Proc. Arthropod. Embryol. Soc. Jpn. 39, 9–13 (2004)

ISSN 1341–1527

Localization of Lepismatid Embryo in the Egg, during the Diapause Stage (Hexapoda: Zygentoma, Lepismatidae)

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Abstract

Comparing the embryogeneses of nine lepismatids, three types were recognized concerning the localization of the early embryo within the egg. The first is the "invaginated germ band type," shown in *Lepisma saccharina*, in which the embryo sinks deep in the yolk during diapause. The second is the "partially invaginated germ band type," shown in *Heterolepisma dispar* and *Isolepisma japonica*, in which the posterior half of the embryo sinks in the yolk, although the anterior half remains at the egg surface. The third is the "superficial germ band type," shown in *Ctenolepisma* spp. (*i. e., C. lineata pilifera, C. longicaudata, C. pinicola, C. villosa* and *Ctenolepisma* sp.) and *Thermobia domestica*, in which the embryo does not sink into the yolk but retains its original, superficial position. Thus, the embryos of Ptilothrichi, including *Ctenolepisma* and *Thermobia*, can be categorized in the superficial germ band type, whereas those of Gymnothrichi, including *Lepisma, Heterolepisma* and *Isolepisma*, could be put in the same category, in which the embryos suffer remarkable invagination to various degrees. The evolutionary transition of the localization of the embryo within the egg in hexapods, in which the invaginated germ band type shown in *L. saccharina* is set at the terminus as representative of lepismatids, has been widely accepted. Against this, the present review concerning the localization of the embryo within the egg in lepismatids, revealed that there exist some other types than that shown in *L. saccharina*, requiring some revaluation.

Introduction

Zygentoma are widely accepted as the apterygote insect closest to early pterygote ancestors (*e. g.*, Hennig, 1969), and they are the most important hexapod group for understanding the groundplan of Dicondylia (= Zygentoma + Pterygota). The comparative embryological approach is one of the most promising methods of phylogenetic analysis. For this reason, we have started comparative embryological studies (Masumoto and Machida, 2002, 2003), using nine lepismatid species belonging to five genera as materials, *i. e., Heterolepisma dispar* Uchida, *Isolepisma japonica* Uchida, *Lepisma saccharina* Linnaeus, *Ctenolepisma lineata pilifera* (Lucas), *C. longicaudata* Escherich, *C. pinicola* Uchida, *C. villosa* (Fabricius), *Ctenolepisma* sp., and *Thermobia domestica* (Packard). In the present study, we describe and compare the localization of these nine lepismatids early embryos within the egg, during the diapause stage.

Materials and Methods

Lepismatids of nine species were collected in 2000 to 2003: *Heterolepisma dispar* Uchida from Shirahama, Wakayama Prefecture; *Isolepisma japonica* Uchida from Shirahama, Wakayama Prefecture, Muroto, Kochi Prefecture, Yonaguni and Kunigami, Okinawa Prefecture; *Lepisma saccharina* Linnaeus from Sanada and Maruko, Nagano Prefecture; *Ctenolepisma lineata pilifera* (Lucas) from Yatsuo, Toyama Prefecture, and Tsukuba, Ibaraki Prefecture; *C. longicaudata* Escherich from Ogasawara, Tokyo Metropolis, and Nishihara, Okinawa Prefecture; *C. pinicola* Uchida

from Sanada, Nagano Prefecture, and Shirotori, Kagawa Prefecture; *C. villosa* (Fabricius) from Yatsuo, Toyama Prefecture, and Ikaruga, Nara Prefecture; *Ctenolepisma* sp. [*ciliata* group; Japanese name: Seguro-shimi; see Ito and Machida (2001)] from Tateyama, Chiba Prefecture; and *Thermobia domestica* commercially imported from Germany.

The eggs laid by these lepismatids under rearing conditions were fixed in Bouin's or Karnovsky's fixative, stained with about 0.05% phenol thionin solution (0.05 g thionin + 0.25 ml phenol/100 ml 40% ethanol) and observed under a light microscope.

Results and Discussion

We compared the blastokineses of nine lepismatids, recognizing three types concerning the localization of the embryo during the diapause stage. The first type is observed in *Lepisma saccharina*, which we call the "invaginated germ band type" (Fig. 1). Before anatrepsis, the embryo is situated on the ventral side near the posterior pole of the egg (Fig. 1A). As a result of anatrepsis, the embryo sinks into the yolk, to take its position deep in the yolk and develop there throughout the diapause stage (Fig. 1B). The second type is observed in *Heterolepisma dispar* and *Isolepisma japonica*, which we call the "partially invaginated germ band type" (Figs. 2, 3). Before anatrepsis, the embryo is situated on the ventral side near the posterior pole of the egg, as in *L. saccharina* (Figs. 2A, 3A). Anatrepsis occurs, and the posterior half of the embryo sinks into the yolk, although the anterior half remains at the egg surface (Figs. 2B, 3B). The third type is observed in five *Ctenolepisma* spp. (*Ctenolepisma lineata pilifera*, *C. longicaudata*, *C. pinicola*, *C. villosa*, *Ctenolepisma* sp.) and *Thermobia domestica*, which we call the "superficial germ band type" (Figs. 4, 5). The embryo is superficially formed on the posterior side of the egg (Figs. 4A, 5A). After anatrepsis, or during the diapause stage, the embryo retains its original, superficial position in the posterior part of the egg (Figs. 4B-1–5, 5B).

Taking the "invaginated germ band type" shown in *L. saccharina* to be representative of zygentoman blastokinesis, the evolutionary transition in hexapods concerning the localization of the embryo within the egg, of which the original terminus is set at Zygentoma, has been proposed and widely accepted (for details, see Heymons, 1897; Sharov, 1966; Jura, 1972; Larink, 1983). As Wellhouse (1953) and Woodland (1957) for *T. domestica* and Truman and Ball (1998) for *C. longicaudata* had already observed, we confirmed that a second germ band type or superficial germ band type does exist among lepismatids. Moreover, we found a third germ band type or partially invaginated germ band type. The above-mentioned evolutionary transition in hexapods concerning the localization of the embryo within the egg should be, therefore, tested and revaluated.

The present study also revealed that the embryos of lepismatids classified into the Ptilothrichi, *i. e.*, *Ctenolepisma* spp. and *T. domestica*, are to be categorized in the "superficial type" and that those of lepismatids classified into the Gymnothrichi, *i. e.*, *L. saccharina*, *H. dispar* and *I. japonica* could be put in the same category, because their embryos are invaginated into the yolk, despite the variant degrees of invagination. This may suggest that the localization of the embryo within the egg during diapause illustrates phylogeny among the lepismatids.

Acknowledgments: For collecting materials, we thank M. Yafuso (*Ctenolepisma longicaudata*), S. Ito (*C. villosa*, *Ctenolepisma* sp.), K. Kiribayashi (*C. lineata pilifera*, *C. villosa*), T. Yamashita (*C. lineata pilifera*, *C. villosa*), T. Oobayashi (*C. longicaudata*), M. Kimura (*Isolepisma japonica*), H. Tamamizu (*Thermobia domestica*), H. Tanase (*Heterolepisma dispar*), K. Miyazaki (*Heterolepisma dispar*), K. Tojo (*C. lineata pilifera*), and the staff of the Sugadaira Montane Research Center, University of Tsukuba (*Lepisma saccharina*). The present study was partially supported by a Grant-in-Aid for Scientific Research from the Japan Society for the Promotion of Science (15570071) to R.M. Contribution No. 188 from the Sugadaira Montane Research Center, University of Tsukuba.

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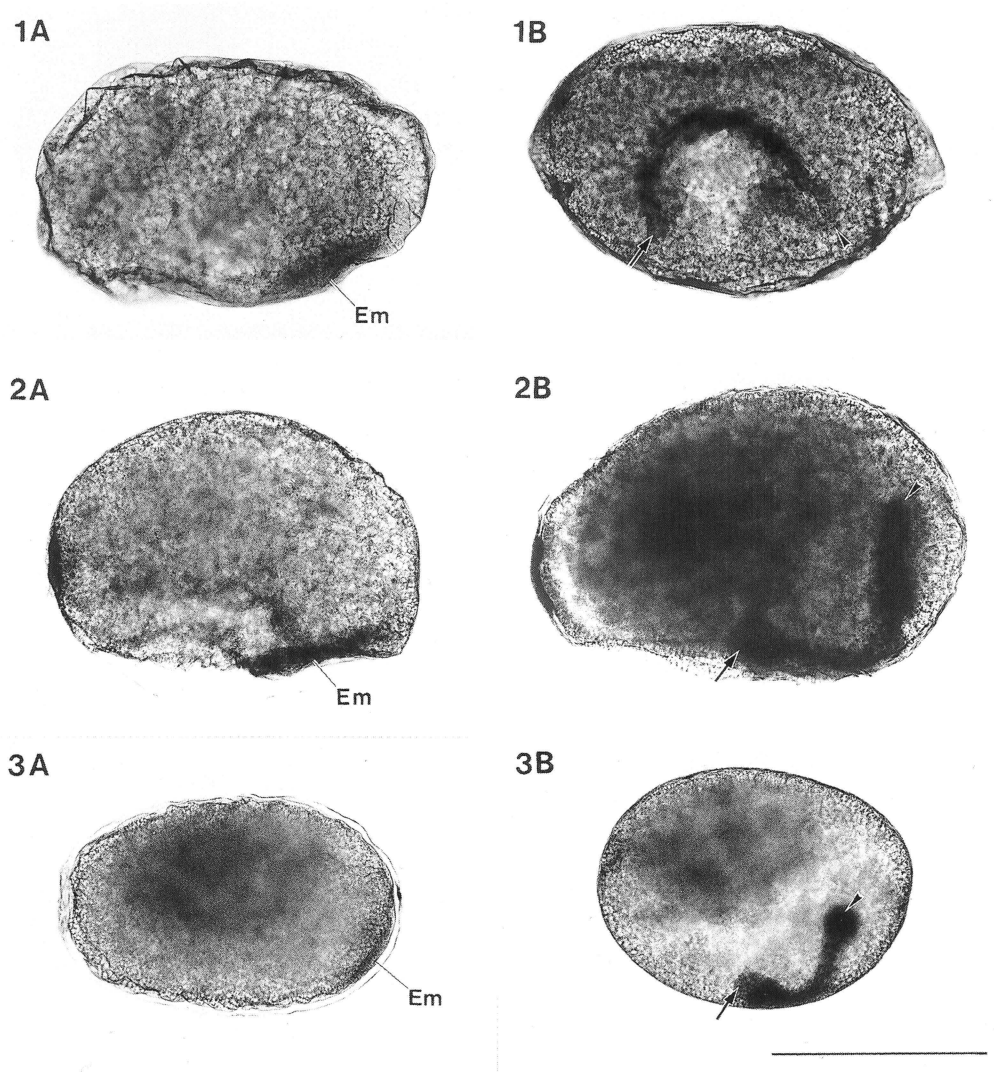


Figs. 1–3 Eggs of Gymnothrichi. Arrows and arrowheads respectively show the cephalic end and posterior limit of the embryo.

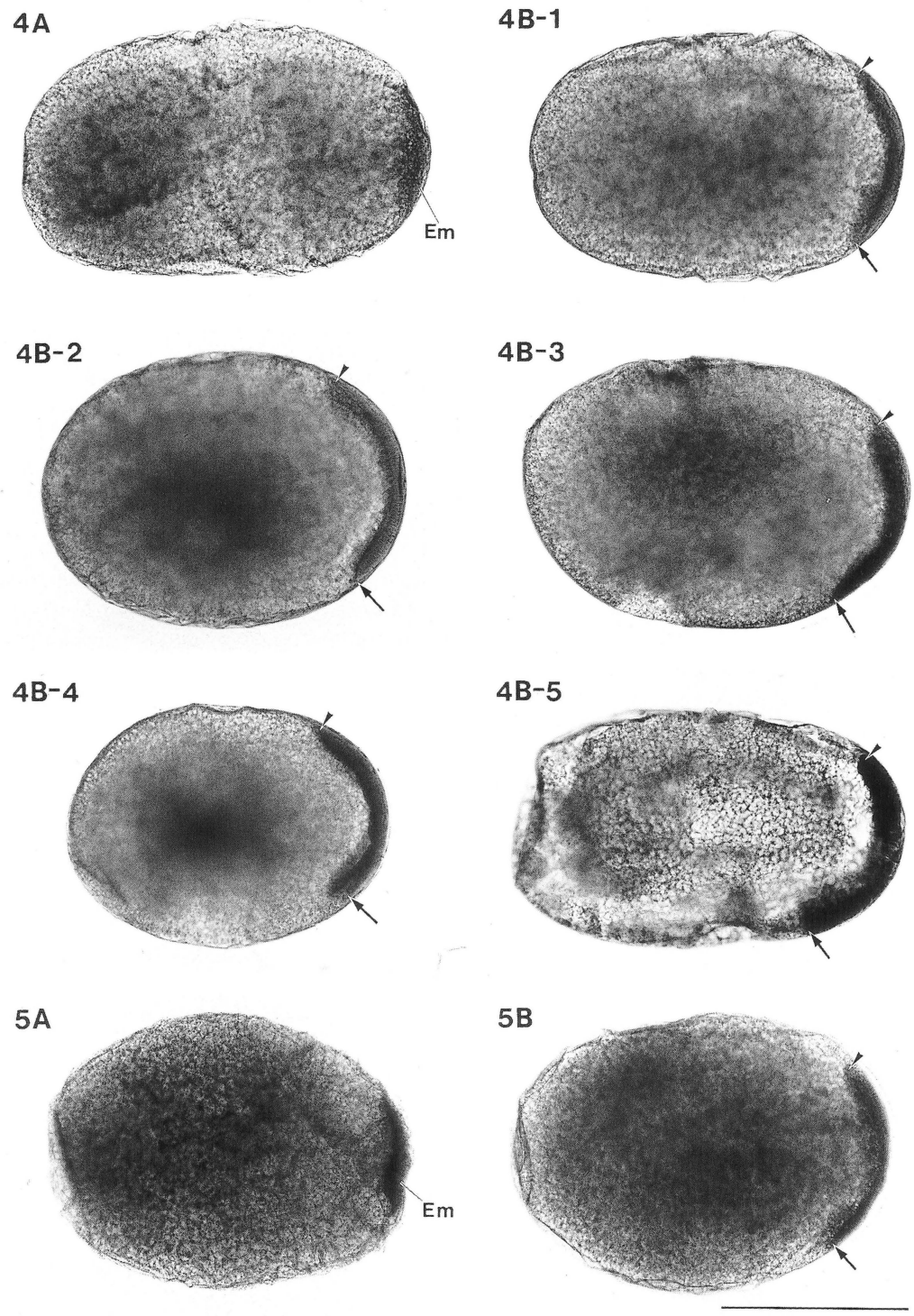
Fig. 1 Invaginated germ band type, shown in *Lepisma saccharina*. Eggs of *L. saccharina* before (A) and after (B) anatrepsis. A. The embryo is superficially formed on the ventral side near the posterior pole of the egg. B. The embryo, sunk deep in the yolk in the diapause stage, is localized there.

Figs. 2, 3 Partially invaginated germ band type, shown in *Heterolepisma dispar* and *Isolepisma japonica*.

Fig. 2 Eggs of *H. dispar* before (A) and after (B) anatrepsis. A. The embryo is superficially formed on the ventral side near the posterior pole of the egg as in *L. saccharina*. B. As a result of anatrepsis, the posterior half of the embryo sinks deep into the yolk, although the anterior half remains at the egg surface.

Fig. 3 Eggs of *I. japonica* before (A) and after (B) anatrepsis. A. The germ band is formed on the ventral side near the posterior pole of the egg as in *L. saccharin* and *H. dispar*. B. As a result of anatrepsis, the posterior half of the embryo sinks deep into the yolk, although the anterior half remains at the egg surface as in *H. dispar*.

Em: embryo. Bar = 500 μm.



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Figs. 4, 5 Eggs of Ptilothrichi, *i. e.*, *Ctenolepisma* spp. and *Thermobia domestica*, embryos of which are categorized into the superficial germ band type. Arrows and arrowheads respectively show the cephalic end and posterior limit of the embryo.

Fig. 4. Eggs of *Ctenolepisma* spp. before (A) and after (B) anatrepsis. A. *Ctenolepisma lineata pilifera* egg before the anatrepsis stage. The embryo is superficially formed at the posterior pole of the egg: those of the other four species of this genus examined, *i. e.*, *C. longicaudata*, *C. pinicola*, *C. villosa*, and *Ctenolepisma* sp., are the same (not shown). B. The embryo in the diapause stage remains at the egg surface. B-1. *C. lineata pilifera*. B-2. *C. longicaudata*. B-3. *C. pinicola*. B-4. *C. villosa*. B-5. *Ctenolepisma* sp.

Fig. 5 Eggs of *T. domestica* before (A) and after (B) anatrepsis. A. The embryo is superficially formed at the posterior pole of the egg as in *Ctenolepisma* spp. B. The embryo in the diapause stage remains at the egg surface as in *Ctenolepisma* spp.

Em: embryo. Bar = 500 μm.