

The Paracoxal Suture in Insect Embryos: Its State and Importance for Understanding the Basalmost Podomeres*

Yukimasa KOBAYASHI

Sayamadai 2–21–18, Sayama-shi, Saitama 350–1304, Japan
E-mail: dineutus@hotmail.co.jp

In the late embryo of the ground beetle *Carabus insulicola*, the subcoxae, or the basalmost podomeres, of thoracic appendages are divided into the proximal subcoxa-1 and distal subcoxa-2 by a semi-circular furrow (Kobayashi et al., 2013). By comparing those subcoxae with the larval pleural sclerites, Kobayashi et al. assumed that subcoxae-1 and 2 correspond to the larval anapleural ring (anapleuron) and katapleural ring (katapleuron), respectively; thus, the semi-circular furrow should be equivalent to the paracoxal suture sensu Matsuda (1970). Kobayashi (2017) further pointed out that the demarcation between subcoxae-1 and 2 could be detected in some holometabolous embryos, such as Megaloptera, Neuroptera, and Trichoptera, but is obscure in the embryos of non-holometabolous taxa.

On the other hand, in the embryo of the orthopteran *Gryllus bimaculatus*, Mashimo and Machida (2017) revealed that the thoracic pleura enlarge rapidly without dividing into subcoxae-1 and 2. They defined the dorsal edge of the developing subcoxa as the boundary between the tergum and appendage (BTA). Based on this definition, they insisted that the paracoxal suture of the *Carabus* embryo is the BTA, and that the boundary between the ‘subcoxa’ and ‘coxa’ in the embryo of the grylloblatodean *Galloisiana yuasai* observed by Uchifune and Machida (2005) is also the BTA. In other words, the subcoxa-1 sensu Kobayashi et al. and the whole subcoxa sensu Uchifune & Machida are the region which should be included in the tergum.

To explore the background of this disagreement in interpretation, I have surveyed the literature (chiefly by Matsuda, 1970) describing the state and distribution of the paracoxal suture in all hexapod orders. As a result, the following are key considerations for discussing the embryonic paracoxal suture. (1) Based on the distribution of pleuro-coxal muscles of Orthoptera, it is assumed that almost all the pterothoracic pleural areas belong to the katapleuron. The anapleuron may potentially exist near the dorsal edge of the pleuron, and consequently the paracoxal suture may disappear secondarily. This state of orthopteran pleura, as pointed out by Matsuda (1970), is considerably specialized, and the result of Mashimo and Machida (2017), in which the paracoxal suture

is not observed in embryogenesis, seems to reflect this specialization. Thus, one should be cautious when generalizing these results. (2) In contrast, in several polyneopteran orders such as Grylloblattodea and Blattodea, the anapleuron is relatively large, and both the small katapleuron and the paracoxal suture are found only in the episternum. In these orders, the paracoxal suture is absent in the epimeron. (3) In most holometabolous orders, the paracoxal suture is present in both the episternum and epimeron of adult pterothoracic pleura. In the larvae, however, there are no data explicitly indicating the state of the paracoxal suture.

I have also reexamined the correspondence between the embryonic subcoxae-1 and 2 and the larval pleural sclerites of *C. insulicola*. In this species, unlike *Gryllus*, it is difficult to assume the rapid enlargement of the subcoxa in late embryonic stages. I have therefore reached the conclusion that the division into subcoxae-1 and 2 is valid, and the embryonic paracoxal suture is not equivalent to the BTA. However, to confirm whether the embryonic subcoxae-1 and 2 really develop into the larval anapleuron and katapleuron, I plan to observe the thoracic muscles of *Carabus* larvae with a micro-CT.

Based on the second consideration described above, the ‘subcoxa’ of the *Galloisiana* embryo (Uchifune and Machida, 2005) is probably equivalent to subcoxa-1. Hence the boundary between the ‘subcoxa’ and ‘coxa’ is not the BTA, probably showing the paracoxal suture plus the boundary between the epimeron and coxal meron.

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