

Relationship between Notoptera and Dermaptera, from the Embryological Standpoint*

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Synopsis

The embryogenesis of Notoptera and Dermaptera is compared, and their relationship is discussed. The periplasm is scanty in the notopteran eggs, and the blastoderm is thin. The embryo of this order is categorized as the short-germ type, and the immersion of embryo into the yolk is of the invagination type. Notoptera and Dermaptera, to which a closer affinity to the former has been attributed by some authors, according to present studies are quite different in some important embryological features, and the closer phylogenetical relationship between them is thought to be doubtful. Brief comparisons of embryogenesis of Notoptera with those of some other orthopteroid orders are also given.

Introduction

Notoptera (Grylloblattodea) are cryptozoic, apterous insects and represent the smallest insect order, inhabiting under stones and in caves in alpine areas of the northern circumpacific region. Since their discovery, they have been attracting the attentions of entomologists, and lot of studies on their taxonomy, morphology, ecology and phylogeny have been done. However, insofar as their phylogenetical affinity, it is controversial, and we have not attained the generally accepted view: some authors attributed their closer affinity to Blattodea (Walker, 1914; Imms, 1927; Snodgrass, 1937;

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Bey-Bienko, 1951; Sharov, 1966), the others to Orthoptera (Crampton, 1933; Snodgrass, 1937; Walker, 1938; Nakamura, 1946; Blackith and Blackith, 1968; Matsuzaki *et al.*, 1979; Nagashima, 1982), to Isoptera (Rae and O'Farrell, 1959), and to Dermaptera (Rae and O'Farrell, 1959; Kadam, 1961; Giles, 1963; Kamp, 1973; Edwards, 1982). Some authors found out ancestral features in Notoptera, but Nagashima *et al.* (1982) regarded them as neoteneously evolved Orthoptera, Baccetti (1981, 1982) as highly specialized orthopteroids, and Matsuzaki *et al.* (1979) as orthopteroid representatives but being not primitive.

For the solution of the phylogenetical controversy, the comparative embryological study may offer important information. In the present paper we pay attention mainly to this standpoint. First we illustrate some features of the embryogenesis of Notoptera and Dermaptera to make comparisons between them, and then examine their phylogenetical relationship. Brief comparisons of embryogenesis of Notoptera with those of some other orthopteroid orders are also given.

Materials and Methods

For the embryological studies of Notoptera and Dermaptera we utilized *Galloisiana nipponensis* (Caudell et King) and *Anisolabis maritima* Gené as materials respectively, and the methods employed were the same as previously described (Ando and Nagashima, 1982; Fuse and Ando, 1983).

Observations

Some features of embryogenesis of a notopteran Galloisiana nipponensis

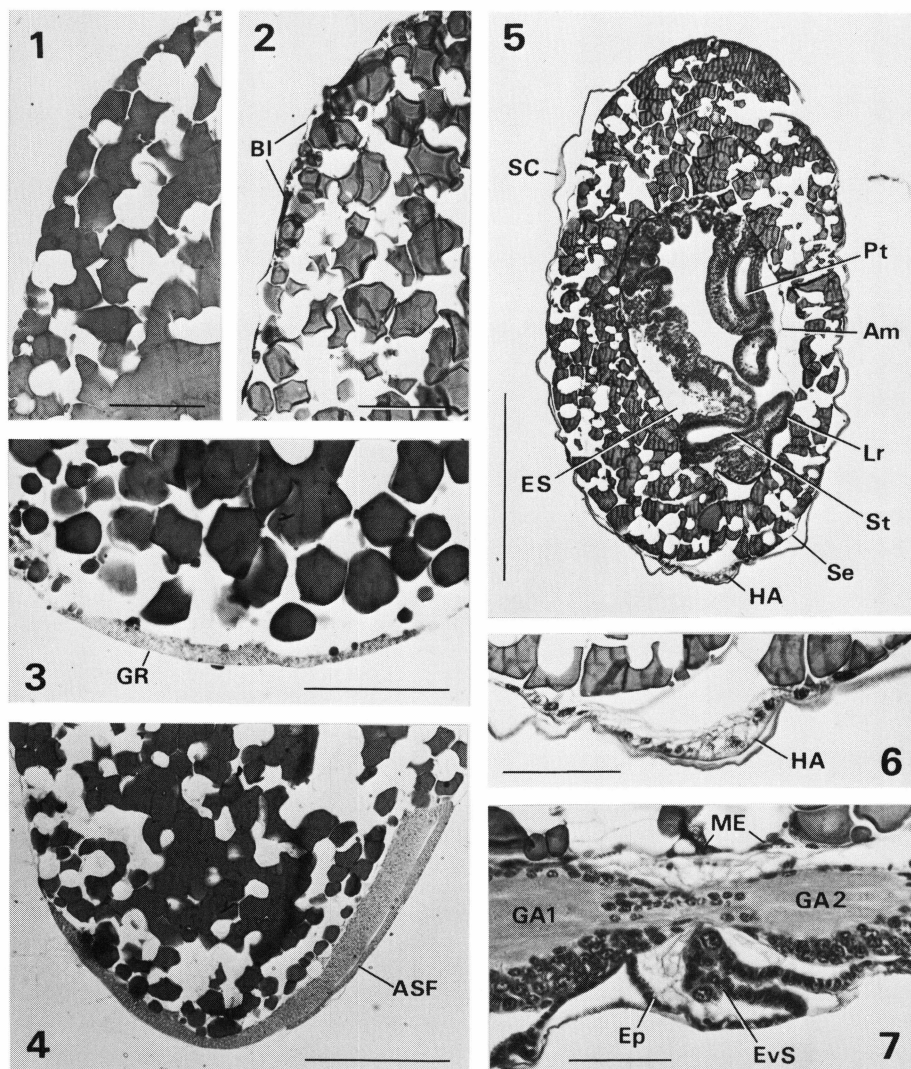
The embryonic development of *G. nipponensis* is already outlined (Ando and Nagashima, 1982).

Eggs of this insect have a very large amount of yolk, scanty cytoplasmic reticula and periplasm, and a very thin blastoderm forms (Figs. 1, 2). The germ rudiment is small (*ca.* 300 μ m in diameter), situated at the posterior end of egg (Fig. 3). Immersion of the embryo into the yolk is accomplished with the posterior amnioserosal fold (*cf.* Fig. 4). As a result of the anatresis, the embryo is deeply situated in the yolk (Fig. 5). Thickened area of the serosa is found at the posterior end of the egg in the stages before katatresis (Figs. 5, 6), which may be interpreted as the hydropylar area. Epineural sinus is moderate-sized (Fig. 5). A unique structure, eversible sac, is formed on the ventral surface of the first abdominal segment (Fig. 7).

Some features of embryogenesis of a dermapteran Anisolabis maritima

The embryonic development of *A. maritima* is already outlined (Fuse and Ando, 1983).

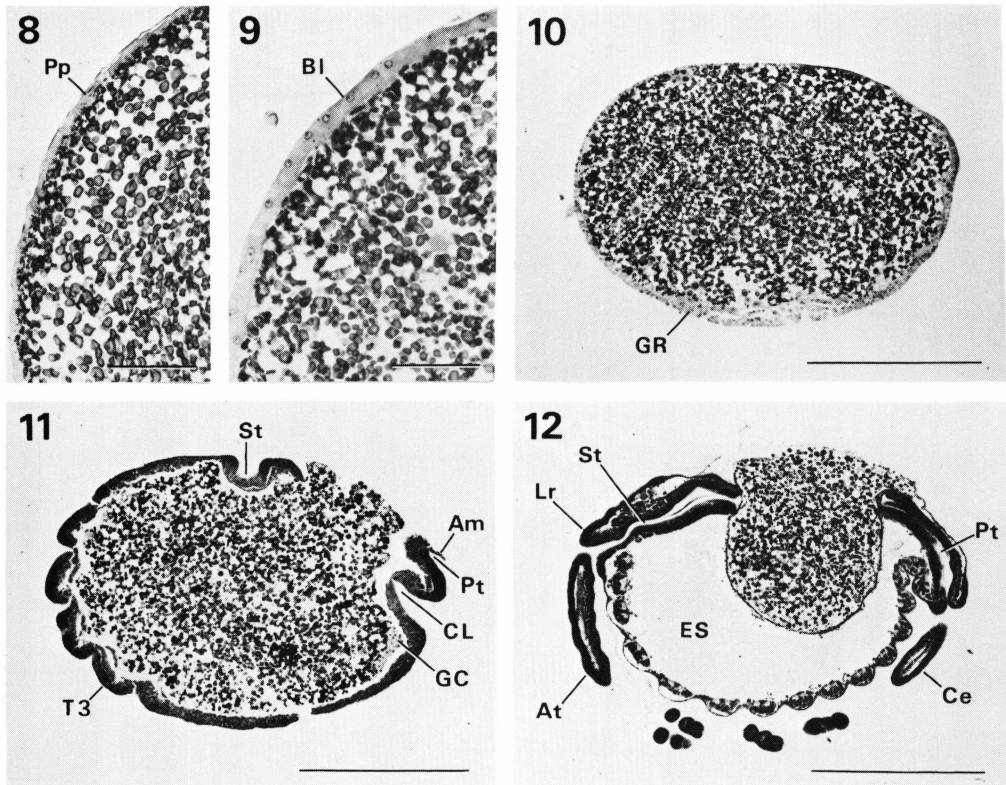
Eggs of this insect have a thick periplasm, and a thick blastoderm forms (Figs. 8,



Figs. 1—7. Sections of eggs of *Galloisiana nipponensis*. Chorion removed.

1. Newly laid egg. Scale: 100 μ m. 2. Blastoderm. Scale: 100 μ m. 3. Germ rudiment. Scale: 100 μ m. 4. Embryo initiating anatrepsis, sagittal. Scale: 100 μ m. 5. Egg just before katrepsis, sagittal. Scale: 500 μ m. 6. Hydropylar area, enlargement of Fig. 5. Scale: 100 μ m. 7. Eversible sac of full grown embryo, sagittal. Scale: 50 μ m.

Am, amnion; ASF, posterior amnioserosal fold; Bl, blastoderm; Ep, epidermis; ES, epineural sinus; EvS, eversible sac; GA1—2, ganglia of first and second abdominal segments; GR, germ rudiment; HA, hydropylar area; Lr, labrum; ME, developing midgut epithelium; Pt, proctodaeum; SC, serosal cuticle; Se, serosa; St, stomodaeum.



Figs. 8–12. Sections of eggs of *Anisolabis maritima*. Chorion removed.

8. Newly laid egg. Scale: 100 μ m. 9. Blastoderm under formation. Scale: 100 μ m. 10. Germ rudiment. Scale: 500 μ m. 11. Young embryo, sagittal. Embryonic membranes removed. Scale: 500 μ m. 12. Embryo just before katatrepsis, sagittal. Embryonic membranes removed. Scale: 500 μ m.

Am, amnion; At, antenna; Bl, blastoderm; Ce, cercus (forceps); CL, caudal loop; ES, epineural sinus; GC, primordial germ cells; GR, germ rudiment; Lr, labrum; Pp, periplasm; Pt, proctodaeum; St, stomodaeum; T3, third thoracic segment.

9). The germ rudiment forms at the ventral side, and it nearly attains in length a half of the circumference of the egg (Fig. 10). The embryo undergoes the development throughout on the egg surface (Figs. 10–12), and is of the superficial type. A large epineural sinus appears (Fig. 12).

Discussion

The embryogenesis of Dermaptera was studied by some workers: *Forficula auricularis* by Heymons (1895) and *Anisolabis maritima* by Fuse and Ando (1983), and viviparous species *Hemimerus talpoides* by Heymons (1912) and *Arixenia jacobsoni* by Hagan (1951). The embryogenesis of the latter two species is of specialized type, especially in

case of *H. talpoides*, and we take no thought of them here.

We find differences between the embryogenesis of the Notoptera and that of the Dermaptera (see also Heymons, 1895; Fuse and Ando, 1983) in some important features. Firstly, according to the thickness of the periplasm or blastoderm: the periplasm is scanty in the former, and rather thin blastoderm forms, while in the latter both periplasm and blastoderm are thick. Secondly, according to the germ type: the small germ rudiment is formed at the posterior end of the egg in the former, whereas that of the latter is rather long, and it nearly attains in length a half of the circumference of the egg. Here we may categorize the embryos of the former and latter ones to the short-germ and long-germ types respectively (see also Krause, 1939). Some authors such as Sander (1984) pointed out the correlation between the germ type and oogenesis, and the cases of Notoptera and Dermaptera well document their statement: the former has a panoistic type ovary (Matsuzaki *et al.*, 1979), and the latter a meroistic (polytrophic) one (Singh, 1967). Thirdly, according to the type of the immersion of embryo: the embryo is immersed deeply into the yolk in the former and it is of invagination type, but in the latter the embryo undergoes the development throughout on the egg surface, and the embryo is of superficial type. These features of the egg or embryogenesis are quite different between Notoptera and Dermaptera, and those in Dermaptera as well as their oogenesis might rather resemble those in holometabolous insects. In addition, in Notoptera hydropylar area forms, while in Dermaptera such a structure is not found, and the eversible sac is also characteristic of Notoptera. On the other hand, in Dermaptera primordial germ cells, which appear in a form of large clump in the yolk, can be clearly distinguished already in the early stage of development, *i. e.* in germ rudiment stage (Heymons, 1895), and a large epineural sinus may be characteristic of Dermaptera as well. We may here maintain that Notoptera and Dermaptera have quite different types of embryogenesis, and that the close relationship between them, which some authors such as Rae and O'Farrell (1959), Kadam (1961) and Giles (1963) from comparative morphological, Kamp (1973) from numerical taxonomical, and Edwards (1982) from ecological bases suggested, should be doubtful and both the orders should belong to the different groups being phylogenetically not closely related.

We may say that some important features found in Notoptera, *i. e.* thin periplasm or blastoderm, panoistic ovary type and the short-germ embryo of invagination type are widely spread within Orthopteroidea (*e. g.* Heymons, 1895; Leuzinger *et al.*, 1926; Roonwal, 1936, 1937; Striabel, 1960), although there are found some exceptions, for example, an orthopteran *Gryllotalpa* has a long-germ type embryo of superficial type (Heymons, 1895). It regards the embryogenesis of Notoptera as representative one within Orthopteroidea, but we could not detect, in our preliminary studies, any embryological bases facilitating the further discussion on the phylogenetical position of Notoptera within Orthopteroidea. In some orthopterans (*e. g.* Slifer, 1938) the hydropylar area is formed on the serosa as in Notoptera, and the fact might reflect some relationship between them. However, of course, this feature alone would not suffice to suppose affinity. For the definite discussion on the affinities of Notoptera within Orthopteroidea, the further detailed studies on the embryogenesis of Notoptera will be derived in future.

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