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## Morphology of the elytral base sclerites

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## ABSTRACT

The elytral base sclerites (= sclerites located at the articular region between the forewing and thorax in Coleoptera) of selected taxa were examined and homologized. Although the elytral base sclerites are highly modified compared to the wing base sclerites of the other neopterans, they can be homologized by using the conservative wing flapping and folding lines as landmarks. A reduction of the first axillary sclerite was identified as a general trend of the elytral base sclerites, although the sclerite usually has a very important function to mediate flight power from the notum to the wing. This result indicates that the functional constraint against the basal sclerites is relaxed because of the lack of an ability to produce flight power by elytra. In contrast, the elytral folding system formed by the basal sclerites is well retained, which probably occurs because proper wing folding is a key for the shelter function of the elytra. The elytral base sclerites apparently contain more homoplasies than the serially homologous hindwing base sclerites of Coleoptera, which suggests that the structure is less useful for higher-level systematics. However, the faster evolutionary rate of the elytral base sclerites suggests there is potential for studying the lower-level phylogeny of Coleoptera.

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## 1. Introduction

The wing base structure consists of several tightly associated sclerites located at the joint region between the wing and thorax. These sclerites play principal roles in wing flapping, rotating, and folding (Brodsky, 1994). Therefore, these sclerites are strongly constrained functionally and are known to evolve very slowly (Hörschemeyer, 2002). In addition, the complicated shapes and articulations of the wing base sclerites make it possible to code considerable numbers of characters useful for phylogenetic estimations. Because of these properties, the wing base structure has been utilized for uncovering deep insect phylogeny (Yoshizawa and Saigusa, 2001; Hörschemeyer, 2002; Yoshizawa, 2007, 2011; Yoshizawa et al., 2017). Overall, the trees estimated from the wing base morphology are congruent with the results from molecular phylogenetic analyses (e.g., Ishiwata et al., 2011) and comprehensive insect phylogenomics (Misof et al., 2014).

Coleoptera are the most diversified insect order. They are characterized by highly modified forewings, called elytra, which function as a shelter against physical damage, predation,

desiccation, and changes in temperature (Linz et al., 2016). The hindwing base structure of Coleoptera, which has a much less modified condition, has been studied for a wide range of taxa and utilized for higher level phylogenetic estimations (Browne and Scholtz, 1998, 1999; Hörschemeyer, 1998). The forewing base structure (i.e., elytral base) of Coleoptera has also been examined in some studies, but most of the observations were conducted as part of an extensive morphological study of single species and thus lacked a comparative point of view (Rivnay, 1928; Bostick, 1945; El-Kifl, 1953; Tremblay, 1958; Doyen, 1966; Larsén, 1966). Some studies made comparative analyses, but comparisons were restricted to closely related taxa only (Stellwaag, 1914; Herbst, 1952; Ahrens, 2006; Frantsevich, 2011; Sípek et al., 2016). Therefore, most of the previous studies lacked reliable arguments about the homology and transformation of elytral base sclerites throughout the order. A couple of unique terms (e.g., basal process: Doyen, 1966; basal lobe: Larsén, 1966; elytral root: Sípek et al., 2016) have been adopted for elytral base sclerites without homologization with the wing base structure of the other Neoptera, which should also be resolved.

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**Table 1**  
Comparisons of the homology schemes of the elytral base sclerites presented here and in previous studies.

Reference[Taxa (family)]present scheme	Tg	HP	BSc	BR	1Ax	2Ax	3Ax	PMP	DMP
Bostick (1945: fig. 17)	—	Costa	Subcosta (ventral)	—	Ax1	Ax2	Ax3 (part)	Ax37 (part)	—
Larsén (1966: fig. 9)	—	Co?	Sco	Rd	1Ax (part)	1Ax (part) + 2Ax	3Ax + 4Ax	—	—
Richmond (1931: fig. 27)	—	ae (elytral apophysis)	—	—	—	—	—	—	—
Stellwaag (1914: figs 8–9 & tab. XI)	—	lateral apophysis	—	Achl	Achl (Ax1: part)	Achl (part)	Achl + Pf (root)	—	median apophysis
Herbst (1952: nomenclature)	—	L (costal lobe)	AO1 (upper apophysis 1)	AO2	Ax1	Ax2	Ax3	—	AO3
Ahrens (2006: fig. 5, app. 3)	—	hs	bsc	fm1	—	Ax2	Ax3	—	bmp
Frantsevich (2011: fig. 3)	—	root	—	—	Ax1	Ax2	Ax3	—	—
Sipek et al. (2016: fig. 2)	—	elytral root	—	—	Ax2	Ax2	Ax3	—	—
El-Kifí (1953: fig. 25)	—	basal process	—	—	lateral plate of mesonotum ?	1Ax	2Ax	3Ax?	—
Doyen (1966: fig. 38)	—	basal process	—	—	—	axillary 2	axillary 3	—	axillary 1
Tremblay (1958: figs 1–2)	1M (mesoptera)	PBA (joint process)	AR-2M (part)	2M (part)	2M (part)	(2Ax)	3M	—	—
Rivnay (1928: fig. 15)	—	apophysis	—	—	—	—	—	—	—

The wing base sclerites are also crucial for identifying the homology of the wing veins (Wootton, 1979). Homology between the elytral and wing regions (such as radial, medial, cubital or anal areas) is less understood, and it has been only aided based on limited fossil records of primitive Coleoptera (Kukalová-Peck and Beutel, 2012; Kirejtshuk et al., 2014). Proper understanding of the elytral base structure may provide a clue to identify the homology of elytral regions and to identify the origin and transformation of these highly modified wings.

In this study, we observed and homologized the elytral base sclerites of selected taxa from Coleoptera. This work will form the basis for future morphological, evolutionary and functional studies of the elytra and the elytral base sclerites.

## 2. Materials and methods

The main purpose of this study was to establish a consistent homology interpretation for the elytral base sclerites. Previously, the elytral base sclerites were examined and homologized for several coleopteran taxa (Table 1). Therefore, taxa were mainly selected from the families or their close relatives (Cerambycidae instead of Chrysomelidae) shown in Table 1. In addition, the elytral base sclerites of a species of Buprestidae (Polyphaga) was examined because of its special interest for the study of morphological transformations. The following taxa were examined: suborder Adephaga: Carabidae (*Calosoma chinense*) and Gyrinidae (*Dineutus orientalis*); suborder Polyphaga: Hydropphilidae (*Hydrophilus acuminatus*), Scarabaeidae (*Trypoxylus dichotomus*), Tenebrionidae (*Andocamaia ryukyuensis*), Cleridae (*Enoclerus moestus*), Buprestidae (*Chrysodema manillarum*) and Cerambycidae (*Prionus insularis*). Dried or alcohol-preserved specimens were used. The thorax of each specimen was removed from the other body parts and was soaked in 10% KOH at room temperature for one night. The soaked material was rinsed with water, followed by 80% ethanol, and then stored and observed in glycerol. To facilitate the observation of dorsal structures, the ventral structures, including the ventral layer of the wings, were removed. Observations were made using Olympus SZ60 and Olympus SZX16 binocular microscopes.

## 3. Results (Figs. 1–8, Table 1)

The first axillary sclerite (1Ax) of the elytral base is highly variable in the shape and the degree of development. In Carabidae, it has a posterior triangular body and an anterior arched head (Fig. 1), which was generally observed in the other neopteran 1Ax. Proximally, it articulates with the notum by two points of the body region, but the posterior articulation is looser. Apically, the head articulates with the middle part of the elytral root (as discussed by Sipek et al., 2016) along the convex axillary fold line. The head of 1Ax and the elytral root are partly fused, but this condition is uniquely observed in Carabidae. Distally, it articulates with the second axillary sclerite by two points of the body region. In Cerambycidae, the fully developed condition of 1Ax was observed, but it is less developed (Fig. 8). The head region is very weakly sclerotized. In Gyrinidae (Fig. 2) and Buprestidae (Fig. 7), the head and body regions were separated into two independent sclerites. In Scarabaeidae (Fig. 4), Tenebrionidae (Fig. 5) and Cleridae (Fig. 6), the head region is completely unsclerotized, so the articulation between 1Ax and elytral root is absent. In Hydrophilidae, 1Ax is completely reduced (Fig. 3).

The second axillary sclerite (2Ax) is well developed throughout the examined taxa but is highly variable. In Carabidae (Fig. 1) and Gyrinidae (Fig. 2), it is triangular and articulates

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