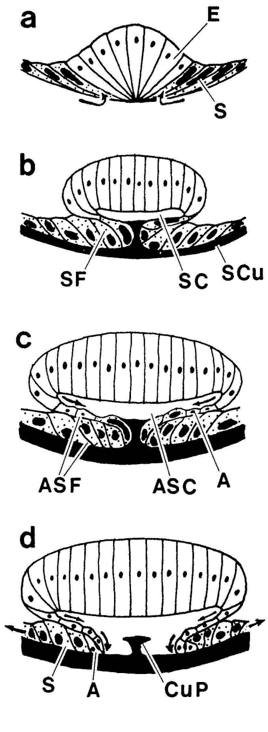

Fig. 2 Schematic diagrams showing formation of amnioserosal fold (a-c) and its unfolding (d) in *Pedetontus unimaculatus*. See text for detail. A:amnion, ASC:amnioserosal cavity, ASF:amnioserosal fold, CuP:cuticular plug, E:embryo, S:serosa, SC:serosal cavity, SCu:serosal cuticle, SF:serosal fold.

rent from the manner in the Thysanura-Pterygota, in which the amnioserosal fold formation is closely linked with the anatrepsis accompanied by formation of amnion.

The amnioserosal fold of Microcoryphia is an ephemeral structure. It exists only in a short period in the earlier stages, and its duration is considerably variable among embryos. On the other hand, in the Thysanura-Pterygota, the amnioserosal fold is maintained for a precise time period covering certain stages of embryogenesis specific for a group. Could the amnioserosal folds different in this way bear any comparable plan in the embryogenesis? As for the amnioserosal fold in the Microcoryphia, there is even a fair possibility that the participation of amnion itself to the fold can be avoided. An example provides a good support to this idea in which withdrawal of embryonic membrane fold (serosal fold) occurred before the formation of amnion.

Consequently, we find significant differences in the amnioserosal folds between the Microcoryphia and Thysanura-Pterygota. It makes us irresolute to identify them unconditionally. We would not of course reject any phylogenetical relationships between them, but they should fairly possibly be related to each other. Further phylogenetical discussions are presented elsewhere.

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