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'Exite'-like Structures on Thoracic Appendicular Bases of a Mayfly *Bleptus fasciatus* Eaton (Insecta: Ephemeroptera, Heptageniidae)*

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Insects account for three quarters of all animal species, and more than 99 percent of them are wing-acquired insects, *i. e.*, Pterygota. Pterygotes have achieved spectacular prosperity and radiation, and the elucidation of their evolution, their morphogenesis and groundplans is one of the most interesting subjects not only in entomology but also animal phylogeny (Janzen, 1977; Wooton, 1986; Kingsolver and Koehl, 1994; Wilson, 1996; Daly *et al*., 1998). Insects were the first organisms to have developed powered flight, perhaps from within the Devonian or even the Early Carboniferous periods (*e. g.*, Engel and Grimaldi, 2004; Grimaldi and Engel, 2005). The most obvious effect of wings is the ability to disperse. A flying insect can readily exploit new habitats, and should the local environment become unfavorable, it can more effectively seek better habitats. Utilizing its flying capabilities it has access to a broader range of biological niches.

With regard to the 'origin of wings,' which has been argued over a long period, various hypotheses have been proposed, such as the 'paranotal lobe theory' (Snodgrass, 1935; Hamilton, 1971; Quartau, 1986) and the 'epicoxal exite (outer lobe or podite of the most basal leg segment) theory' (Kukalová-Peck, 1978, 1991). Of these hypotheses, presently, the latter may be currently accepted. The epicoxal exite hypothesis of wing origin can be reconciled with another recurring view that wings are derived from tracheal gills of ancestral aquatic "protopterygotes." The abdominal winglets (or gills) of the protopterygote may be serially homologous with thoracic wings (Kukalová-Peck, 1991). According to this theory, the gill itself is a modified epicoxal exite of a hypothetical, basal leg podite. The articulating epicoxal exite of the most proximal appendicular segment then became modified into a gill and then into a wing. On the other hand, the movable abdominal gills of the modern aquatic mayfly nymphs may be homologous with the abdominal winglets of the protopterygote, and be serially homologous with thoracic wings (Kukalová-Peck, 1991). Indeed, the gills of some mayflies look like tiny wings, and the tracheation in the gills resembles the venation in the wings. In addition, recent developmental biological evidence has also supported the 'exite or gill theory' by comparing the expression of genes found in 'crustacean gills' with the two genes found in wings of the insects (Averof and Cohen, 1997).

On verifying direct homology of wing to epicoxal exite, it becomes important to compare the serial homology between wings (or epicoxal exites) with other proximal exites of appendages (*e. g.*, subcoxal, coxal, trochanteral and prefemural exites). Unfortunately, the significant 'exite structures' of proximal appendicular podites do not remain in present pterygote insects (Kukalová-Peck, 1991). Those have been only recognized in the Paleozoic fossil insects (Carboniferous to Permian; about 350–250 million years ago). Because according to each insects habitat, under the effect of phylogenetical evolution, each of their appendages adapted and modified according to their functions (sometimes with the accompanying structural simplification or degeneration of non-functional structures).

However, we recently found the structures to be regarded as the remnants of subcoxal and coxal exites in the headwater-specific heptageniid mayfly *Bleptus fasciatus*, belonging to one of the most basal pterygote clades Ephemeroptera (Fig. 1A, B), which is endemic to mountain areas of Japan (except Hokkaido island and Ryukyu islands) and Korea (Miyairi and Tojo, 2007). In the coxal exites, the tracheation can be clearly observed (Fig. 2). Through this discovery amongst present winged insects, long required research has become possible into the verification of the serial homology between the 'coxal

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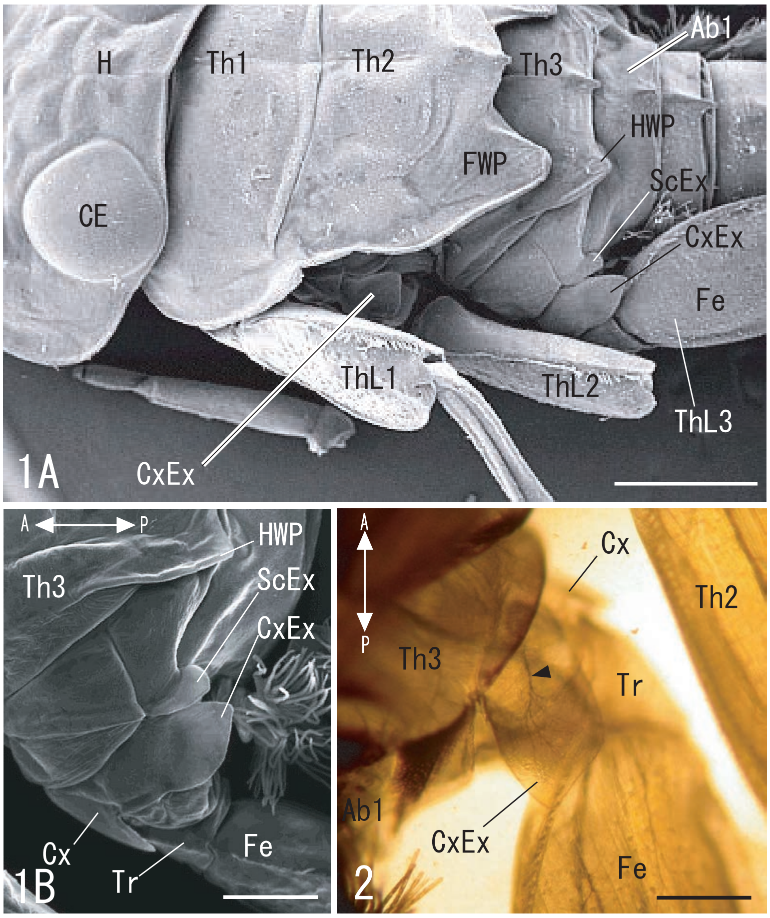

Figs. 1–2 External features of the heptageniid mayfly *Bleptus fasciatus* nymph.

Fig. 1 SEM micrographs. A. Dorso-lateral view. Note the coxal exite (CxEx), the subcoxal exite (ScEx) and the hind wing pad (HWP = 'epicoxal exite?'). B. Enlargement of the base of left hind leg (lateral view).

Fig. 2 A Light micrograph of the base of right hind leg (dorsal view). The tracheation (arrowhead) is clearly observed in the coxsal exite.

Ab1: first abdominal segment, A-P: anterior-posterior axis, CE: compound eye, Cx: coxa, CxEx: coxal exite, Fe: femur, FWP: fore wing pad, H: head, HWP: hind wing pad, ScEx: subcoxal exite, Th1–3: pro-, meso- and metathorax, ThL1–3: pro-, meso- and metaleg, Tr: trochanter. Scales = 1A : 1mm; 1B : 500μm; 2 : 300 μm.

exite - subcoxal exite - epicoxal exite (*i. e.*, wing),' and that between the 'epicoxal exite (*i. e.*, wing) - gill' with various newly available approaches.

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