

Rotation in Developing Embryos of *Tanypteryx pryeri* Selys (Petaluridae) and *Davidius nanus* Selys and *Sieboldius albardae* Selys (Gomphidae) (Insecta: Odonata)

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The rotation of embryo in insect eggs is a type of blastokinesis, which occurs around the long axis of the egg, different from the kataspsis (=revolution) of hemimetabolous embryos, which is antero-posterior turn of an embryo, and is a necessary process for dorsal closure of the embryo. Occurrence of the rotation was fragmentarily reported from nine hemimetabolous orders with only exception of Heteroptera which was systematically investigated by Cobben (1968) through almost all the families.

In Odonata, the rotation was first described by Seidel (1929) for *Platycnemis pennipes* (Zygoptera, Platycnemididae), in which the germ band rotated 180° at revolution. Ando (1962) carried out a comparative embryology of the order, but he did not mention the rotation of embryo. Recently I investigated embryogenesis of Odonata, in particular on the rotation of embryo in the egg, referable to five families, covering three suborders and revealed that there were three different types of rotation at subordinal level, and moreover there were two types of rotation at family level in Anisoptera (Miyakawa, 1987). The rotation angles were 180° in Zygoptera, 90° in Anisozygoptera, and 0° in aeshnid Anisoptera. However, in exophytic eggs of libellulid Anisoptera, embryos showed a different type of rotation, i. e., a gravity-dependent rotation just before or after revolution to take a venter-up position. Time and cause of the rotation were divergent according to taxa. Four causes were suggested: (1) Rotation at the beginning of revolution in zygopteran and anisozygopteran embryos is caused by bilaterally asymmetric fusion of amnion and serosa at the embryonic head, which results in rotation when it ruptures. (2) The 180° rotation of zygopteran embryos does not always occur at the revolution but it occurs also after revolution in some cases. Post-revolutionary rotations are caused by change of embryonic form as development proceeds to fit the embryo to the dorso-ventrally asymmetric, banana-form egg shell. (3) Libellulid gravity-dependent rotation is caused by only difference in the specific gravity between the embryo and the yolk, the latter being denser than the former. (4) Irregular rotations of grown embryos seen in various taxa are attributed to occasional activities of trunk muscles. In my previous paper (Miyakawa, 1987), however, I did not include Petaluridae and Gomphidae, which are the most archaic families of Anisoptera.

Petaluridae has a complete set of ovipositor-parts like Anisozygoptera and anisopteran Aeshnidae, but the oviposition is not true endophytic and the eggs are not elongate but ellipsoidal. Gomphidae, on the contrary, has a degenerated ovipositor and lays ellipsoidal eggs exophytically like modern Libellulidae.

On the other hand, early germ bands of Petaluridae and Gomphidae develop in yolk ("invaginated" type, Ando, 1962), of which type is widely seen in primitive odonate taxa, such as Zygoptera, Anisozygoptera, and aeshnid Anisoptera, all of which are exclusively endophytic. Thus it is interesting to know what types of the embryo rotation occur in Petaluridae and Gomphidae. If the embryo rotation depends on phylogenetic position, then those of the two families may resemble those of *Epiophlebia* (Anisozygoptera) or *Aeshna* (Anisoptera), and if it depends on the egg shape in relation to oviposition manner, then the embryo rotation may resemble those of modern *Orthetrum* and *Sympetrum* (Libellulidae).

The live eggs of *Tanypteryx pryeri* ($n=5$) (Petaluridae), and *Davidius nanus* ($n=20$) and *Sieboldius albardae* ($n=22$) (Gomphidae) were fixed on water-filled glasses (see also Miyakawa, 1987), and directions of embryo relative to each egg shell were observed throughout the development. If necessary, the direction of egg initially fixed was altered later to examine whether rotation was gravity-dependent or not. These observations and experiments revealed that embryos of these species of the two families perform, as a rule, a gravity-dependent rotation at or just after revolution, quite similarly to the embryo rotation of Libellulidae (Miyakawa, 1987). These results may allow us to conclude that in the exophytic, ellipsoidal eggs the embryos perform a gravity-dependent rotation to take a venter-up position without reference to phylogenetic position (Table 1).

Table 1 Rotation of embryo in odonate eggs so far known.

Suborder / Family	N	Oviposition	Egg shape	Rotation
<i>Zygoptera</i>				
Calopterygidae	1 gen. 2 sp.*	endophytic	elongate	180°, at and after revolution
Coenagrionidae	1 gen. 1 sp.*	"	"	"
Platycnemididae	1 gen. 1 sp.*	"	"	"
<i>Anisozygoptera</i>				
Epiophlebiidae	1 gen. 1 sp.*	"	"	90°, at revolution
<i>Anisoptera</i>				
Aeshnidae	2 gen. 3 sp.*, **	"	"	0°
Petaluridae	1 gen. 1 sp.	exophytic	ellipsoidal	gravity-dependent, to take a venter-up position after revolution
Gomphidae	2 gen. 2 sp.	"	"	"
Corduliidae	1 gen. 1 sp.**	"	"	"
Libellulidae	2 gen. 3 sp.*	"	"	"

For taxa with asterisks see Miyakawa (1987)* and my unpublished data.**

References

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