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## The wing base of the palaeodictyopteran genus *Dunbaria* Tillyard: Where are we now?

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## ABSTRACT

The structure of insect wing articulation is considered as reliable source of high level characters for phylogenetic analyses. However, the correct identification of homologous structures among the main groups of Pterygota is a hotly debated issue. Therefore, the reconstruction of the wing bases in Paleozoic extinct relatives is of great interest, but at the same time it should be treated with extreme caution due to distortions caused by taphonomic effects. The present study is focused on the wing base in *Dunbaria* (Spilapteridae). The articulation in *Dunbaria quinquefasciata* is mainly formed by a prominent upright axillary plate while the humeral plate is markedly reduced. Due to unique preservation of surface relief of the axillary plate, its composition shows a detailed pattern of three fused axillary sclerites and presumable position of the sclerite 3Ax. The obtained structures were compared among Spilapteridae and to other palaeodictyopterans *Ostrava nigra* (Homoiopteridae) and *Namuroningxia elegans* (Namuroningxiidae). The comparative study uncovered two patterns of 3Ax in *Dunbaria* and *Namuroningxia*, which correspond to their different suprafamilial classification. In contrast to previous studies these new results reveal the homologous structural elements in the wing base between Paleozoic Palaeodictyoptera and their extant relatives of Ephemeroptera, Odonata and Neoptera.

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### 1. Introduction

The insect wing base has been studied for more than a century with some classical works like Snodgrass (1909). The wing base is bearing a valuable set of characters with high potential to help with the resolution of the insect phylogeny on various levels as has been shown in a number of studies (e.g., Hörschemeyer, 2002; Yoshizawa, 2011). However, the homology of articular elements among the main lineages of Pterygota as mayflies (Ephemeroptera), dragonflies (Odonata) and Neoptera implies inconsistencies among different authors and hitherto represents an unresolved problem in entomology (see e.g., Willkommen and Hörschemeyer, 2007a, b; Willkommen, 2008; Ninomiya and Yoshizawa, 2009). Evolutionary history of these pterygote lineages is traceable since the latest Early Carboniferous suggesting the deep divergences at least of early Carboniferous age or rather the Devonian (Prokop et al.,

2005; Engel et al., 2013). However, the current estimations based on calibrated phylogenetic trees, support the first divergence between Palaeoptera and Neoptera in the Late Devonian about 360 Mya or even earlier (Misof et al., 2014; Wang et al., 2016). Another group of Pterygota relevant to this debate is extinct Palaeodictyoptera, which systematic position remains unresolved and is either considered as sister group of Palaeoptera, sister group of Neoptera or even, based on the characters of the mouthparts as sister group of Hypoperlida (Kukalová-Peck, 1991; Rasnitsyn, 2002; Sroka et al., 2015; Prokop et al., 2017a). However, the number of shared apomorphies in the wing venation and structure of genitalia rather supports a rather inclusive position for Palaeodictyoptera close to the early diverging groups of pterygotes as Odonatoptera, Ephemeroptera, and Neoptera (e.g., Prokop et al., 2016a; Pecharová and Prokop, 2018). Moreover, the morphology of nymphal wing pads in Palaeodictyoptera and their growth during the postembryonic development supports the hypothesis on the dual origin of insect wings (Prokop et al., 2017b). Although, this composite model was already suggested by Crampton (1916) and later developed by Rasnitsyn (1981), it is

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currently receiving support from various studies like embryology and evo-devo (e.g., Niwa et al., 2010; Clark-Hachtel et al., 2013; Mashimo and Machida, 2017; Linz and Tomoyasu, 2018).

The examples of earlier studies on wing base morphology of other extinct insect groups (e.g., Paoliida, Permopsocida) demonstrated that some fossils with 3D preservation in amber resin or even ironstone nodules allow to study delicate structures and provide crucial support for the systematic placement (e.g., Prokop et al., 2012; Yoshizawa and Lienhard, 2016; Huang et al., 2016).

The wing base morphology of Palaeodictyoptera has been already documented in several species albeit a relatively low potential for the preservation of notably three-dimensional structures like sclerites and membranes. Kukulová (1960) described the first basivenal sclerites of *Ostrava nigra* Kukulová, 1960 (Homiopteridae) from Namurian C of the Czech Republic comparing the subcostoradial plate of Palaeodictyoptera to the radioanal plate of Odonata. In a subsequent study the same author focused on pteralia of several other palaeodictyopteran species, such as *Moravia convergens* Kukulová-Peck, 1964 (Calvertiellidae), *Dictyoptilus sepultus* (Meunier, 1910) (Eugereonidae), *Stenodictya parisiana* Kukulová, 1970 (Dictyoneuridae); those have been demonstrated to show the fused subcosto-anal plate and differences in attachment of anal veins and axillary region between Palaeodictyoptera and Ephemeroptera (Kukulová-Peck, 1974). Müller (1978) re-described an old type specimen of *Eugereon boeckingi* Dohrn, 1866 (Eugereonidae) from the middle Permian of Saar-Nahe Basin in Germany including the restoration of the forewing base. He suggested that the basivenal plates as subcostoradial, medial, cubital, and anal were well separated. Kukulová-Peck (1978, 1983) provided more complex interpretations of the wing base in Palaeodictyoptera suggesting that the articular sclerites are delimited by sutures and form columns of sclerites aligned with veins as proxalaria (P), axalaria (Ax), fulcalaria (F) and basivenalia (B). These were at the same time demonstrated on several examples of nymphal wing pads of *Adolarrhya bairdi* Kukulová-Peck and Richardson, 1983 (Homiopteridae), *Paimbia fenestrata* Sinitshenkova, 1979 and *Parathesoneura carpenteri* Sharov and Sinitshenkova, 1977 (both Tchirkovaeidae) and also adult wings like *Mazonopteron wolfforum* Kukulová-Peck and Richardson, 1983 (Homiopteridae) and even on an extant dragonfly *Uropetala carovei* (Petaluridae) and a mayfly *Siphonurus* sp. (Siphonuridae) (Kukulová-Peck, 1983; Fig. 16). Albeit this concept attempted to show the regular architecture as ground-plan and homologies of articular elements of the wing base among different groups of Palaeoptera, it is viewed by some authors as hypothetical and rather controversial (e.g., Rasnitsyn, 1981; Willmann, 1997). An additional study focused on the wings and the wing base in the palaeodictyopteran family Homiopteridae is following the same concept, the so called “protowing model” (Kukulová-Peck and Richardson, 1983). Brodsky (1994: 94, Fig. 5.11) proposed another interpretation of the wing base in *M. wolfforum* and reconsidered the structure of the Palaeodictyoptera wing apparatus particularly in respect of flight abilities.

Petrulevičius and Gutiérrez (2016: Fig. 4) described an odonopteran *Kirchnerala treintamil* (Geroptera) suggesting that the anterior articular plate consists of precostal and costal pteralia, but at the same time indicating that subcostal pteralia (proxalare and basivenale) are not so noticeable. Although, their interpretation followed the hypothesis proposed by Kukulová-Peck (1983), surprisingly their drawing is missing proxalaria, while an additional unmarked sclerite is present between basivenalia and fulcalaria in the anterior articular plate. Albeit the reasonable preservation of subcostal pteralia the columns of four sclerites were not found (Petrulevičius and Gutiérrez, 2016: Figs. 3 and 4).

In this study, we examined the wing base of the genus *Dunbaria* Tillyard in Dunbar and Tillyard, 1924, which belongs to the largest palaeo-dictyopteran family Spilapteridae with 20 genera assigned (Liu et al., 2015; Prokop et al., 2016b). The family has the longest duration among Palaodictyoptera spanning from the early Late Carboniferous to the Late Permian strata and at the same time includes one of the earliest recorded winged insects (Brauckmann and Schneider, 1996; Wolfe et al., 2016). The members of Spilapteridae commonly bear prothoracic lobes interpreted by some authors as winglets, hind wings broader than fore wings and both pairs of wings often with a pattern of dark stripes or spots (Kukulová, 1969; Carpenter, 1992; Li et al., 2013). Moreover, a supposed nymph of Spilapteridae has been recently described showing a partly preserved rostrum, the heteronomous wing pads and an abdomen with prominent laterotergites (Prokop et al., 2016b). Our study is additionally focused on so far overlooked peculiarities in the wing venation of *Dunbaria* species and sum up the flight abilities to get a more complex picture of this extinct insect.

## 2. Material and methods

### 2.1. Material

The examined specimens in this study come from the following institutional collections: Capital Normal University, Beijing, China (acronym: CNU); Municipal Museum of Ostrava (acronym: MMO); National Museum, Praha (acronym: NMP); Paleontological Institute of Russian Academy of Sciences, Moscow, Russia (acronym: PIN); and Yale Peabody Museum, New Haven, USA (acronym: YPM).

### 2.2. Observation, line drawings and photographs

The material was examined under a stereomicroscope Zeiss Discovery V12 coupled with PlanApo S objectives and incident light CL 6000 and Schott ringlight. The specimens were dry or under a film layer of 70–80% ethanol. The wing joints were drawn directly using a stereomicroscope Leica MZ 12.5 fitted with a camera lucida. Photographs were taken using a digital camera Canon D550 (Canon Inc., Tokyo, Japan) with lenses EF 50 mm and MP-E 65 mm. Original photographs were processed using the image-editing software Adobe Photoshop CS (Adobe Systems, San Jose, California), and the same images were processed by the focus-stacking software Helicon Focus Pro (Helicon Soft Ltd., Kharkov, Ukraine) or Zerene Stacker (Zerene Systems LLC). Scanning electron micrographs were taken using an environmental electron microscope Hitachi S-3700N (Hitachi Ltd, Chiyoda, Tokyo, Japan) at an accelerating voltage of 15 kV with a turntable sample holder located at the National Museum in Praha.

### 2.3. Anatomical abbreviations

We follow the terminology of muscles after Matsuda (1970) and wing base morphology after Willkommen (2008) and Ninomiya and Yoshizawa (2009). The terminology of the composite leading edge of the wing as proposed for Odonata by Riek and Kukulová-Peck (1984) and Bechly (1996). The terminology used for the microstructures on wing leading edge follows D'Andrea and Carfi (1991).

The following symbols are used: psc – prescutum, sc – scutum, sl – scutellum, ANP/MNP/PPN – anterior/median/posterior notal wing process, BC – basicostale, BSc – basisubcostale, BR – basi-radiale, BAn – basianale, T – tegula, Hp – humeral plate, Axp – axillary plate, Mp – median plate; PMP – proximal median plate; veins: PC – precosta, CA/CP – costal anterior/posterior, Sca/ScP – subcostal anterior/posterior, RA/RP – radial anterior/posterior,

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