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Embryonic Development of the Scorpion Fly, *Panorpodes paradoxa* (Mecoptera, Panorpodidae) with Special Reference to Larval Eye Development

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Synopsis

Embryonic development in the scorpion fly, *Panorpodes paradoxa* (Mecoptera: Panorpodidae), with special reference to larval eye development, was first described.

The mode of development of optic lobe, rudimental postretinal fibers, and optic plate observed in *Pd. paradoxa* was almost identical with that observed in other mecopteran *Panorpa pryeri*, previously described by the author. This indicates that the mode of larval eye development in Mecoptera is basically the same with that observed in hemimetabolous insect embryos. In *Pd. paradoxa*, however, development of rudimental postretinal fibers and optic plate was abortive; they degenerate and finally disappear by the end of embryonic revolution. As a result, a newly hatched larva of *Pd. paradoxa* has no eyes at all.

Absence of larval eyes in *Panorpodes* may thus be interpreted as caenogenetic. This observation may further suggest that this caenogenetic character is very useful to consider phylogenetic relationship between *Pd. paradoxa* and *P. pryeri*.

Introduction

Mecopteran insects have been considered the most primitive among holometabolous insects, and this the reason why study of this insect group is very necessary to reveal phylogenetic relationship among holometabolans. Comparative embryology is supposed to be the most effective method for this purpose. Unfortunately however, embryological information on this insect group is still very fragmentary, even though several papers have recently appeared (Ando, 1960, 1973; Ando and Haga, 1974; Ando and Suzuki, 1977; Suzuki, 1982; Suzuki and Ando, 1981; Wolf, 1961).

Intention of present author is to study embryogenesis of mecopterans to make clear the relationship among this insect group, and then ultimately to elucidate phylogeny of holometabolous insects from embryological viewpoint. In the present paper, the author describes an outline of the embryogenesis after gross morphological observation of *Panorpodes*

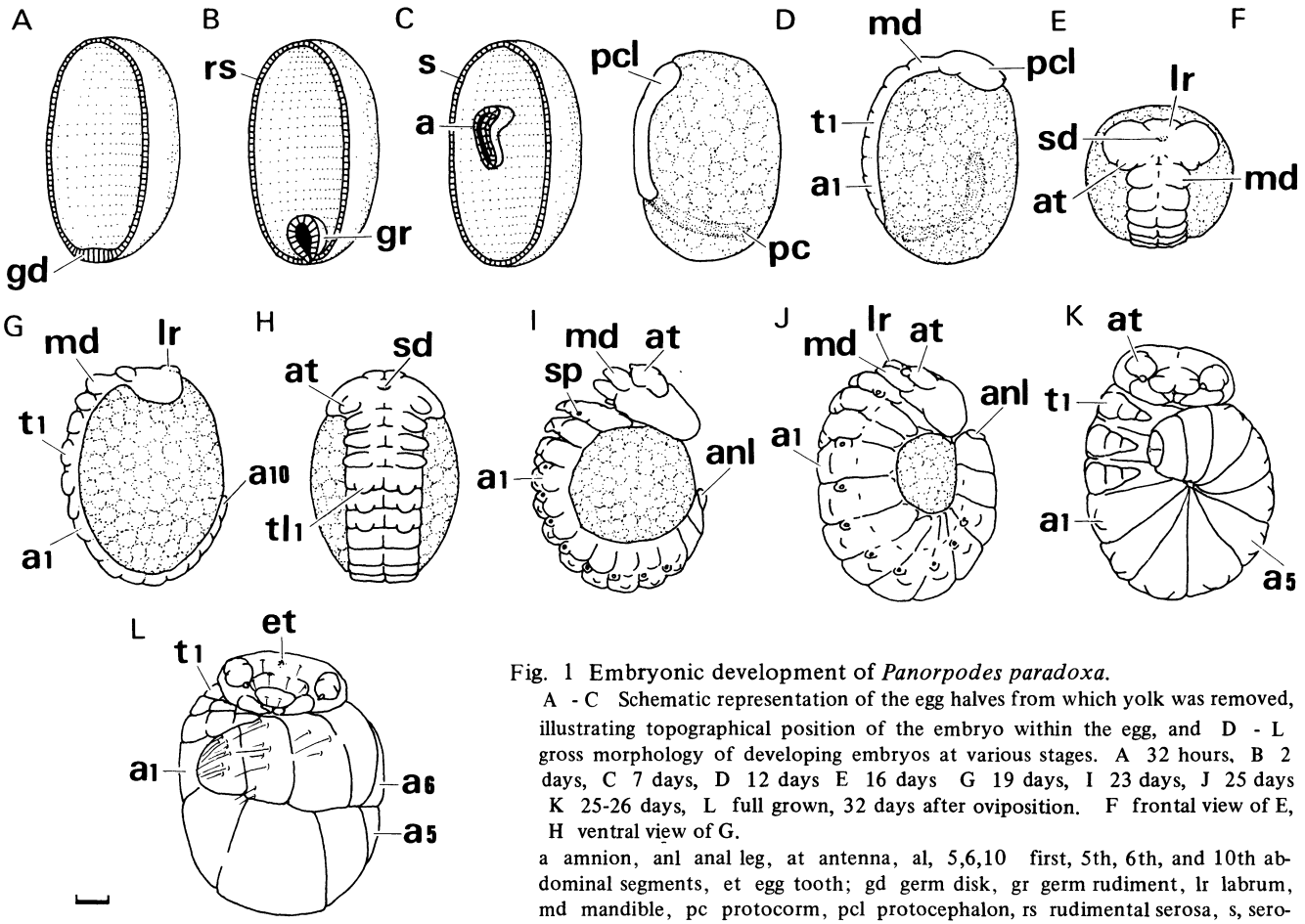


Fig. 1 Embryonic development of *Panorpodes paradoxa*.

A - C Schematic representation of the egg halves from which yolk was removed, illustrating topographical position of the embryo within the egg, and D - L gross morphology of developing embryos at various stages. A 32 hours, B 2 days, C 7 days, D 12 days E 16 days G 19 days, I 23 days, J 25 days K 25-26 days, L full grown, 32 days after oviposition. F frontal view of E, H ventral view of G.

a amnion, anl anal leg, at antenna, al, 5,6,10 first, 5th, 6th, and 10th abdominal segments, et egg tooth; gd germ disk, gr germ rudiment, lr labrum, md mandible, pc protocorm, pcl protocephalon, rs rudimental serosa, s, serosa, sd stomodaeum, sp spiracle, tl, first thoracic segment, tll first thoracic leg. Scale = 100 μm.

paradoxa MacLachlan(Panorpodidae), neither embryonic nor postembryonic development of which has hitherto been known. Detailed histological observation of embryonic larval eye development in *Pd. paradoxa* was given, as occurrence of larval compound eyes in *Panorpa pryeri* MacLachlan (Panorpidae) has already been described (Ando and Suzuki, 1977). From these observation the author will discuss the relationship between Panorpidae and Panorpodidae.

Materials and Methods

Pregnant females of *Panorpodes paradoxa* MacLachlan were collected at and near Sugadaira, Nagano Prefecture, Japan, from June to July during 1979-1982. Ten to fifteen insects were reared in a each mesh-walled cage and wet tissue paper was set for the site of their egg-laying. Newly laid eggs on or in the tissue paper were kept at 21°C. The eggs and larvae were fixed in alcoholic Bouin's fluid for 30 min (warmed to 40°C or at room temperature). They were cut into 6-8 μm-thick, and stained with Delafield's hematoxylin and eosin. The eggs, whose choria were removed and stained in toto with Mayer's hematoxylin, were used for the study of the external morphology of embryos. Drawings were made with the aid of Abbe's camera lucida. The first instar larvae for scanning electron microscopy were dehydrated through an ethyl alcohol-isoamil acetate series after fixation. Then they were dried by the critical point drying method and coated with gold. Observations were examined under the scanning electron microscope, JSM T-200 of JEOL.

Results

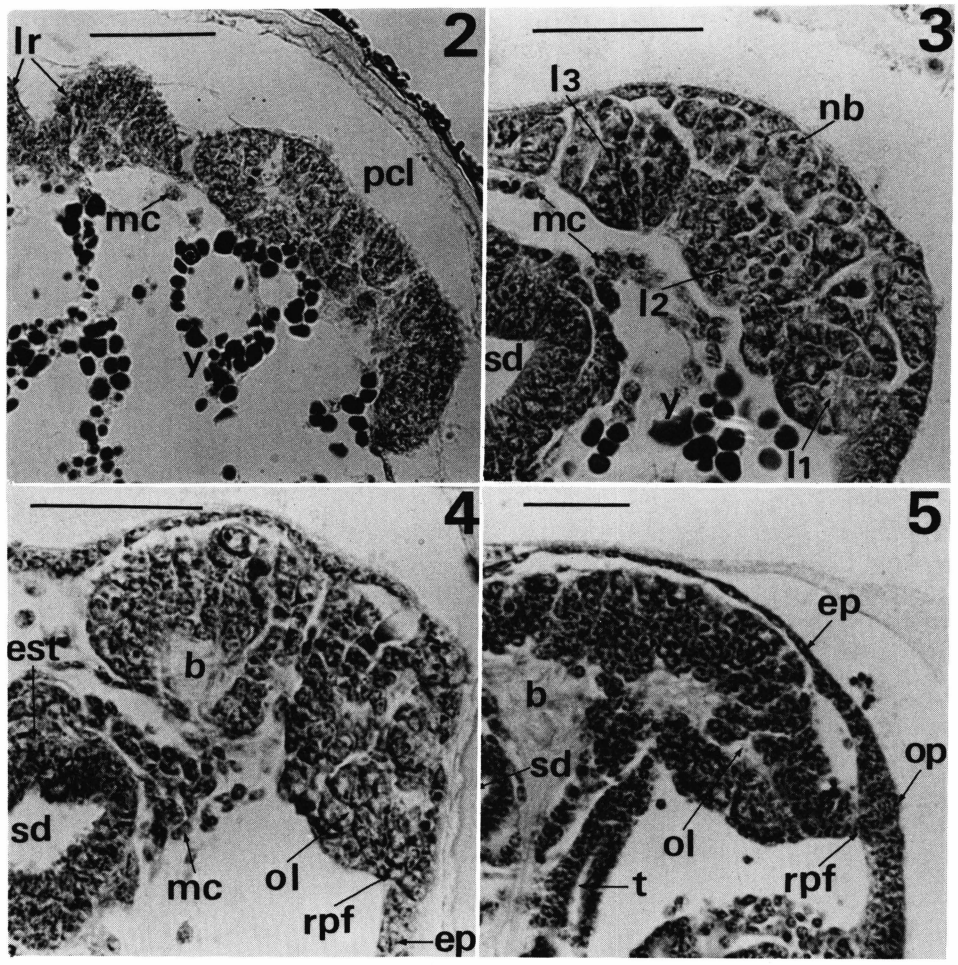
The shape of the newly laid eggs of *Pd. paradoxa* is oval and is 750-800 by *ca.* 500 μm. The chorion is very thin and creamy white just after oviposition, but it changes dark within several hours. The egg period is 28-40 (mean, 32.6) days (21°C).

1. Outline of the embryonic development of *Pd. paradoxa*

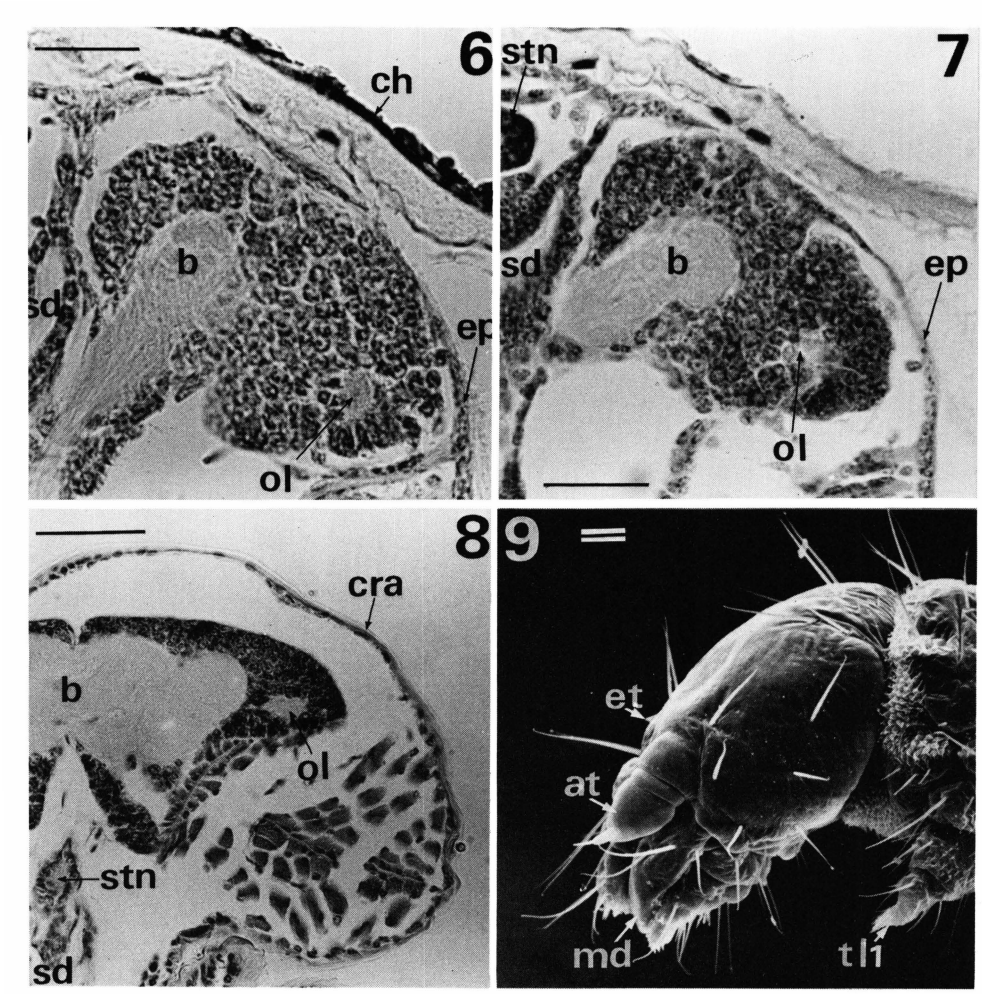
At one day after oviposition, energids reach the egg periphery, and cellular blastoderm is completed. At 32 hr after oviposition, the blastoderm becomes thickened especially near the posterior egg pole (Fig. 1-A) and this thikened region of the blastoderm, 100-150μm in diameter, is the embryonic area, *i. e.*, germ disk. The germ disk becomes sac-shaped and begins to sink into the yolk (Fig. 1-B) at 2 days after oviposition, and the germ rudiment or embryo takes a position at the core of the egg (Fig. 1-C) at 7 days after oviposition.

At 12 days after oviposition, the embryo surfaces from the yolk, but the posterior half of the protocorm still remains in the yolk (Fig. 1-D). At 16 days after oviposition, anterior to the third abdominal segment of the embryo appears on the yolk (Figs. 1-E, F), and the remaining part of the embryo finally comes out from the yolk at 19th day, and anlagen of gnathal and thoracic appendages may be seen at this stage (Figs. 1-G, H).

At 23 days after oviposition, gnathal segments become compact and paired spiracles are observed on the first, third thoracic and first eight abdominal segments (Fig. 1-I). At 25 days after oviposition, the head and caudal end of the embryo almost touch with each other



Figs. 2-5 Embryonic larval eye development in *Panorpodes paradoxa* (I).
Left part of horizontal (2) and transverse (3-5) sections through head of embryo. 2) 16 days, 3) 18 days, 4) 20 days, 5) 23 days after oviposition.
b brain, ep epidermis, est evagination of stomatogastric nervous system, lr labrum, l1-3 lobi 1-3 of protocerebrum, mc mesodermal cell, nb neuroblast, ol optic lobe, op optic plate, pcl protocephalon, rpf rudimental postretinal fibers, sd stomodaeum, t tentorium, y, yolk. Scales : 50 μm.



Figs. 6-9 Embryonic larval eye development in *Panorpodes paradoxa* (II).
Left part of transverse (6,7) and horizontal (8) sections through head of embryo (6, 7) and newly hatched larva (8). 6) 25 days, 7) 26 days, 8) 33 days after oviposition, 9) lateral view of head of newly hatched larva.
at antenna, b brain, ch chorion, cra cranium, ep epidermis, et egg tooth, md mandible, ol optic lobe, sd stomodaeum, stn stomatogastric nervous system, tll first thoracic leg. Scales : 50 μm.

(Fig. 1-J), and the embryo undergoes revolution (Fig. 1-K). Just before hatching, the embryo bears relatively long setae (Fig. 1-L) and mandibular tips become fulvous.

2. Embryonic larval eye development of *Pd. paradoxa*

In the course of the above-mentioned embryogenesis, the larval eye development of *Pd. paradoxa* occurs by the following process.

At 16 days after oviposition, the ectoderm of protocephalon becomes multi-layered, though neuroblasts which form the future protocerebrum are not yet observed (Fig. 2). At 18 days after oviposition, neuroblasts, which are round (12-13 μm in diameter) and stained lightly with hematoxylin, become discernible in the ectoderm of the protocephalon (Fig. 3). The future protocerebrum consists of three parts, namely lobi 1, 2 and 3 (Fig. 3), and the lobi 2 and 3 are made by proliferation of neuroblasts. As seen in Fig. 3, neuroblasts are hardly observed in the area of the ectoderm from where the lobus 1 is formed; lobus 1 thus seems to be formed exclusively from invagination of the ectoderm.

At 20 days after oviposition, the lobi 1, 2 and 3 begin to be compact and become separated from the epidermis of the embryonic head (Fig. 4). The lobus 1, which forms a optic lobe later, however, still possesses the connection with the head epidermis, and this connection is rudimental postretinal fibers (Fig. 4, rpf). At 23 days after oviposition, the developing brain becomes more compact as the cephalognathal segments begin to gather (Fig. 5). Simultaneously the epidermis, with which the rudimental postretinal fibers contact, thickens to *ca.* 20 μm. This thickening is the rudimental optic plate (Fig. 5, op), though the cell differentiation does not occur in there.

However, at 25 days after oviposition, *i. e.*, at just before revolution, the rudimental postretinal fibers start to degenerate. Connection between the epidermis and optic lobe has become almost rudimentary, and the thickening of the optic plate also may no longer be seen (Fig. 6). At revolution the connection between the epidermis and optic lobe disappears completely (Fig. 7) and the connection never occurs again, and it is impossible to distinguish the optic plate from the surrounding epidermis.

Fig. 8 shows the part of the head of the just hatched larva in the horizontal section. Although optic lobe is still present, larval eyes are absent. The electron micrograph (Fig. 9) shows the lateral view of the hatched larval head of *Pd. paradoxa.* In *Panorpa,* larval eyes exist near the base of the antennae (Ando and Suzuki, 1977; Bierbrodt, 1943; Byers, 1963; Miyake, 1912; Riek, 1973; Yie, 1951), but the larval eyes in *Pd. paradoxa* are never observed at any part of the head.

Discussion

Judging from the Issiki's description (1959), the first instar larvae of *Pd. paradoxa* considerably differ from the larvae of other mecopteran families in point of the following characters; 1) larval eyes are absent, 2) paired abdominal legs on the first eight abdominal segments are absent, and 3) existence of the eleventh abdominal segment, which is very rare for larvae of the holometabolous insects. As for the first character, other mecopteran lar-

vae have compound eyes similar to that observed among the hemimetabolous insect larvae, and so far as their embryonic development and structure are concerned, the mecopteran larval eyes seem to be slightly modified from hemimetabolous larval eyes (Ando, 1957; Ando and Suzuki, 1977; Paulus, 1979; Riek, 1970; Rottmar, 1966; Snodgrass, 1935). This may indicate that Mecoptera occupies the rather primitive status among all holometabolans.

Present author considers that occurrence of larval eye degeneration in insects could be classified into following three grades.

The first grade may be observed in the externally eyeless grylloblattids, *Galloisiana* (Nagashima, 1979), in which eye structure was completely formed but only eye pigment was lacking. The second grade may be that the eye rudiments appear at first, but then degenerate and disappear in the course of embryogenesis. The third grade may be known as true eyeless, in which case eye rudiments may never appear during the embryogenesis.

As a result of present study, it may be possible to conclude that larval eye formation of *Pd. paradoxa* clearly belongs to the second grade. The thickening of the optic plate in *Pd. paradoxa* occurs when cephalognathal segments start to concentrate, as in the case of *P. pryeri* (Ando and Suzuki, 1977; Suzuki and Ando, 1981). In the embryos of *P. pryeri* approaching to revolution, the active cell differentiation occurs in the developing optic plate and retinular cells, Semper's cells and crystalline cones are formed (Ando and Suzuki, 1977). In *Pd. paradoxa,* on the other hand, before the commencement of cell differentiation in the optic plate, thickness of the optic plate starts to decrease, which indicates degeneration of this plate. Therefore, absence of the larval eyes in *Pd. paradoxa* may be concluded as due to caenogenesis, and not palingenesis.

The larvae of *Brachypanorpa,* the other genus of Panorpodidae, are also eyeless (Byers and Thornhill, 1983), and it could be supposed that they became eyeless because of the same reason of *Panorpodes,* namely caenogenesis. This conclusion that the larvae of *Panorpodes* and *Brachypanorpa* lost their eyes caenogenetically may suggest that they are phylogentically distant from *P. pryeri* of Panorpidae to some extent, and may support the Byers' conclusion (1965) that subfamily Panorpodinae, which consists of genera *Panorpodes* and *Brachypanorpa,* should be independent of family Panorpidae, and family Panorpodidae is to be established.

Several factors such as habitat, food preference, and behavior of these larvae might have collectively brought about this degeneration of larval compound eyes in *Panorpodes paradoxa.* Consequently, it will be available to investigate such factors during postembryonic development as a means of searching for the cause which led these larvae to eyeless.

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