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The "Polyneopteran Comparative Embryological Project": Present and Future*

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"Polyneoptera," or the basal neopteran group, is a large group currently represented by eleven diverse orders, *i. e*., Plecoptera, Embioptera, Phasmatodea, Orthoptera, Mantodea, Blattodea, Isoptera, Grylloblattodea, Mantophasmatodea, Dermaptera, and Zoraptera (Boudreaux, 1979; Klass *et al*., 2003). However, not only their interordinal relationships remain highly controversial (Kristensen, 1989; Grimaldi and Engel, 2005; Terry and Whiting, 2005), but even the accuracy of the taxon suspect (cf. Klass, 2009). Irrespective of these phylogenetical issues, the "polyneopteran" orders are the most significant in elucidating the groundplan and evolution of Neoptera, which have achieved spectacular prosperity, since "polyneopteran" orders are almost certainly directly derived from early radiations of Neoptera in the Carboniferous (Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005).

Our "Polyneopteran Comparative Embryological Project" has hitherto dealt with Grylloblattodea, Mantophasmatodea, Embioptera, Phasmatodea and Dermaptera: 1) to propose a closer affinity between Grylloblattodea and Mantophasmatodea (= Chimaeraptera *sensu* Uchifune and Machida, 2005) (Machida *et al*., 2004; Tsutsumi *et al*., 2004; Uchifune and Machida, 2005; Uchifune *et al*., 2006), based on embryological features such as blastokinesis and egg structures, 2) to reinforce the affinity between Embioptera and Phasmatodea (= Eukinolabia *sensu* Terry and Whiting, 2005) (Jintsu *et al*., 2007), based on the egg structure, and 3) to provide evidence to correlate Dermaptera and Endopterygota, based on germ band formation (Kusakari and Machida, 2005).

To promote our "Polyneopteran Comparative Embryological Project," we should accumulate much more embryological information to extend critical discussions of each polyneopteran member. Then, aiming at progressive arguments on phylogenetical issues concerning "Polyneoptera," making "clusters" may be promising. In this respect, Chimaeraptera and Eukinolabia are first focused on. 1) To verify the cluster Chimaeraptera, composed of Grylloblattodea and Mantophasmatodea, which our comparative embryological studies have proposed, full understanding of the embryogenesis of Mantophasmatodea is required. 2) As for the cluster Eukinolabia, Embioptera and Phasmatodea too closely resemble each other not to postulate their affinity. Nevertheless, Embioptera and Phasmatodea show marked contrasts in some major embryological features, such as the germ band type and the manner of blastokinesis, which have been used as key characters in insect comparative embryology: in Embioptera a broad germ anlage forms and the embryo takes its position deep in the yolk during the intertrepsis (Kershaw, 1914; Jintsu and Machida, 2009), but in Phasmatodea a small germ anlage forms and the embryo maintains its original position on the surface of the yolk throughout embryogenesis (Bedford, 1970). How can these differences between Embioptera and Phasmatodea be elucidated? This is not only important to test the cluster Eukinolabia, but is also significant in the reevaluation of comparative embryological characters, to render steady progress in insect comparative embryology.

3) In the context of the reevaluation of comparative embryological characters, Dictyoptera and Orthoptera may be the best models. Dictyoptera, composed of Blattodea, Mantodea and Isoptera, are well supported by various disciplines. However, several major differences in embryogenesis among these three orders have made the groundplan of Dictyoptera impossible to reconstruct, and moreover, in a single order Blattodea, *Blattela* and *Periplaneta* undergo utterly different blastokinesis: for example, as for the blastokinesis, in isopterans the blastokinesis is accompanied by a complete reverse of embryo's axis (Striebel, 1960), but the reverse of embryo's axis is not involved in the blastokinesis of mantodeans, of which embryos instead undergo the

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rotation around the egg's long axis (Hagan, 1917); embryos of a blattodean *Blattela* retain their original position throughout the embryogenesis (Wheeler, 1889), but those of another blattodean *Periplaneta* play a complete reverse of their axis during the blastokinesis (Heymons, 1895). The case is true of Orthoptera. Diverse members of the order show wide-ranging variations in significant embryological features such as the localization of embryos and manner of blastokinesis, not only between the suborders Ensifera and Caelifera but even among infra-subordinal levels of each suborder (Korotneff, 1885; Wheeler, 1893; Heymons, 1895; Roonwal, 1936). Careful and not superficial but critical reexaminations of Dictyoptera and Orthoptera must contribute a sound basis for insect comparative embryology, and simultaneously develop a steady phylogenetical argument concerning these groups.

4) Our embryological study of Dermaptera suggested that Dermaptera could be elucidated from the framework of "Dermaptera + Acercaria (or Paraneoptera) + Endopterygota (or Holometabola)." In this respect, a comparative embryological study on Dermaptera is greatly desired, using all the families as materials, including primitive dermapteran representatives Diplatyidae and Pygidicranidae, which must be helpful to reconstruct the dermapteran groundplan and to test the "Dermaptera + Acercaria + Endopterygota" hypothesis: our team has already succeeded in obtaining a sufficient number of eggs of diplatyid *Diplatys flavicollis* and examined its egg-laying behavior and egg structure (Shimizu and Machida, 2009).

Other than Dermaptera, there are two "polyneopteran" orders whose affinity to Acercaria and/or Endopterygota has been suggested, *i. e*., Plecoptera and Zoraptera. 5) Although Plecoptera have been assigned to a status as the basalmost clade of "Polyneoptera" and Neoptera (Bourdreaux, 1979), often their affinity to Acercaria and/or Endopterygota has been proposed (Ross, 1956; Hamilton, 1972) and recently, the affiliation of Plecoptera to Eukinolabia has been mentioned (Zompro, 2004). Comparative embryological studies have suggested the resemblance of Plecoptera to Isoptera in the possession of a bladder-like early embryo on one hand, and on the other to Grylloblattodea, Orthoptera, and Mantodea in the possession of specialized serosal derivatives (Kishimoto and Ando, 1985 vs. Wheeler, 1893; Knower, 1900; Hagan, 1917; Uchifune and Machida, 2005). Critical and thorough examinations of plecopteran embryology are strongly expected. 6) Zoraptera have been related to various "polyneopteran" orders and often assigned to Acercaria (Hennig, 1953; Boudreaux, 1979; Grimaldi and Engel, 2005; Terry and Whiting, 2005; Yoshizawa, 2007). Zoraptera are one of the most controversial groups in the argument of neopteran phylogeny. Our embryological knowledge on Zoraptera remains totally lacking. As far as concerning whether they belong to "Polyneoptera" or Acercaria, the embryological approach must be the most promising. Acercaria are a well-established group in light of comparative embryology, and are characterized by that the embryo of the typical semi-long germ type, deeply invaginating into the yolk, elongates with an S-shaped posture (Phthiraptera: Schölzel, 1937; Hemiptera: Butt, 1949; Psocoptera: Goss, 1953; Thysanoptera: Haga, 1985). Zorapteran embryology is greatly desired.

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