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Short communication

Homology of the wing base sclerites in Ephemeroptera (Insecta: Pterygota) – A reply to Willkommen and Hörnschemeyer

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Abstract

We revised the homology of wing base structure in Ephemeroptera (Insecta: Pterygota) proposed by Willkommen and Hörnschemeyer in a recent issue of *Arthropod Structure and Development*. The first free sclerite (s1) in Ephemeroptera should be homologized with a part of the first axillary sclerite (1Ax) of Neoptera, together with the second free sclerite, whereas the authors recognized s1 as a detached part of the anterior notal wing process. The fifth free sclerite of Ephemeroptera should be homologized with the median notal wing process of Neoptera, rather than it being homologous with a part of 1Ax in Neoptera, as the authors postulated. Hypothesized secondary fusion of the axillary sclerites in Ephemeroptera and Odonata proposed by the authors is premature, because the basal phylogeny of Pterygota is still poorly understood, and an alternative interpretation of morphological evolution (i.e., that undifferentiated axillary sclerites represent the ground plan of Pterygota) can also be drawn from the Ephemeroptera + Neoptera hypothesis.

Keywords: Palaeopterans; Neoptera; Axillary sclerites; Articulations; Folding line; Notal wing process

1. Introduction

Morphology of the wing base structure in insects is very difficult to interpret. In particular, the completely different wing folding mechanisms in palaeopterans (Ephemeroptera and Odonata) and Neoptera (all other winged insects) make it extremely difficult to homologize their wing base structure (reviewed in Willkommen and Hörnschemeyer, 2007).

In a recent issue of this journal, Willkommen and Hörnschemeyer (2007) (referred to as W&H from this point on) addressed this very difficult problem. On the basis of detailed examinations of the external morphology and musculature in Ephemeroptera, they proposed homology of the wing base sclerites between Ephemeroptera and Neoptera. They also discussed the ground plan condition of the wing base morphology and wing folding mechanism in insects based on their morphological observations and phylogenetic hypotheses presented by previous authors (e.g., Ogden and Whiting, 2003).

In the course of our series of studies on the polyneopteran (Yoshizawa, 2007) and palaeopteran wing base, we have also attempted to homologize the wing base structure between Ephemeroptera and Neoptera. Although our interpretations are largely in agreement with those presented by W&H, further support for their conclusions and evidence for alternative interpretations have resulted from our observations.

2. Materials and methods

The following taxa of Ephemeroptera were examined in this study: Baetidae – Genus undet.; Dipteromimidae – *Dipteromimus*; Ephemerellidae – *Uracanthella*; Ephemeridae – *Ephemera*; Ephemeropteridae – Genus undet.; Heptageniidae – *Ecdyonurus*, *Epeorus*; Isonychiidae – *Isonychia*; Siphlonuridae – *Siphlonurus*. Neopteran taxa examined were listed in Yoshizawa (2007). Dissecting and observing methods followed Yoshizawa (2007), and terminology followed W&H.

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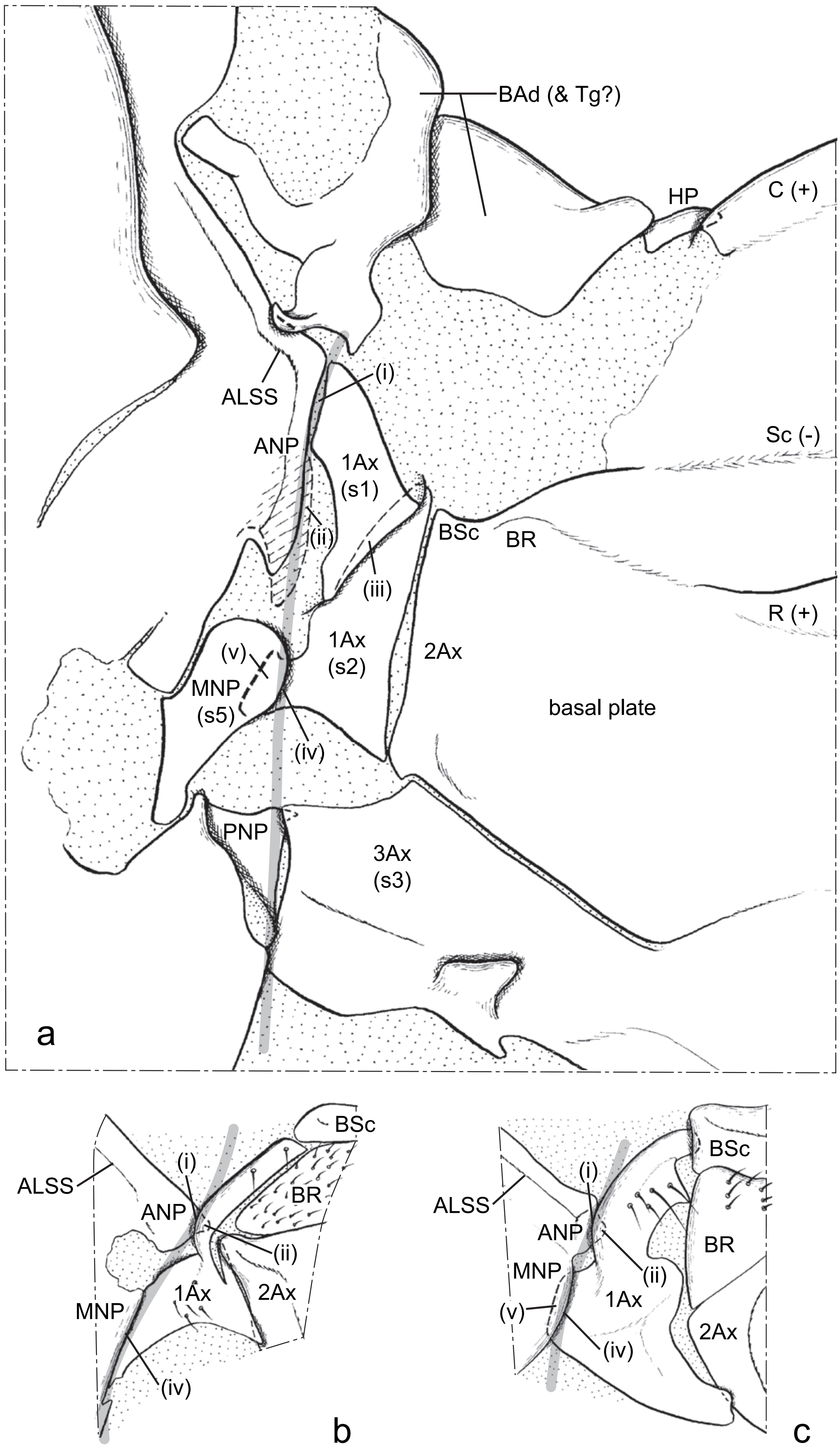

Fig. 1. Forewing base of (a) Ephemeroptera: *Isonychia japonica*, (b) Plecoptera: *Nemoura* sp. and (c) Mecoptera: *Panorpa japonica*. Parts (b) and (c) show first axillary sclerite and related structures, only. Gray lines indicate the basal hinge. Abbreviations: ALSS, anterolateral scutal suture; BAd, dorsal part of basalar sclerite; BR, basiradiale; BSc, basisubcostale; HP, humeral plate; PNP, posterior notal wing process; Tg, tegula; (+), convex vein; (−), concave vein. See text for other abbreviations and Roman numerals.

3. Results and discussion

Apart from a few points, our interpretations are in agreement with those presented by W&H. Therefore, we focus only on the controversial points below.

3.1. Homology of the first axillary sclerite (1Ax) and related sclerites

In Neoptera (Fig. 1b, c), 1Ax articulates proximally to the notum with two wing processes, anterior (ANP) and median notal processes (MNP). The folding line formed by these two articulations is the basal hinge. These articulations and folding line bear a principal function in the wing flapping and folding (Wootton, 1979) and thus are highly conserved throughout the Neoptera. The apex of ANP extends beneath the anteroproximal margin of 1Ax. In contrast, the posteroproximal part of 1Ax usually extends beneath MNP.

The first free sclerite (s1) in Ephemeroptera (Fig. 1a) was considered by W&H as a detached part of ANP. However, three points of evidence indicate that s1 cannot be homologized with ANP but represents a part of 1Ax together with s2 (see Fig. 1 for characters mentioned by Roman numerals): (i) the basal hinge runs between the notum and s1; (ii) the lateral margin of the notum next to s1 has an apodeme and s1 is placed over the apodeme; (iii) the distal margin of s1 is sometimes placed on the upper side of 1Ax (s2), and this condition is contrary to the neopteran ANP (lower) and 1Ax (upper) (character ii in Fig. 1b, c). In addition, s1 and s2 are completely fused with each other in a species of Baestidae examined in this study, which may provide further support for our interpretation.

The s5 in Ephemeroptera (Fig. 1a) was identified as MNP by W&H, but they also mentioned the possibility that s5 could represent a part of 1Ax. However, the latter possibility can be clearly excluded by the following two observations: (iv) the basal hinge runs between s5 and 1Ax (s2); (v) the posteroproximal corner of 1Ax (s2) extends beneath s5. In some Ephemeroptera (e.g., *Epeorus*, *Siphlonurus*), s5 is fused to the notum which represents the same condition as that observed in Neoptera.

3.2. Ground plan of the wing base

W&H estimated the polarity of wing base evolution based on two hypotheses of the basal diversification of Pterygota, i.e., monophyly of Palaeoptera or sister group relationship between Odonata + and Neoptera (=Metapterygota) (reviewed in Ogden and Whiting, 2003). They concluded that the wing base structure of Neoptera (i.e., presence of three separate axillary sclerites) is more similar to the ground plan condition of Pterygota, and secondary fusion of the axillary sclerites in Ephemeroptera and Odonata is most likely. However, they did not care for another possible hypothesis, i.e., a sister group relationship between Ephemeroptera + and Neoptera (Lemche, 1940; Brinck, 1962; Matsuda, 1970; Ogden and Whiting, 2003; Kjer, 2004). In addition, a clear border (e.g., suture) and evidence of the secondary fusion between 2Ax and the basal plate cannot be identified in the present study (Fig. 1a). Based on the latter phylogenetic hypothesis and our morphological observation, differentiation of 1Ax and 3Ax from the basal plate as observed in Ephemeroptera and Neoptera can also be regarded as their synapomorphy, and undifferentiated axillary sclerites as seen in Odonata may represent the ground plan condition of Pterygota. Even under the Palaeoptera or Metapterygota hypotheses, undifferentiated 2Ax from the basal plate is an equally or more parsimonious explanation as the ground plan condition of Pterygota.

3.3. Conclusion

W&H's study is based on the detailed examination of external and muscle morphology and presents strong evidence for the homology between the ephemeropteran and neopteran wing bases. However, some ambiguities remain in their interpretation. Our examination of the articulations and folding line in the wing base successfully removes these ambiguities, clarifying homology of ephemeropteran and neopteran wing base structures. Further morphological investigation of the wing base sclerites and a stable phylogenetic hypothesis on the basal diversification of Pterygota are still needed for thorough understanding of the origin and transformation of the insect wing base structure.

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