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A revised interpretation of the wing base structure in Odonata

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Abstract. Homology of the wing base structure in the Odonata is highly controversial, and many different interpretations for this structure have been proposed to date. In extreme cases, two independent origins of the insect wings have been suggested based on comparative morphology between the odonate and other pterygote wing bases. Difficulties in establishing homology of the wing base structures between Odonata and other Pterygota are mainly due to their extreme differences in morphology and function. In the present paper, we established homology of the wing base structures between Neoptera, Ephemeroptera and Odonata using highly conservative and unambiguously identifiable characters (the basal wing hinge and subcostal veins) as principal landmarks. As a result, the odonate wing base structure was reasonably homologized with those of Ephemeroptera and Neoptera. Based on the present interpretation, the ancestral condition of the wing base structure in insects is also discussed.

Introduction

In number of species, the Pterygota (winged insects) occupy more than 98% of the most diversified eukaryote class, Insecta (Grimaldi & Engel, 2005). They were the first living things to take flight, and this ability of flight greatly improved their capabilities of dispersal, evasion of predators, and mate location (Engel & Grimaldi, 2004; Grimaldi & Engel, 2005). The acquisition of wings is considered to be a key morphological innovation which led to the present diversity of insects, and therefore uncovering the origin and evolution of the insect wings and flight is important in understanding the evolution and diversification of insects (Grimaldi & Engel, 2005; Hörnschemeyer & Willkommen, 2007). The origin of insect wings and flight has attracted attention and has been studied from many different points of view (reviewed by Boxshall, 2004), such as morphology of the extant (Snodgrass, 1935; Hamilton, 1971; Willkommen & Hörnschemeyer, 2007) and fossil (Kukalová-Peck, 1983, 1991) insects, functional morphology (Marden & Kramer, 1994, 1995; Hasenfuss, 2002), physical modeling (Kingsolver & Koehl, 1985, 1994; Wootton & Ellington, 1991) and developmental genetics (Averof & Cohen, 1997; Goto & Hayashi, 1997; Damen et al., 2002).

The insect wing is a complex system composed of membranes, veins, folding and flexion lines, and marginal setae. The combination of all these elegant structures is what provides insects with the capability of flight (Brodsky, 1994). Furthermore, the wing base structure plays an important role in insect flight. The wing base structure is a complicated system composed of the notal margin, axillary sclerites, median plates, and vein bases, as well as articulations and folding lines formed by these structures (Wootton, 1979). The wing base structure transmit flight power from the thorax to wing veins. Also, rotation of the wing is controlled directly by muscles inserted to the wing base sclerites (Brodsky, 1994).

Therefore, reconstruction of the ancestral condition of the wing base structure is essential in understanding how the insect wings originated and evolved (Hörnschemeyer & Willkommen, 2007; Willkommen & Hörnschemeyer, 2007).

In reconstructing the ancestral condition of the wing base structure, the seemingly most promising approach would be to analyze the ancestral fossil insects (Kukalová-Peck, 1983, 1991). The analysis of the tiny and complicated wing base morphology, however, is extremely difficult even in extant insect orders, such that of the utility of less preserved fossil insect wings is questionable (Meier, 1993). The second best, but most practical approach is to analyze the wing base structure of extant insects. Among the extant insect orders, the Odonata (dragonflies and damselflies) are considered to be the most basal winged insects, together with the Ephemeroptera (mayflies) (= Palaeoptera: Kristensen, 1991). The wing folding mechanism in palaeopterans is completely different from that in Neoptera (= winged insects excluding palaeopterans) and, generally, the wing folding mechanism observed in Neoptera (backward wing folding) is considered to represent a more derived condition than the palaeopteran wing folding (no backward wing folding) (Martynov, 1925; La Greca, 1980; see also Willkommen & Hörnschemeyer, 2007 and Hasenfuss, 2008 for alternative interpretation). Therefore, the wing base structure of palaeopteran orders is critical in understanding the ancestral condition of the insect wing base.

Homology of the wing base structure is relatively well established in Neoptera (e.g., Matsuda, 1970; Yoshizawa & Saigusa, 2001; Hörnschemeyer, 2002; Hörnschemeyer & Willkommen, 2007; Yoshizawa, 2007) and palaeopteran Ephemeroptera (Willkommen & Hörnschemeyer, 2007; Yoshizawa & Ninomiya, 2007). In contrast, the wing base structure in Odonata is understood only poorly, and many different interpretations have been proposed (Chao, 1953; Tannert, 1958; Matsuda, 1970, 1981; La Greca, 1980; Brodsky, 1994). Among these, the most extreme interpretations are those proposed by Matsuda (1970, 1981) and La Greca (1980), who conclude that the wing base structure of Odonata cannot be homologized with that of Ephemeroptera and Neoptera, and insect wings must have evolved twice, independently. Monophyly of Pterygota is now strongly supported with morphology and molecular data (Kristensen, 1991; Grimaldi & Engel, 2005; Yoshizawa & Johnson, 2005; Kjer et al., 2006; Mallatt & Giribet, 2006; Misof et al., 2007) and thus independent origins of the insect wings generally are not accepted. However, homology of odonate wing base is very poorly established, and Matsuda's and La Greca's interpretations of odonate wing base structure have not yet been tested critically.

Difficulties in establishing homology of the wing base structures between Odonata and other Pterygota are due mainly to their significant differences in appearance and function. The axillary areas of Ephemeroptera and Neoptera are composed of several detached sclerites, whereas in Odonata there is only a single sclerite (= the axillary plate). In contrast, the costal margin of Odonata shows much more complicated morphology than that of Ephemeroptera and Neoptera. Wing flapping is promoted by the indirect flight muscles in Ephemeroptera and Neoptera whereas it is promoted by the direct flight muscles in Odonata. Despite these significant differences, the previous approaches in establishing the odonate wing base homology were based largely on the superficial similarity and relative positions of sclerites, and all failed to homologize the odonate wing base confidently (Tannert, 1958; Matsuda, 1970, 1981; La Greca, 1980; Brodsky, 1994). In identifying their homology, putting reliable landmarks (the points of which homology can be decided unambiguously) is critical, and the basal hinge is a hopeful candidate for the principal landmark (Yoshizawa, 2007; Yoshizawa & Ninomiya, 2007). The basal hinge is the most basal folding line bearing a principal function in the wing flapping (Wootton, 1979) and thus is highly conserved throughout the winged insects. The second landmark would be the subcostal vein (Sc). Although homology of some veins in Odonata is controversial, there is consensus on homology of the Sc vein throughout the insect orders (Riek & Kukalová-Peck, 1984; Brodsky, 1994; Rehn, 2003; Trueman, unpubl. cited in Gullan & Cranston, 2005; Bechly, 2007). Sc

can be identified without doubted as the second anterior-most concave vein. Because of its functional importance, the relative position of the Sc vein to the costal and radial veins is constrained and thus is conserved (Wootton, 1981).

Here we establish homology of the wing base structure in Odonata using the basal hinge and Sc vein as landmarks. As a result, homology of the wing base structures between Odonata, Ephemeroptera and Neoptera can be established reasonably. Misinterpretations in the previous researches are identified. Based on the newly established scheme of the insect wing base morphology, we discuss the ancestral condition of the wing base structure.

Materials and Methods

Taxa examined are listed in Appendix 1. Ephemeropteran and neopteran taxa examined were listed previously (Yoshizawa, 2007; Yoshizawa & Ninomiya, 2007). Both dried and wet (preserved in 80 or 98% ethanol) specimens were used for examinations. Thoraces were removed from the specimen and soaked with 10% KOH for 24 hours at room temperature. The soaked specimen was rinsed with distilled water and then with 80% ethanol, and examination was carried out in 80% ethanol or 50% glycerol using a Olympus SZ60 binocular dissecting microscope. Dissecting and observing techniques followed Yoshizawa (2007). The odonate wing bases are highly 3-dimensional structure. Therefore, in observing articulations between the notum and axillae, the wing was stretched artificially downward (bottom of Figs. 1, 3-4). Freshly killed and undissected specimens of *Aeshna nigroflava* and *Sympetrum infuscatum* were used for further examination of the movement of wing articulations. All specimens examined are stored in the Hokkaido University Insect Collection as vouchers.

Terminology of the notal and wing base structures which could be adopted throughout the winged insect orders followed Brodsky (1994). Specific terms for the ephemeropteran wing base structure followed Yoshizawa & Ninomiya (2007). Homology of some odonate wing base structures is controversial so that the most neutral terms were adopted following Tannert (1958: proximal and distal costal plates) and Hatch (1966: prescutum, semi-detached scutal plates, and axillary plate). Several new terms were coined, which are mentioned in the text. Terms and abbreviations adopted in this paper for the odonate wing base structure are summarized in Fig. 1.

The following descriptions of morphological characters were based only on the forewing base structure. However, the wing base structures of Odonata showed homogeneous condition in both wings. Therefore, in general, the following descriptions can also be applicable to the hindwing base structure.

Results

The landmarks

In all examined specimens, the basal hinge runs along the proximal margins of the proximal costal plate and the axillary plate (Figs. 1-4). The semi-detached scutal plates and processes extending from the prescutum, scutum and scutellum are located internal to the basal hinge. This condition was confirmed in freshly killed specimens of *Aeshna nigroflava* and *Sympetrum infuscatum*.

The subcostal vein (Sc) was identified easily as the second anterior-most and concave vein in all the specimens examined (Figs. 1-4). The basisubcostale (BSc) was also identified unambiguously by tracing the ventral Sc vein basally. BSc is separated from the axillary plate by a narrow membranous notch proximally, but they are fused with each other distally. Medially, a longitudinal (i.e., along the long wing axis) ridge was observed clearly on BSc.

The notum

A process, termed here as prescutal process (PsP), extends from the lateral region of

the prescutum (Figs. 1, 3, 4). The semi-detached scutal plates (SDP) are placed posterodistal to PsP and anterolateral to the scutum. SDP and PsP usually are bordered by a groove, and a deep hemispherical concavity toward SDP is frequently invaginated from the groove. There is a deep concavity between the scutum and SDP, and a tendon is inserted to the concavity.

SDP can be subdivided into three parts. This subdivision is especially clear in Anisoptera (Fig. 3) and Zygoptera (Fig. 4). In these groups, the median part of SDP (mSDP) clearly is separated from a sclerite placed posterior to mSDP (pSDP). pSDP is closely associated with the axillary plate but these sclerites do not form articulation between them. A sclerite placed distal to mSDP and associated with PCP is the distal SDP (dSDP). It is distinct in Anisoptera (Fig. 3) and Zygoptera (Fig. 4), but mSDP and dSDP are partly fused in Anisozygoptera (Fig. 1). The anterior part of mSDP extends laterally toward PCP, and the extended part overlaps to the anterior tip of dSDP. The posterolateral corner of dSDP extends laterally, and the extension is approximated closely with PCP. In Zygoptera, an additional extension is observed anterior to the posterolateral corner, and this additional extension composes a tight articulation with PCP (Fig. 4). Such extension and articulation are not observed in Anisozygoptera and Anisoptera, but only a weak expansion is observed on the lateral margin of dSDP in these suborders (Fig. 1). The posterior region of pSDP strongly swells posterodorsally and is completely (Zygoptera: Fig. 4) or partly (Anisozygoptera and Anisoptera: Figs. 1, 3) separated from the other part of pSDP.

Along the basal hinge, three articulations were confirmed between the axillary plate and notum (Figs. 1-4, bottom). The anterior articulation is formed by a strongly swollen projection extending from the scutum. The apical tip of the projection extends beneath the proximal margin of the axillary plate. The median articulation is formed by a sclerite placed posterior to the projection. The sclerite is separated clearly from the projection by narrow membranous region. The internal margin of the axillary plate extends beneath the distal margin of the sclerite. The posterior articulation is formed by a projection extending from the scutellum and the posteroproximal corner of the axillary plate. An apparent sulcus can be seen at the base of the projection.

The costal plates

The costal plates are sclerites located distal to the basal hinge and basal to the costal vein (Figs. 1, 3-4). The costal plates comprise two sclerites, the proximal and distal costal plates (PCP and DCP). PCP is strongly swollen anteriorly and dorsally. It can be divided into two areas by a deep longitudinal groove. On the anterior lobe of PCP, a tendon is inserted internally to which direct flight muscles are attached. The posterior lobe of PCP is usually subdivided into two regions by a shallow longitudinal groove. PCP is associated distally with DCP. In Anisozygoptera and Zygoptera, DCP is tightly associated with C vein distally, and they are separated only by a narrow membranous region (Figs. 1, 4). In Anisoptera, their association is looser, and they are associated tightly only at the posterior region (Fig. 3). On DCP, no insertions of muscle or tendon were observed.

The axillary plate

The axillary area is defined here as the wing base region distal to the basal hinge and posterior to BSc. In Odonata, a strongly swollen sclerite, the axillary plate (AxP), is situated in the axillary area (Figs. 1-4). In Anisozygoptera and Zygoptera, there is a pair of weak humps at the area where AxP articulates with the scutum (Figs. 1, 4). In Zygoptera, there is a narrow membranous region distal to the posterior hump (Fig. 4). In Anisoptera, a pair of flat sclerites extends from the proximal margin of AxP, and the posterior sclerite articulates with the scutal process (Fig. 3 bottom). The anterior hump of Anisozygoptera and Zygoptera (Figs. 1, 4), and the anterior flat sclerite of Anisoptera (Fig. 3) are tightly associated with the proximal tip of BSc. From the proximal part of AxP just posterior to the AxP-scutal

articulation, a narrow membranous region is invaginated deeply toward the posterior corner of AxP (Figs. 1-4). The structure located proximal to the notch is strongly sclerotized, and its anterior tip strongly projects anteriorly.

The R and M veins arise from the anterior margin of AxP (Figs. 1, 3-4). These veins are associated tightly with each other basally, but are clearly distinguishable. The basal ends of these veins are unclear, but the base of R vein seems to be at the base of the paired hump in Anisozygoptera and Zygoptera (Figs. 1, 4), and the base of the proximal flattened extension of Anisoptera (Fig. 3). The base of M vein seems to be at median part of AxP. The Cu vein arises from the distal part of AxP, where AxP strongly expanded distally over the base of Cu vein (Figs. 1, 3-4).

AxP is somewhat truncated posterodistally and continues to a flat sclerite where insertion of a muscle can be confirmed (Figs. 1-4). On the sclerite, a membranous region is usually observed just distal to the point of muscular insertion. However, such a membranous region cannot be observed in some large anisopterans (e.g., *Anotogaster sieboldi*, *Epiphthalmia elegans*, *Orthetrum* spp., *Sympetrum* spp.). The A vein arises from the posterodistal part of the flattened region (Figs. 1, 3-4).

Discussion

Homology of the costal plates (Fig. 5)

Judging from the positional congruence (i.e., just basal to the C vein), the distal costal plate (DCP) in Odonata can be homologized unambiguously with the humeral plate (HP) of Neoptera and Ephemeroptera (Matsuda, 1970; Pfau, 1986; Brodsky, 1994). In contrast, homology of the proximal costal plate (PCP) of Odonata needs further analysis.

A key feature in interpreting the homology of PCP is the presence of an internal tendon and muscles inserted to it. The muscles are the direct flight muscles which perform wing flapping (Pfau, 1986). In addition, the muscles perform pronation of wings (Pfau, 1986; Newman & Wootton, 1988). As well as wing flapping, pronation is one of the most important motions in flapping flight (Tennekes, 1996). Therefore, in the winged insects, this function should have been retained throughout the group.

In Neoptera, the basalare (Ba) and muscle inserted to it perform pronation of wing (Pfau, 1986; Nalbach, 1989; Brodsky, 1994; Balint & Dickson, 2001). This may suggest homology between Ba and PCP. However, morphological and functional differences of these structures also are significant. For example, Ba of Neoptera is located beneath the wing and only is connected with HP at a point (Brodsky, 1994; Hörnschemeyer, 2002), whereas PCP in Odonata widely occupies dorsal and costal regions of the wing and is associated widely with HP (= DCP) (Figs. 1, 3-4). In addition, the direct flight muscle is not observed on neopteran Ba, and only promotes wing flapping (Brodsky, 1994). Therefore, it is difficult to homologize the odonate PCP and neopteran Ba directly.

However, the ephemeropteran Ba shows an intermediate condition. On the basis of external and musculatural morphology, homology of the neopteran and ephemeropteran Ba has been well established by Brodsky (1974) and Willkommen & Hörnschemeyer (2007). Ba of Ephemeroptera occupies the dorsal region of the wing and has strong connection with HP (Yoshizawa & Ninomiya, 2007), and this condition is in good morphological agreement with PCP of Odonata. In addition, ephemeropteran Ba assists wing flapping as well as pronation of wing (Brodsky, 1970; Pfau, 1986; Willkommen & Hörnschemeyer, 2007), and it is also in good functional agreement with the odonate PCP.

Judging from the above evidence, it is most reasonable to homologize the odonate PCP with Ba of Neoptera and Ephemeroptera. Chao (1953) and Matsuda (1970) homologized PCP with HP, but this interpretation cannot be justified morphologically and functionally. Based on the positional similarity, Yoshizawa & Ninomiya (2007) mentioned also that the dorsal part of the ephemeropteran Ba (= PCP of Odonata) may be, at least in

part, homologous with the tegula of Neoptera. In Ephemeroptera, the anterior end of the basal hinge is not clearly observed (Yoshizawa & Ninomiya, 2007) but, in Odonata, anterior end of the basal hinge apparently runs along the proximal margin of PCP (Figs. 1, 3-4). The tegula of Neoptera is located internal to the basal hinge (Yoshizawa & Saigusa, 2001; Yoshizawa, 2007). Therefore, PCP cannot be homologized with the tegula, and the potential homology proposed by Yoshizawa & Ninomiya (2007) is unjustifiable.

Homology of the axillary plate and notal processes (Fig. 5)

The basal hinge bears the principal function in wing folding and flapping (Wootton, 1979). In addition, as confirmed by Yoshizawa (2007) and Yoshizawa & Ninomiya (2007), positions and conditions of the articulations along the basal hinge are highly conserved throughout the Neoptera and Ephemeroptera. Therefore, these features are very important in determining the homology of the wing base structure between Odonata, Ephemeroptera and Neoptera. In Ephemeroptera and Neoptera, the following three articulations are consistently observed along the basal hinge posterior to BSc: (1) the anterior notal wing process (ANP) and the anteroproximal part of the first axillary sclerite (1Ax) : ANP arises from the scutum, and the tip of ANP extends beneath the proximal margin of 1Ax; (2) the median notal wing process (MNP) and the posteroproximal corner of 1Ax: MNP arises from the scutum (Neoptera) or is a free sclerite placed posterior to ANP (Ephemeroptera), and the posteroproximal part of 1Ax extends beneath the distal margin of MNP; (3) the posterior notal wing process (PNP) and proximal tip of 3Ax: PNP arises from the scutellum.

As mentioned above, the Sc vein and BSc of Odonata can be identified undoubtedly from the positional and morphological congruence of Sc vein with that in Neoptera and Ephemeroptera. Homology of BSc between Odonata and Neoptera is also corroborated by the presence of median longitudinal ridge on BSc in both groups (Figs. 1, 3-4: Yoshizawa & Saigusa, 2001; Yoshizawa, 2007), although such ridge is absent in Ephemeroptera (Yoshizawa & Ninomiya, 2007). Therefore, the region posterior to BSc can be identified as the axillary area throughout the winged insects, and AxP is the only sclerite placed in the axillary area of Odonata.

We confirm three articulation points between AxP and the notum in Odonata (Figs. 1-4). The anterior articulation is composed of the anteroproximal margin of AxP and a process extending from the scutum, and AxP is placed over the tip of the process. The median articulation is composed of the mid-proximal margin of AxP and a free sclerite placed posterior to the scutal process, and the distal margin of the free sclerite is placed over AxP. The posterior articulation is composed of the posteroproximal corner of AxP and a process extending from the scutellum. Numbers and conditions of these articulations are in complete agreement with the above mentioned articulations (1)-(3) observed consistently through the neopteran and ephemeropteran wing bases. Therefore, it is reasonable to estimate that the above three articulations observed between the notum and AxP in Odonata are homologous with ANP, MNP and PNP of Neoptera and Ephemeroptera. It is estimated from the articulatory conditions that the anteroproximal region of AxP corresponds 1Ax, and posterior region of AxP corresponds 3Ax of Neoptera and Ephemeroptera (Fig. 5).

The above estimation can also be corroborated by some other morphological features. In Neoptera and Ephemeroptera, the anterior tip of 1Ax is closely associated with the proximal tip of BSc. In Odonata, the anteroproximal region of AxP is associated closely with the proximal tip of BSc (Figs. 1, 3-4). The agreement of these morphological structures corroborates the present interpretation, i.e., the anteroproximal region of AxP in Odonata corresponds to 1Ax of Neoptera and Ephemeroptera. In Zygoptera, a narrow membranous region can be observed on AxP (Fig. 4) which somewhat looks like representing the border between 1Ax and 2Ax as observed in Neoptera and Ephemeroptera. However, such membranous region cannot be observed in Anisozygoptera and Anisoptera (Figs. 1-3). It is not clear whether the presence of the membranous region represents the most ancestral

condition of the odonate wing base and whether it represents the border between 1Ax and 2Ax.

Concerning to the homology of odonate 3Ax, the following points of evidence corroborate the present interpretation estimated from the notal articulation. First, in Neoptera and Ephemeroptera, the muscles t-p14 (both groups) and t-p13 (only Neoptera) are inserted to 3Ax (Matsuda, 1970; Brodsky, 1994; Willkommen & Hörnschemeyer, 2007). Also in Odonata, t-p14 muscle is inserted on the posterior region of AxP (Pfau, 1986; Brodsky, 1994; present observation). This muscle performs supination of the wings during flapping, and this function is retained throughout the winged insects (Pfau, 1986; Rheuben & Kammer, 1987; Neuman & Wootton, 1988; Brodsky, 1994). Second, in Neoptera and Ephemeroptera, 3Ax is linked to (Ephemeroptera) or articulated with (Neoptera) the base of A vein. In Odonata, the A vein arises from the posterodistal part of AxP (Figs. 1-4). Therefore, evidence from the musculature and venation also supports that the posterior region of AxP corresponds to 3Ax of Neoptera and Ephemeroptera.

Judging from the positional congruence (i.e., distal to 1Ax and anterior to 3Ax), the anterodistal region of AxP can be homologized with 2Ax + median plates of Neoptera or the basal plate of Ephemeroptera (= undivided 2Ax and median plate: Yoshizawa & Ninomiya, 2007) (Fig. 5). In Neoptera and Ephemeroptera, 2Ax is associated with the base of the radial (R) vein, and the median plates (MP) are associated with the bases of medial (M) and cubital (Cu) veins (Matsuda, 1970; Brodsky, 1994). In Odonata, the veins R and M are arising from the anterior part of AxP, and vein Cu arises from the mid-distal part of AxP (Figs. 1, 3-4). These venational associations are also in complete agreement with those observed on 2Ax and MP of Neoptera and the basal plate in Ephemeroptera.

The interpretation proposed for the odonate wing base structure by Brodsky (1994) is largely in agreement with ours, but there are two disagreements. The sclerites interpreted as 1Ax by Brodsky (1994) apparently are located internal to the basal hinge and thus should be homologized with ANP and MNP (Fig. 5). In our interpretation, true 1Ax is included in his 2Ax + BR + proximal median plate. The sclerite interpreted as a part of PNP by Brodsky (1994) apparently is located distal to the basal hinge and is continuous to AxP. Therefore, the sclerite should be homologized with a part of 3Ax (Fig. 5). His "basal part of PNP" corresponds to PNP in the present sense.

Chao (1953), Tannert (1958) and Matsuda (1970, 1981) considered the semi-detached scutal plate (SDP) to be a homologous structure with 1Ax of Neoptera. However, as mentioned above, SDP is placed internal to the basal hinge (Figs. 1, 3-4). Therefore, by using the basal hinge as a landmark (Yoshizawa & Ninomiya, 2007), their interpretation is rejected. In addition, they homologized the prescutal process (PsP) with the anterior notal wing process (ANP) of Neoptera because it is placed proximal to SDP (= 1Ax in their interpretation). However, PsP arises from the region anterior to tergal apophysis (= phragma of Neoptera: Matsuda, 1970: Figs. 3-4). In Neoptera, the process extending from the region anterior to phragma is the prealar arm (Fig. 5). Therefore, interpretation on the homology of ANP by Chao (1953), Tannert (1958) and Matsuda (1970, 1980) is unjustified. Matsuda (1970, 1981) mentioned the possibility of independent origins of the wings in Odonata and other Pterygota based on this morphological interpretation, but now this hypothesis loses its morphological basis.

La Greca (1980) mentioned heterogeneous nature of the odonate wing base and its independent origin from the wings of other Pterygota. According to him, 1Ax of Neoptera and Ephemeroptera has its origin on the lateral margin of the notum and thus cannot be homologized with any parts of the odonate AxP or vein bases. From this assumption, the basal hinge of Odonata and other Pterygota is argued as not homologous. However, the articulations between the notum and axillary plates are in complete agreement between Odonata and other Pterygota in their number and conditions (Figs. 1-4), and independent origins of such a complicated character system are implausible. In addition, as discussed

above, other morphological evidence (musculature and relationships between AxP and vein bases) also supports that AxP corresponds to the axillary sclerites and median plates of other Pterygota (Fig. 5). Therefore, homology of the basal hinge throughout the winged insects is the most reasonable interpretation.

In summary, all the points of evidence identified in this study strongly suggest that AxP of Odonata is the undivided (or fused) structure corresponding to 1Ax, 2Ax, 3Ax, basiradiale (BR), proximal median plate and distal median plate of Neoptera or 1Ax, 3Ax and basal plate of Ephemeroptera. In contrast, no clear border which indicates subdivision of AxP can be observed in Odonata, except for a narrow membranous region observed only in Zygoptera (Fig. 4) which may represent the border between 1Ax and 2Ax. Transformation series of the wing base sclerites is discussed in the next section.

The ancestral condition of the pterygote wing base

Homology of the wing base structures between Odonata, Ephemeroptera and Neoptera can be reasonably established (above). Therefore, the morphological interpretations of the odonate wing base proposed by Matsuda (1970, 1981) and La Greca (1980) are rejected and, judging from the wing base morphology, a single origin of the insect wings and flight is the most plausible interpretation (but see also Trueman, 2004 who argued that, although wing itself probably has common origin, flight might have originated independently between Odonata and other Pterygota). Recent analyses of molecular data also supported monophyly of the winged insects (Yoshizawa & Johnson, 2005; Kjer et al., 2006; Mallatt & Giribet, 2006; Misof et al., 2007). Therefore, estimating the ancestral condition of the extant insect wings based on morphology of the Odonata, Ephemeroptera and Neoptera is justifiable.

Our examination together with previous studies (Yoshizawa & Saigusa, 2001; Hörnschemeyer, 2002; Willkommen & Hörnschemeyer, 2007; Yoshizawa, 2007; Yoshizawa & Ninomiya, 2007) allow determination that the following features are unique to the palaeopterans: (1) basalare occupying costal to dorsal regions of wing base; (2) median notal wing process separated from scutum; (3) absence of axillary folding lines and associated articulations and (4) 2Ax, BR and median plate not separated from each other.

Generally, the ability of backward wing folding in Neoptera is considered to represent an apomorphic condition (Martynov, 1925; Carpenter, 1963; Grimaldi & Engel, 2005). Contrary to this, Willkommen & Hörnschemeyer (2007) assumed that the ability of backward wing folding and presence of three separated axillary sclerites as observed in Neoptera represent the ancestral condition of the winged insects, and the basal plate of Ephemeroptera and the axillary plate of Odonata are derived from that condition by fusion of the sclerites independently or maybe in their common ancestor. Similar assumption was also proposed by Kukalová-Peck (1983, 1991) and Hasenfuss (2002, 2008). Kukalová-Peck (1983, 1991) considered the fusion of axillary sclerites and lack of backward wing folding to be autapomorphies of Palaeoptera. Willkommen & Hörnschemeyer (2007) mentioned that such fusions developed to provide more stability for the wing base: keeping gliding position in Ephemeroptera or providing highly manoeuvrable hunting flight in Odonata, however, the verification for their interpretation seems weak. Willkommen & Hörnschemeyer (2007) mentioned butterflies (Lepidoptera: Papilionoidea) as an example of apparent secondary loss of wing foldings (Ivanov, 1996); however the wing base structure of butterflies comprises the fundamental elements of neopteran axillary sclerites and median plates, and fusion of the sclerites is never observed (Ivanov, 1996; K. Yoshizawa, personal examination), although they are very active fliers and stability of the wing base is important. Convergent loss of wing folding seems frequent, but does not support frequent secondary fusion of the wing base sclerites.

Rather, from a cladistic point of view, the opposite interpretation can be regarded as more parsimonious: i.e., undivided 2Ax + basiradiale + median plate and lack of backward

wing folding as observed in palaeopterans represent the ancestral condition of the extant winged insects, and separation of 2Ax and presence of the axillary folding lines are autapomorphies of Neoptera. This supposition is more parsimonious under Metapterygota (monophyly of Odonata + Neoptera) or Chiasmomyaria (Ephemeroptera + Neoptera) hypotheses. Under the Palaeoptera hypothesis (Odonata + Ephemeroptera), both interpretations are equally parsimonious. Now all phylogenetic hypotheses mentioned above have some morphological and molecular support (Hovmöller et al., 2002; Ogden & Whiting, 2003; Whitfield & Kjer, 2008), although morphological support for the Palaeoptera hypothesis is highly questionable (Kristensen, 1991; Soldán, 1997; Willmann, 1998). Establishing a sound phylogenetic hypothesis for the basal diversification of Pterygota is critical to reveal the ancestral condition of the insect wing base structure and wing folding mechanism. Unfortunately, the present data cannot end this controversy because of the lack of outgroups, but we emphasize that the hypothesis proposed by Willkommen & Hörnschemeyer (2007) cannot be regarded as a single best interpretation from amongst the above-mentioned phylogenetic hypotheses.

As well as the wing folding mechanism and state of axillary sclerites, the ancestral condition of basalare (dorsally expanded or not) and median notal wing process (separated from the scutum or not) cannot be estimated unambiguously without sound phylogenetic hypothesis of the early diversification of the winged insects. However, the functional aspect may be helpful in predicting the character state polarity of the basalare. The dorsal extension of the basalare in Odonata probably is associated tightly with their flight mechanism, i.e., wing flapping by direct flight muscles. In Odonata, the direct flight muscles are inserted on the dorsal part of basalare via a tendon, and this provides the principal power for wing flapping (Tannert, 1958; Pfau, 1986; Brodsky, 1994). Therefore, broad dorsal extension of basalare and its tight connection with humeral plate as observed in Odonata are important to transmit power from the muscle to the costal vein effectively (Pfau, 1986). In contrast, the principal function of the ephemeropteran basalare is to perform pronation of the wing and has only a supplemental function for wing flapping (Pfau, 1986). Nevertheless, the basalare in Ephemeroptera does extend broadly, dorsally as in Odonata. This implies that functional convergence of the dorsal extension of basalare is less plausible, and this condition is likely to represent the ancestral state of Pterygota.

Although the present study does not provide support for the ground plan scheme of axillary sclerites as proposed by Kukalová-Peck (1983, 1991), separation of the median notal wing process (and maybe also posterior notal wing process) from the scutum as observed in Ephemeroptera and Odonata seems to provide partial support for that scheme. Kukalová-Peck (1983, 1991) interpreted the anterior, median and posterior notal wing processes as all separated from the notum in the common ancestor of the winged insects. In these and previous observations (Yoshizawa & Ninomiya, 2007), separation of MNP from the scutum is very clearly detected in two basal orders of Pterygota (Figs. 1-4). Therefore, it is plausible that the separation of MNP represents the ancestral condition of the winged insect, as predicted by Kukalová-Peck (1983, 1991). Separation of PNP from the scutellum is observed in all ephemeropterans (Yoshizawa & Ninomiya, 2007) and some orders in Neoptera (Hörnschemeyer, 2002; Yoshizawa, 2007). Although PNP of Odonata is tightly fused to the scutellum, a clear line can be seen at the base of PNP. If this line represents their structural border, then a separated PNP also may represent the most ancestral condition of the winged insects (Kukalová-Peck, 1983, 1991). Separation of the PNP in Neoptera is interpreted generally as a derived condition within the group (Hörnschemeyer, 2002; Yoshizawa, 2007), but this interpretation may need to be revised.

Concluding comments

Homology of the wing base structure in Odonata has been one of the most controversial topics in insect morphology. By using two unambiguously homologized structures as

principal landmarks, we have established a reasonable new scheme for homology of the wing base structure in Odonata. Although beyond the scope of the present study, the new scheme of the wing base structure will be useful also for estimation of the intraordinal relationships of Odonata (Rehn, 2003; Bybee et al., 2008) or to decide the highly controversial homology of odonate wing veins (Riek & Kukalová-Peck, 1984; Brodsky, 1994; Rehn, 2003; Trueman, unpubl. cited in Gullan & Cranston, 2005; Bechly, 2007).

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Figure captions

Fig. 1. Right forewing base structure of *Epiophlebia superstes* (Anisozygoptera: Epiophlebiidae), dorsal view, showing whole structure (top) and magnified articular region (bottom). Abbreviations: m, d, pSDP = median, distal, posterior semi-detached scutal plate.

Fig. 2. Internal structure of the articular region of the left forewing base of *Epiophlebia superstes* (Anisozygoptera: Epiophlebiidae), internal view. Abbreviations: AxP = axillary plate; SC = scutum; SCT = scutellum.

Fig. 3. Right forewing base structure of *Tanypteryx pryeri* (Anisoptera: Petaluridae), dorsal view, showing whole structure (top) and magnified articular region (bottom). Abbreviations: AxP = axillary plate; BSc = basisubcostale; DCP, PCP = distal and proximal costal plate; d, m, pSDP = distal, median, posterior semi-detached plate; PsP = pre-scutal process; SC = scutum; SCT = scutellum.

Fig. 4. Right forewing base structure of *Coeliccia ryukyuensis ryukyuensis* (Zygoptera: Platycnemididae), dorsal view, showing whole structure (top) and magnified articular region (bottom). Abbreviations: AxP = axillary plate; BSc = basisubcostale; DCP, PCP = distal and proximal costal plate; d, m, pSDP = distal, median, posterior semi-detached plate; PsP = pre-scutal process; SC = scutum; SCT = scutellum.

Fig. 5. Right forewing base structure of *Epiophlebia superstes* (Anisozygoptera: Epiophlebiidae) showing the present interpretation of the sclerites (previous interpretations in parentheses). Abbreviations: 1, 2, 3Ax = first, second, third axillary sclerite; ANP, MNP, PNP = anterior, median, posterior notal wing process; AxP = axillary plate; BSc = basisubcostale; PCP, DCP = proximal, distal costal plate; SC = scutum; SCT = scutellum; SDP = semi-detached plate. In AxP, the regions corresponding to 1Ax (lighter) and 3Ax (darker) are indicated by shade.

Appendix 1. Odonate taxa examined

ZYGOPTERA

Coenagrionidae

- Ischnura senegalensis* (Rambur)
- Enallagma boreale circulatum* Selys
- Nehalennia speciosa* (Charpentier)
- Cercion calamorum calamorum* (Ris)
- Cercion sexlineatum* (Selys)
- Cercion hieroglyphicum* (Brauer)
- Cercion sieboldii* (Selys)
- Coenagrion lanceolatum* (Selys)

Platycnemididae

- Coelliccia ryukyuensis ryukyuensis* Asahina

Lestidae

- Lestes sponsa* (Hansemann)
- Sympecma paedisca paedisca* (Eversmann)

Megapodagrionidae

- Rhipidolestes hiraoi* Yamamoto

Euphaeidae

- Euphae yayeyamana* Oguma

Calopterygidae

- Calopteryx cornelia* Selys
- Calopteryx atrata* Selys
- Mnais pruinosa* Selys
- Mnais nawai* Yamamoto

ANISOZYGOPTERA

Epiophlebiidae

- Epiophlebia superstes* (Selys)

ANISOPTERA

Petaluridae

- Tanypteryx pryeri* (Selys)

Gomphidae

- Gomphus postocularis* Selys
- Davidius moiwanus moiwanus* (Okumura)
- Sieboldius albardae* Selys
- Ictinogomphus pertinax* (Selys)

Cordulegastridae

- Anotogaster sieboldii* (Selys)
- Chlorogomphus brunneus costalis* Asahina

Aeshnidae

- Aeshna nigroflava* Martin

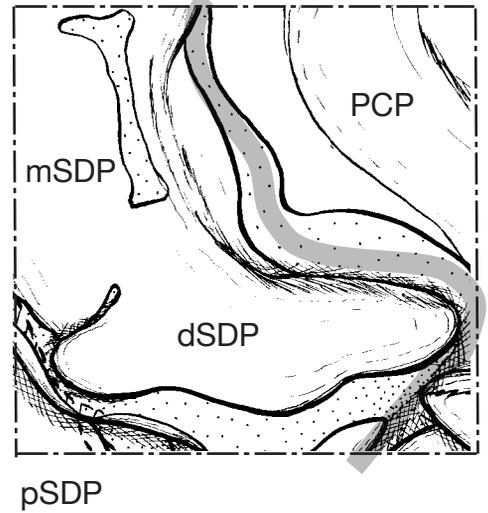
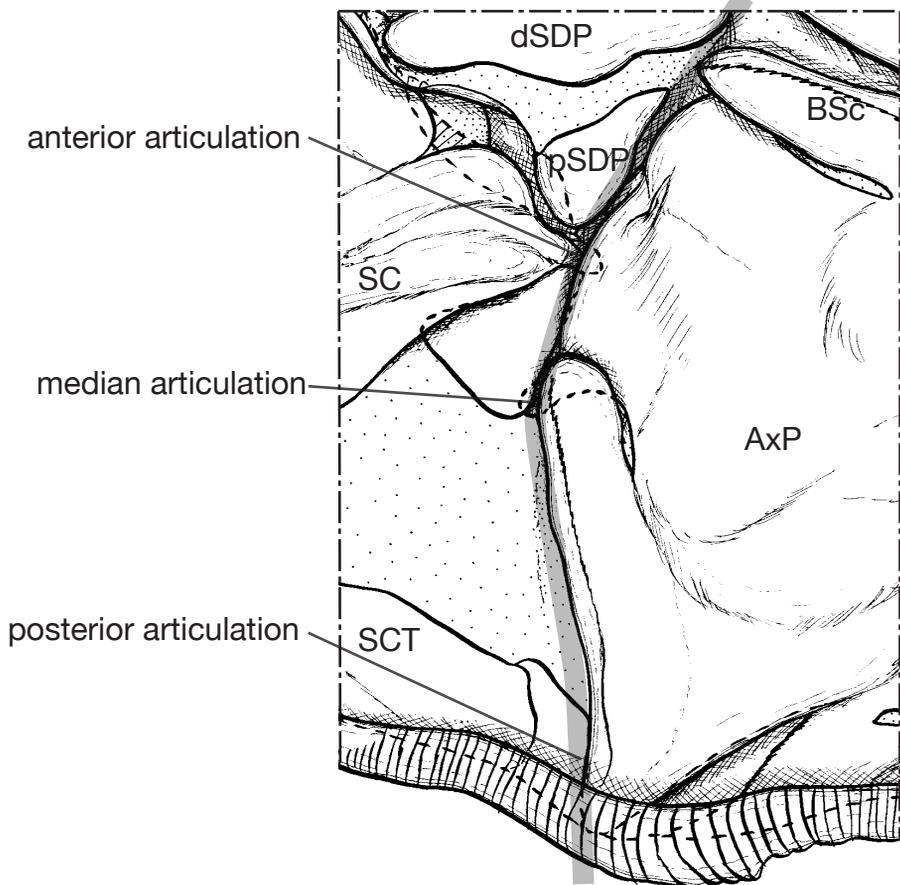
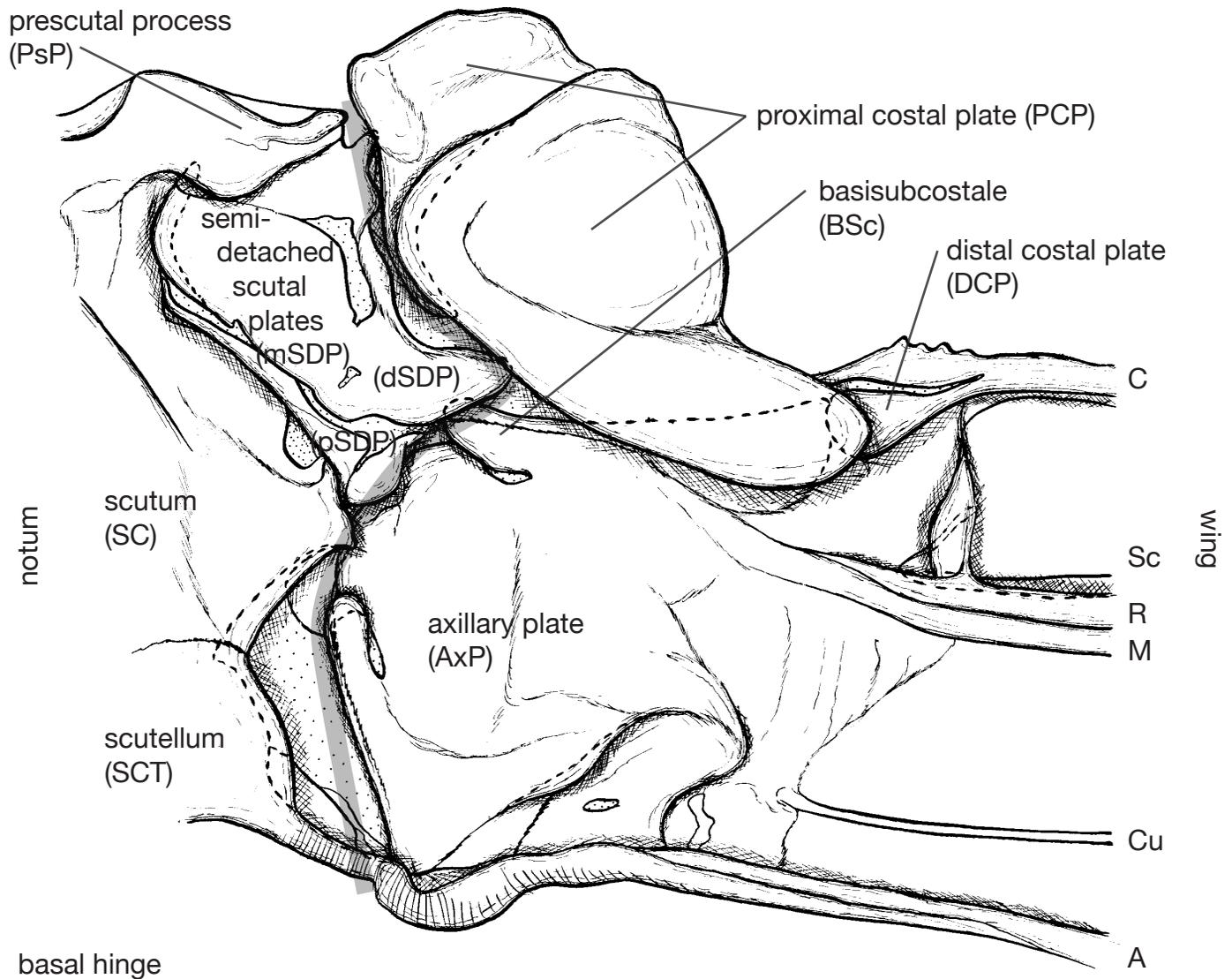
Corduliidae

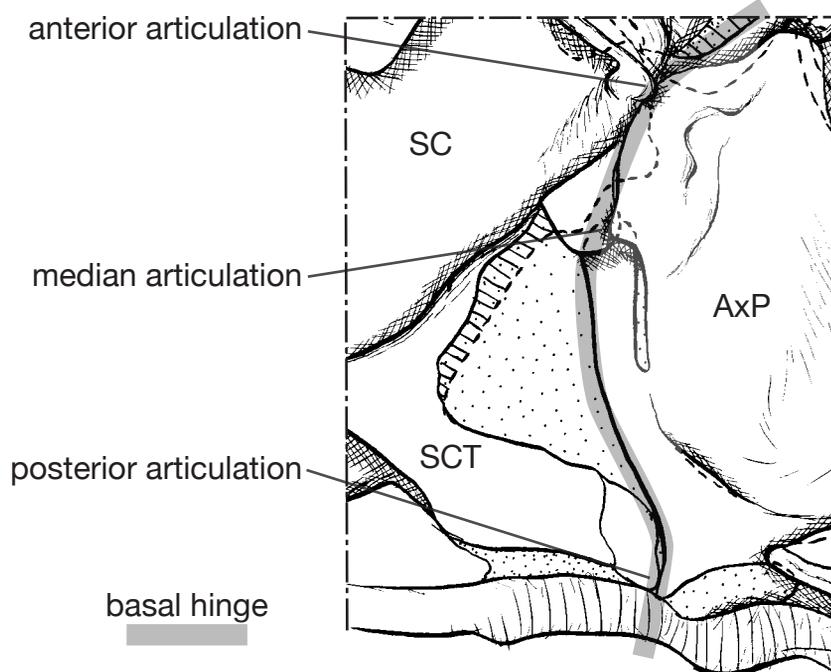
- Epithea bimaculata sibirica* (Selys)
- Somatochlora viridiaenea* (Uhler)
- Somatochlora uchidai* Foerster
- Epophthalmia elegans* (Brauer)

Libellulidae

- Lyriothemis pachygastra* (Selys)
- Orthetrum japonicum japonicum* (Uhler)

Orthetrum albistylum speciosum (Uhler)
Orthetrum triangulare melania (Selys)
Libellula quadrimaculata asahinai Schmidt
Nannophya pygmaea Rambur
Acisoma panorpoides panorpoides Rambur
Sympetrum pedemontanum elatum (Selys)
Sympetrum depressiusculum (Selys)
Sympetrum eroticum eroticum (Selys)
Sympetrum infuscatum (Selys)
Pantala flavescens (Fabricius)
Rhyothemis variegata imperatrix Selys







basal hinge

