- 1 ASD-D-17-00081\_revised ms
- 2 for submission to Arthropod Structure & Development: Special Issue of Wings and Flight

```
3
```

# 4 Morphology of the elytral base sclerites

- 5
- 6 Miwa Sugimoto, Naoki Ogawa, Kazunori Yoshizawa\*
- 7
- 8 Systematic Entomology, School of Agriculture, Hokkaido University, Sapporo 060-8589,
- 9 Japan
- 10
- 11 \*correspondence: psocid@res.agr.hokudai.ac.jp
- 12

#### 13 Abstract

The elytral base sclerites (= sclerites located at the articular region between the forewing and 14 thorax in Coleoptera) of selected taxa were examined and homologized. Although the elytral 15 base sclerites are highly modified compared to the wing base sclerites of the other neopterans, 16 17 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 18 19 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 20 against the basal sclerites is relaxed because of the lack of an ability to produce flight power 21 by elytra. In contrast, the elytral folding system formed by the basal sclerites is well retained, 22 23 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 24 25 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 26 sclerites suggests there is potential for studying the lower-level phylogeny of Coleoptera. 27 28

- 29 1. Introduction
- 30

The wing base structure consists of several tightly associated sclerites located at the 31 joint region between the wing and thorax. These sclerites play principal roles in wing 32 33 flapping, rotating, and folding (Brodsky, 1994). Therefore, these sclerites are strongly constrained functionally and are known to evolve very slowly (Hörnschemeyer, 2002). In 34 35 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 36 these properties, the wing base structure has been utilized for uncovering deep insect 37 phylogeny (Yoshizawa & Saigusa, 2001; Hörnschemeyer, 2002; Yoshizawa, 2007, 2011; 38 39 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) 40 41 and comprehensive insect phylogenomics (Misof et al., 2014). Coleoptera are the most diversified insect order. They are characterized by highly 42 43 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 44 structure of Coleoptera, which has a much less modified condition, has been studied for a 45 wide range of taxa and utilized for higher level phylogenetic estimations (Browne & Scholtz, 46 1998, 1999; Hörnschemeyer, 1998). The forewing base structure (i.e., elytral base) of 47 Coleoptera has also been examined in some studies, but most of the observations were 48 49 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; 50 Doyen, 1966; Larsén, 1966). Some studies made comparative analyses, but comparisons were 51 52 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 53 54 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; 55 elytral root: Sípek et al., 2016) have been adopted for elytral base sclerites without 56 57 homologization with the wing base structure of the other Neoptera, which should also be 58 resolved.

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 & 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.

69

## 70 2. Materials and Methods

71

72 The main purpose of this study was to establish a consistent homology interpretation 73 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 74 75 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 76 examined because of its special interest for the study of morphological transformations. The 77 following taxa were examined: suborder Adephaga: Carabidae (Calosoma chinense) and 78 Gyrinidae (Dineutus orientalis); suborder Polyphaga: Hytrophilidae (Hydrophilus 79 acuminatus), Scarabaeidae (Trypoxylus dichotomus), Tenebrionidae (Andocamaia 80 rvukvuensis), Cleridae (Enoclerus moestus), Buprestidae (Chrysodema manillarum) and 81 Cerambycidae (Prionus insularis). Dried or alcohol-preserved specimens were used. The 82 thorax of each specimen was removed from the other body parts and was soaked in 10%83 84 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 85 86 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 87 88 binocular microscopes.

89

## 90 **3. Results**

- 91 (Figs. 1–8, Table 1)
- 92

The first axillary sclerite (1Ax) of the elytral base is highly variable in the shape and 93 the degree of development. In Carabidae, it has a posterior triangular body and an anterior 94 arched head (Fig. 1), which was generally observed in the other neopteran 1Ax. Proximally, 95 it articulates with the notum by two points of the body region, but the posterior articulation is 96 97 looser. Apically, the head articulates with the middle part of the elytral root (as discussed by Sípek et al., 2016) along the convex axillary fold line. The head of 1Ax and the elytral root 98 are partly fused, but this condition is uniquely observed in Carabidae. Distally, it articulates 99 with the second axillary sclerite by two points of the body region. In Cerambycidae, the fully 100 developed condition of 1Ax was observed, but it is less developed (Fig. 8). The head region 101 is very weakly sclerotized. In Gyrinidae (Fig. 2) and Buprestidae (Fig. 7), the head and body 102 103 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 104 105 the articulation between 1Ax and elytral root is absent. In Hydrophilidae, 1Ax is completely

106 reduced (Fig. 3).

107 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 108 with the third axillary sclerite (3Ax) at its posterior tip. Although they are much narrower, 109 these conditions are similar to conditions observed in the other neopteran wing base. In 110 contrast, 2Ax has additional lobes and projections in all polyphagans: i.e., the region 111 proximal to the 2Ax-3Ax articulation extends posteriorly and frequently forms a lobe-like 112 structure (indicated by "\*" in Figs 3-8). In Hydrophilidae (Fig. 3), Tenebrionidae (Fig. 5), 113 Cleridae (Fig. 6) and Buprestidae (Fig. 7), 2Ax also has a strongly sclerotized lobe 114 anterodistally (indicated by "+"), and its apex articulates with the elytral root along the 115 116 convex axillary fold line. In Hydrophilidae (Fig. 3), Tenebrionidae (Fig. 5), Cleridae (Fig. 6), Buprestidae (Fig. 7) and Cerambycidae (Fig. 8) in which 1Ax is either reduced or absent, the 117 118 anteroproximal region of 2Ax has a well-developed lobe (indicated by "#") by which 2Ax articulates with the notum (except for Cerambycidae in which 1Ax is fully retained, although 119 120 weakly sclerotized: Fig. 8). In Carabidae (Fig. 1), Gyrinidae (Fig. 2) and Cerambycidae (Fig. 8), 2Ax is separated from the elytral root by a narrow membranous furrow along the convex 121 122 axillary fold line, but they are connected by a sclerotized band in Hydrophilidae (Fig. 3), Scarabaeidae (Fig. 4), Tenebrionidae (Fig. 5), Cleridae (Fig. 6) and Buprestidae (Fig. 7). 123 124 The third axillary sclerite (3Ax) is highly variable in shape but always has three arms,

as observed in the other neopteran wing base (Figs. 1–8). The anterior arm articulates with
2Ax along the concave axillary fold line. The distal arm articulates with the posterior margin
of the base of the elytral base along the convex axillary fold line; the posterior arm articulates
with the posterior notal wing process to forming posterior articulation of the basal hinge. The
3Ax-notal articulation seems looser in some taxa (e.g., Hydrophilidae, Fig. 3), but it is an
artifact caused by the preparation of specimens for facilitating clear observation of elytral
base sclerites.

The proximal median plate (PMP) of Neoptera is surrounded by 2Ax, 3Ax and the 132 distal median plate, and it is delimited proximally by the concave axillary fold line and 133 distally by the convex axillary fold line. However, in all the taxa examined here, the region is 134 broadly membranous which shows reduction of PMP in the elytral base (Figs, 1-8). In 135 contrast, broad sclerotization anterior to 3Ax can be seen in some taxa (e.g., Carabidae: Fig. 136 1). In addition, in Tenebrionidae (Fig. 5) and Cerambycidae (Fig. 8), this sclerotized region 137 articulates with 2Ax along some distances. These results indicate that this anterior expansion 138 139 of 3Ax represents a remnant of the reduced PMP. Reduction of PMP has also been identified in the Auchenorrhyncha and Coleorrhyncha of Hemiptera (Yoshizawa & Saigusa, 2001; 140 Yoshizawa et al., 2017), but its independent origins between Coleoptera and Hemiptera is 141 evident. 142

The distal median plate (DMP) of Neoptera is delimited proximally by the convex
axillary fold line. In the elytral base, the line runs from the 1Ax-elytral root or 2Ax-elytral
root articulations through the posterior margin of the elytral root to the 3Ax-elytra
articulation (Figs 1–8). Therefore, the expanded posterodistal region of the elytral root was
identified as DMP.

The basisubcostale (BSc) of Neoptera can consistently be identified by its articulation with the head of 1Ax. Therefore, judging from the conditions observed in Carabidae (Fig. 1) and Cerambycidae (Fig. 8), the median part of the elytral root can be unambiguously identified as BSc. In Hydrophilidae (Fig. 3), Scarabaeidae (Fig. 4), Tenebrionidae (Fig. 5) and Cleridae (Fig. 6), the head of 1Ax is absent, and BSc articulates with the tip of the anterodistal extension of 2Ax (indicated by "+").

Judging from the anterior borderline of BSc, as observed in Carabidae (Fig. 1),
Gyrinidae (Fig. 2) and Tenebrionidae (Fig. 5), the anterior region of the elytral root can be
interpreted as the humeral plate (HP). The border between BSc and HP is unclear in the other

157 taxa.

The basiradiale (BR) of Neoptera can be identified by its relationship with the 158 anterodistal part of 2Ax. In the elytral base, the anterodistal region of 2Ax always articulates 159 with the elytral root. This part of the elytral root was identified as BR. The 2Ax and BR are 160 161 separated along the convex axillary fold line by a narrow membranous furrow in Carabidae (Fig. 1), Gyrinidae (Fig. 2) and Cerambycidae (Fig. 8), but they are connected by a strap of 162 bending cuticle in other taxa (Figs. 3–7), through which the convex axillary fold line is 163 running. Fusion between 2Ax and BR is widely observed in the neuropteroid orders (Zhao et 164 al., 2014), which are close relatives of Coleoptera. 165

The identity of tegula (Tg) in the elytral base was less convincing. In general, the tegula 166 is located at the most proximal part of the anterior margin of the wing base, and it is less 167 sclerotized and frequently covered by short hairs. In Carabidae, a hairy pad is observed at the 168 anterior corner of the notum (Fig. 1), and this condition is superficially very similar to Tg, as 169 observed in other winged insects. In contrast, an isolated and well sclerotized plate can be 170 171 seen on the anterior wing margin of Cleridae (Fig. 6) and Cerambycidae (Fig. 8). Judging from their position, these sclerites are likely represents Tg. In other taxa that were examined, 172 no separable structure corresponding to Tg could be observed. 173

174

#### 175 4. Discussion

176

177 In Carabidae, almost all fundamental elements of the neopteran wing base are retained in the elytral base (i.e., Tg, HP, 1, 2 and 3Ax, PMP, DMP, BSc and BR: Fig. 1), and they can 178 easily be homologized with the wing base sclerites of the other Neoptera by using the wing 179 180 folding lines as landmarks. In addition, each sclerite of the carabid elytral base also shows a similar condition that can be observed in the wing base of other Neoptera (e.g., 1Ax consists 181 182 of a triangular body and elongated head; 2Ax is triangular; and 3Ax has three arms). In contrast, the elytral base sclerites of the other coleopteran taxa are more divergent from those 183 184 observed in the other neopteran wing base structures. Comparisons between the present and previous interpretations of the elytral base sclerites are provided in Table 1. Several previous 185 186 misinterpretations were identified, which mainly occurred because previous authors tried to homologize these highly modified elytral base sclerites without considering the 187 188 transformation of these sclerites throughout Coleoptera and without using convincing

189 landmarks (i.e., the wing folding lines as employed here and previous studies: Wootton,

- 190 1979). In addition, homology of a unique elytral structure, which has been called by a couple
- 191 of local terms (basal process or elytral root) can also be identified convincingly in relation to
- 192 elytral base sclerites (composite structure of HP, BSc, BR and DMP: Table 1).

193 Generally, the wing base sclerites are very conservative and are slowly evolving structures because of strong functional constraints acting on them (Hörnshemeyer, 2002). In 194 contrast, the elytral base sclerites are more variable, and several modifications never seen in 195 the wing base sclerites of the other Neoptera were identified. For example, 1Ax is divided 196 into two separated sclerites in Gyrinidae (Adephaga: Fig. 2) and Buprestidae (Polyphaga: Fig. 197 7). Furthermore, these two taxa are apparently distantly related (they belong to different 198 199 suborders), which shows the independent occurrences of unusual modifications. They are also completely different in their choice of habitat (aquatic Gyrinidae and arboreal 200 201 Buprestidae), and thus similar modifications in 1Ax cannot be explained by convergence resulting from behavioral similarity. The modifications of the elytral base are also a contrast 202 203 to the much more stable hindwing base sclerites of Coleoptera (Hörnschemeyer, 1998). The occurrence of such a contrasting evolutionary trend seen between serially homologous 204 structures (elytral base and hindwing base sclerites) indicates there were different 205 evolutionary pressures acting on these two structures. There are two possibilities for causing 206 such unusual evolutionary trends in the elytral base: relaxed constraint and different selective 207 208 pressures.

Among the various modifications observed in the elytral base, reduction of 1Ax seems to be a general trend, which includes weak sclerotization (Cerambycidae: Fig. 8), division

- 211 into two sclerites (Gyrinidae and Buprestidae: Figs. 2 and 7), absence of the head
- 212 (Scarabaeidae, Tenebrionidae and Cleridae: Figs. 4–6), and complete absence

213 (Hydrophilidae: Fig. 3). Furthermore, the division of 1Ax and absence of the head were

detected in distantly related taxa and thus multiple occurrences were evident. The 1Ax is

located next to the thorax and plays a key function in mediating the power generated by the

thorax to the wings (Brodsky, 1994). Tight associations between the thorax and 1Ax as well

- as 1Ax and BSc/2Ax are very important for generating flapping movements. Therefore, the
- 218 lack of 1Ax is very rarely observed among flying insects but is known also from the
- 219 hindwing base of froghoppers (Hemiptera: Cicadomorpha: Cercopoidea). The reduction of
- 1Ax is also a general trend in the infraorder Cicadomorpha (Yoshizawa & Wagatsuma, 2012).

In this group, the metathorax is almost entirely occupied by the jumping muscles, and the 221 flight muscles are extremely reduced or almost completely absent. Therefore, the metathorax 222 lacks the ability to produce strong flight power (Ogawa & Yoshizawa, 2017). In both cases 223 (elytra and hindwings of Cicadomorpha), the lack of an ability to produce active flight power 224 225 and the reduction of 1Ax seem to be connective evolutionary events. It is very likely that 1Ax of both groups has been relaxed from the functional constraint resulting from the lack of a 226 227 function to mediate the flight power, which probably explains the general trend of the 1Ax reduction observed in the elytral base. 228

229 In contrast, to achieve the important protection function (Linz et al., 2016), tight associations between the left and right elytra as well as between the elytra and body must be 230 231 established. Therefore, accurate control of the elytral closing movement may act as a different evolutionary constraint for the elytral base sclerite. For example, in contrast to the 232 reduction of 1Ax, 2Ax and 3Ax of the elytral base are well developed in all the examined 233 taxa (Figs 1–8). The basal hinge and the concave and convex axillary folding lines are the 234 235 principal lines for achieving wing folding. The concave axillary folding line is formed by the 2Ax-3Ax articulation, and the convex axillary folding line is formed by the 2Ax-BR 236 articulation anteriorly and the 3Ax-elytra articulation posteriorly, which are all firmly formed 237 in the elytral base. In the taxa with reduced 1Ax, tight articulation between 2Ax and the 238 notum was observed, which forms the anterior articulation of the basal hinge along with the 239 posterior articulation between 3Ax and the notum. These results suggest that the elytral base 240 241 sclerite are strongly constrained for maintaining accurate closure movements. This assumption may be tested by comparing the elytral base between species with different 242 modes of elytral opening. For example, rose chafers (Scarabaeidae: Cetoniinae) have a 243 244 specialized elytral locking system and do not open elytra even during flight (Sîpek et al., 2016). In this subfamily, significant reduction of 2Ax and 3Ax are known (Herbst, 1952; 245 246 Sípek et al., 2016). Therefore, it is conceivable that lack of the opening-closing function of elytra in Cetoniinae caused relaxed constraint against the accurate elytral closing mechanism 247 248 and then caused reduction of 2Ax and 3Ax.

Although the elytral base sclerites seem homoplasious, they may also involve some phylogenetic signal for the higher-level systematics. For example, the lobe located posteroproximal to the 2Ax-3Ax articulation (\* in Figs. 3–8) is uniquely and consistently observed in Polyphaga. In the other neopteran wing base, 3Ax articulates with the posterior

| 253  | tip of 2Ax so that the lobe located posterior to the articular point, as observed in Polyphaga,   |
|--|---|
| 254  | apparently represents an apomorphic condition. The faster evolution rate of the elytral base  |
| 255  | sclerites suggests their potential for uncovering the lower-level phylogeny of Coleoptera. In   |
| 256  | this study, we selected only one species from each representative taxon so that the utility of  |
| 257  | this characteristic system for the lower-level phylogeny would not be discussed. The  |
| 258  | homology scheme of the elytral base sclerites presented here should provide a basis for future  |
| 259  | morphological, evolutionary and functional studies of this characteristic system.   |
| 260  |   |
| 261  | Acknowledgments   |
| 262  |   |
| 263  | We thank Masahiro Ôhara and Namiki Kikuchi for providing valuable samples for this study.   |
| 264  | This study was conducted as part of MS's master thesis and is also partially supported by the   |
| 265  | JSPS pre-doctoral fellowship and by the JSPS research grants 15J03697 to NO and   |
| 266  | 15H04409 to KY.   |
| 267  |   |
|  |   |
| 268  | References  |
| 268<br>269   | References  |
| 268<br>269<br>270  | References Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based   |
| 268<br>269<br>270<br>271   | References Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based on morphological characters (Coleoptera: Scarabaeidae). Systematic Entomology 31,   |
| 268<br>269<br>270<br>271<br>272  | References<br>Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based<br>on morphological characters (Coleoptera: Scarabaeidae). Systematic Entomology 31,<br>113–144.   |
| 268<br>269<br>270<br>271<br>272<br>273   | References<br>Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based<br>on morphological characters (Coleoptera: Scarabaeidae). Systematic Entomology 31,<br>113–144.<br>Bostick, B.O., 1945. The morphology of the carabid beetle <i>Calosoma scrutator</i> (Fabricius).   |
| 268<br>269<br>270<br>271<br>272<br>273<br>274  | <ul> <li>References</li> <li>Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based on morphological characters (Coleoptera: Scarabaeidae). Systematic Entomology 31, 113–144.</li> <li>Bostick, B.O., 1945. The morphology of the carabid beetle <i>Calosoma scrutator</i> (Fabricius). Annals of the Entomological Society of America 38, 14–32.</li> </ul>   |
| 268<br>269<br>270<br>271<br>272<br>273<br>274<br>275   | <ul> <li>References</li> <li>Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based on morphological characters (Coleoptera: Scarabaeidae). Systematic Entomology 31, 113–144.</li> <li>Bostick, B.O., 1945. The morphology of the carabid beetle <i>Calosoma scrutator</i> (Fabricius). Annals of the Entomological Society of America 38, 14–32.</li> <li>Brodsky, A.K., 1994. <i>The Evolution of Insect Flight</i>. Oxford University Press, Oxford.</li> </ul>   |
| 268<br>269<br>270<br>271<br>272<br>273<br>274<br>275<br>276                                    | <ul> <li>References</li> <li>Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based on morphological characters (Coleoptera: Scarabaeidae). Systematic Entomology 31, 113–144.</li> <li>Bostick, B.O., 1945. The morphology of the carabid beetle <i>Calosoma scrutator</i> (Fabricius). Annals of the Entomological Society of America 38, 14–32.</li> <li>Brodsky, A.K., 1994. <i>The Evolution of Insect Flight</i>. Oxford University Press, Oxford.</li> <li>Browne, J., Scholtz, C.H., 1998. Evolution of the scarab hindwing articulation and wing base:</li> </ul>  |
| 268<br>269<br>270<br>271<br>272<br>273<br>274<br>275<br>276<br>277                             | <ul> <li>References</li> <li>Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based on morphological characters (Coleoptera: Scarabaeidae). Systematic Entomology 31, 113–144.</li> <li>Bostick, B.O., 1945. The morphology of the carabid beetle <i>Calosoma scrutator</i> (Fabricius). Annals of the Entomological Society of America 38, 14–32.</li> <li>Brodsky, A.K., 1994. <i>The Evolution of Insect Flight</i>. Oxford University Press, Oxford.</li> <li>Browne, J., Scholtz, C.H., 1998. Evolution of the scarab hindwing articulation and wing base: a contribution toward the phylogeny of the Scarabaeidae (Scarabaeoidea: Coleoptera).</li> </ul>   |
| 268<br>269<br>270<br>271<br>272<br>273<br>274<br>275<br>276<br>277<br>278                      | <ul> <li>References</li> <li>Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based on morphological characters (Coleoptera: Scarabaeidae). Systematic Entomology 31, 113–144.</li> <li>Bostick, B.O., 1945. The morphology of the carabid beetle <i>Calosoma scrutator</i> (Fabricius). Annals of the Entomological Society of America 38, 14–32.</li> <li>Brodsky, A.K., 1994. <i>The Evolution of Insect Flight</i>. Oxford University Press, Oxford.</li> <li>Browne, J., Scholtz, C.H., 1998. Evolution of the scarab hindwing articulation and wing base: a contribution toward the phylogeny of the Scarabaeidae (Scarabaeoidea: Coleoptera). Systematic Entomology 23, 307–326.</li> </ul>  |
| 268<br>269<br>270<br>271<br>272<br>273<br>274<br>275<br>276<br>277<br>278<br>279               | <ul> <li>References</li> <li>Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based on morphological characters (Coleoptera: Scarabaeidae). Systematic Entomology 31, 113–144.</li> <li>Bostick, B.O., 1945. The morphology of the carabid beetle <i>Calosoma scrutator</i> (Fabricius). Annals of the Entomological Society of America 38, 14–32.</li> <li>Brodsky, A.K., 1994. <i>The Evolution of Insect Flight</i>. Oxford University Press, Oxford.</li> <li>Browne, J., Scholtz, C.H., 1998. Evolution of the scarab hindwing articulation and wing base: a contribution toward the phylogeny of the Scarabaeidae (Scarabaeoidea: Coleoptera). Systematic Entomology 23, 307–326.</li> <li>Browne, J., Scholtz, C.H., 1999. A phylogeny of the families of Scarabaeoidea (Coleoptera).</li> </ul>   |
| 268<br>269<br>270<br>271<br>272<br>273<br>274<br>275<br>276<br>277<br>278<br>279<br>280        | <ul> <li>References</li> <li>Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based<br/>on morphological characters (Coleoptera: Scarabaeidae). Systematic Entomology 31,<br/>113–144.</li> <li>Bostick, B.O., 1945. The morphology of the carabid beetle <i>Calosoma scrutator</i> (Fabricius).<br/>Annals of the Entomological Society of America 38, 14–32.</li> <li>Brodsky, A.K., 1994. <i>The Evolution of Insect Flight</i>. Oxford University Press, Oxford.</li> <li>Browne, J., Scholtz, C.H., 1998. Evolution of the scarab hindwing articulation and wing base:<br/>a contribution toward the phylogeny of the Scarabaeidae (Scarabaeoidea: Coleoptera).<br/>Systematic Entomology 23, 307–326.</li> <li>Browne, J., Scholtz, C.H., 1999. A phylogeny of the families of Scarabaeoidea (Coleoptera).<br/>Systematic Entomology 24, 51–84.</li> </ul>  |
| 268<br>269<br>270<br>271<br>272<br>273<br>274<br>275<br>276<br>277<br>278<br>279<br>280<br>281 | <ul> <li>References</li> <li>Ahrens, D., 2006. The phylogeny of Sericini and their position within the Scarabaeidae based<br/>on morphological characters (Coleoptera: Scarabaeidae). Systematic Entomology 31,<br/>113–144.</li> <li>Bostick, B.O., 1945. The morphology of the carabid beetle <i>Calosoma scrutator</i> (Fabricius).<br/>Annals of the Entomological Society of America 38, 14–32.</li> <li>Brodsky, A.K., 1994. <i>The Evolution of Insect Flight</i>. Oxford University Press, Oxford.</li> <li>Browne, J., Scholtz, C.H., 1998. Evolution of the scarab hindwing articulation and wing base:<br/>a contribution toward the phylogeny of the Scarabaeidae (Scarabaeoidea: Coleoptera).<br/>Systematic Entomology 23, 307–326.</li> <li>Browne, J., Scholtz, C.H., 1999. A phylogeny of the families of Scarabaeoidea (Coleoptera).<br/>Systematic Entomology 24, 51–84.</li> <li>Doyen, J.T., 1966. The skeletal anatomy of <i>Tenebrio molitor</i> (Coleoptera: Tenebrionidae).</li> </ul> |

- El-Kifl, A.H., 1953. Morphology of the adult *Tribolium confusum* Duv. and its differentiation
  from *Tribolium (Stene) castaneum* Herbst. Bulletin de la Societe Fouad 1er
  d'entomologie 22, 173–249.
- Frantsevich, L., 2011. Mechanisms modeling the double rotation of the elytra in beetles
  (*Coleoptera*). Journal of Bionic Engineering 8, 395–405.
- Herbst, H.G., 1952. Studien über die Flügeldecken der Rutelinen und Cetoniinen (Coleoptera
  Scarabaeidae). Das Elytralgelenk. Zoologische Jahrbücher. Abteilung für Anatomie und
  Ontogenie der Tiere. 72, 1–66.
- Hörnschemeyer, T., 1998. Morphologie und Evolution des Flügelgelenks der Coleoptera und
  Neuropterida. Bonner Zoologische Monographien 43, 1–126.
- Hörnschemeyer, T., 2002. Phylogenetic significance of the wing-base of the Holometabola
  (Insecta). Zoologica Scripta 31, 17–29.
- Ishiwata, K., Sasaki, G., Ogawa, J., Miyata, T., Su, Z.H., 2011. Phylogenetic relationships
- among insect orders based on three nuclear protein-coding gene sequences. Molecular
  Phylogenetics and Evolution 58, 169–180.
- Kirejtshuk, A.G., Poschmann, M., Prokop, J., Garrouste, R., Nel, A., 2014. Evolution of the
  elytral venation and structural adaptations in the oldest Palaeozoic beetles (Insecta:
- 300 Coleoptera: Tshekardocoleidae). Journal of Systematic Paleontology 12, 575–600.
- Kukalová-Peck, J., Beutel, R.G., 2012. Is the Carbiniferous †*Adiphlebia lacoana* really the
  "oldest beetle"? Critical reassessment and description of a new Permian beetle family.
  European Journal of Entomology 109, 633–645.
- Larsén, O., 1966. On the morphology and function of the locomotor organs of the Gyrinidae
  and other Coleoptera. Opuscula entomologica Supplementum 30, 1–214.
- Linz, D.M., Hu, A.W., Sitvarin, M.I., Tomoyasu, Y., 2016. Functional value of elytra under
  various stresses in the red flour beetle, *Tribolium castaneum*. Scientific Reports 6,
  34813.
- 309 Misof, B., Liu, S., Meusemann, K., Peters, R.S., Donath, A., Mayer, C., Frandsen, P.B., Ware,
- 310 J., Flouri, T., Beutel, R.G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler,
- 311 T., Rust, J., Aberer, A.J., Aspock, U., Aspock, H., Bartel, D., Blanke, A., Berger, S.,
- Bohm, A., Buckley, T.R., Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M.,
- 313 Greve, C., Grobe, P., Gu, S., Huang, Y., Jermiin, L.S., Kawahara, A.Y., Krogmann, L.,
- 314 Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li, Z., Li, J., Lu, H., Machida, R., Mashimo,

| 315 | Y., Kapli, P., McKenna, D.D., Meng, G., Nakagaki, Y., Navarrete- Heredia, J.L., Ott,        |
|-----|---|
| 316 | M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., von Reumont, B. M., Schutte, K.,         |
| 317 | Sekiya, K., Shimizu, S., Slipinski, A., Stamatakis, A., Song, W., Su, X., Szucsich, N.U.,   |
| 318 | Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein, M.,         |
| 319 | Tong, X., Uchifune, T., Walzl, M.G., Wiegmann, B.M., Wilbrandt, J., Wipfler, B.,            |
| 320 | Wong, T.K., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D.K., Yoshizawa, K.,       |
| 321 | Zhang, Q., Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou, L., Ziesmann, T.,     |
| 322 | Zou, S., Li, Y., Xu, X., Zhang, Y., Yang, H., Wang, J., Wang, J., Kjer, K.M., Zhou, X.,     |
| 323 | 2014. Phylogenomics resolves the timing and pattern of insect evolution. Science 346,       |
| 324 | 763–767.  |
| 325 | Ogawa, N., Yoshizawa, K., 2017. Morphological dissection of a behavioral trait: thoracic    |
| 326 | musclature clarifies independent development of jumping mechanisms between sister           |
| 327 | groups, planthoppers and leafhoppers (Insecta: Hemiptera: Auchenorrhyncha).                 |
| 328 | Organisms Diversity & Evolution 17, 521–530.  |
| 329 | Richmond, E.A., 1931. The external morphology of Hydrophilus obtusatus Say (Coleoptera:     |
| 330 | Hydrophilidae). Journal of the New York Entomological Society 39, 191-251.                  |
| 331 | Rivnay, E., 1928. External morphology of the Colorado potato beetle (Leptinotarsa           |
| 332 | decemlineata Say). Journal of the New York Entomological Society 36, 125-145.               |
| 333 | Sípek, P., Fabrizi, S., Eberle, J., Ahrens, D., 2016. A molecular phylogeny of rose chafers |
| 334 | (Coleoptera: Scarabaeidae: Cetoniinae) reveals a complex and concerted morphological        |
| 335 | evolution related to their flight mode. Molecular Phylogenetics and Evolution 101, 163-     |
| 336 | 175.  |
| 337 | Stellwaag, F., 1914. Der Flugapparat der Lamellicornier. Zeitschrift für wissenschaftliche  |
| 338 | Zoologie. 108, 359–429.   |
| 339 | Tremblay, E. 1958. Studio morfo-biologico sulla Necrobia rufipes De G. Bollettino del       |
| 340 | Laboratorio di agricoltura "Filippo Silvestri" Portici 16, 9–140.                           |
| 341 | Wootton, R.J., 1979. Function, homology and terminology in insect wings. Systematic         |
| 342 | Entomology 4, 81–93.  |
| 343 | Yoshizawa, K., 2007. The Zoraptera problem: evidence for Zoraptera + Embiodea from the      |
| 344 | wing base. Systematic Entomology 32, 197–204.   |
| 345 | Yoshizawa, K., 2011. Monophyletic Polyneoptera recovered by wing base structure.            |
| 346 | Systematic Entomology 36, 377–394.  |
|     |   |

| 347 | Yoshizawa, K., Saigusa, T., 2001.Phylogenetic analysis of paraneopteran orders (Insecta:        |
|-----|---|
| 348 | Neoptera) based on forewing base structure, with comments on monophyly of                       |
| 349 | Auchenorrhyncha (Hemiptera). Systematic Entomology 26, 1–13.                                    |
| 350 | Yoshizawa, K., Wagatsuma, M., 2012. Phylogenetic relationships among superfamilies of           |
| 351 | Cicadomorpha (Hemiptera: Auchenorrhyncha) inferred from the wing base structure.                |
| 352 | Entomological Science 15, 408–421.  |
| 353 | Yoshizawa, K., Ogawa, N., Dietrich, C.H., 2017. Wing base structure supports Coleorrhyncha      |
| 354 | + Auchenorrhyncha (Insecta: Hemiptera). Journal of Zoological Systematics and                   |
| 355 | Evolutionary Research 55, 199–207.  |
| 356 | Zhao, C., Liu, X., Yang, D., 2014. Wing base structural data support the sister relationship of |
|     |   |

357 Megaloptera and Neuroptera (Insecta: Neuropterida). PLoS ONE 9, e114695.

359 Figure captions

- 361 Fig. 1. Elytral base structure of *Calosoma chinense* (Adephaga: Carabidae)
- 362 Fig. 2. Elytral base structure of *Dineutus orientalis* (Adephaga: Gyrinidae)
- 363 Fig. 3. Elytral base structure of *Hydrophilus acuminatus* (Polyphaga: Hytrophilidae)
- Fig. 4. Elytral base structure of *Trypoxylus dichotomus* (Polyphaga: Scarabaeidae)
- 365 Fig. 5. Elytral base structure of *Andocamaia ryukyuensis* (Polyphaga: Tenebrionidae)
- 366 Fig. 6. Elytral base structure of *Enoclerus moestus* (Polyphaga: Cleridae)
- 367 Fig. 7. Elytral base structure of *Chrysodema manillarum* (Polyphaga: Buprestidae)
- 368 Fig. 8. Elytral base structure of *Prionus insularis* (Polyphaga: Cerambycidae)

| Reference I Taxa (family) \ present scheme |   | Tg                  | HP                     | BSc                       | BR               | 1Ax                          | 2Ax              | ЗАх               | РМР         | DMP                 |
|--|---|---------------------|------------------------|---------------------------|------------------|------------------------------|------------------|-------------------|-------------|---------------------|
| Bostick (1945: fig. 17)                    | Carabiidae  | _                   | Costa                  | Subcosta<br>(ventral)     | _                | Ax1                          | Ax2              | Ax3 (part)        | Ax3? (part) | _                   |
| Larsén (1966: fig. 9)                      | Gyrinidae   | _                   | Co?                    | Sco                       | Rd               | 1Ax (part)                   | 1Ax (part) + 2Ax | 3Ax + 4Ax         | _           | _                   |
| Richmond (1931: fig. 27)                   | Hydrophilidae                                       | _                   | ae (elytral apophysis) |                           | _                | _                            | _                | _                 | -           | _                   |
| Stellwaag (1914: figs 8–9 & tab. XI)       | Scarabaeoidea                                       | _                   | lateral apophysis      |                           | Achl (Ax1: part) | _                            | Achl (part)      | AchII + Pf (root) | _           | median<br>apophysis |
| Herbst (1952: nomenclature)                | Scarabaeidae  | _                   | L (costal lobe)        | AO1(upper<br>apophysis 1) | AO2              | Ax1                          | Ax2              | АхЗ               | _           | AO3                 |
| Ahrens (2006: fig. 5, app. 3)              | Scarabaeidae  | _                   | hs                     | bsc                       | fm1              | _                            | Ax2              | Ax3               | _           | bmp                 |
| Frantsevich (2011: fig. 3)                 | Scarabaeidae  | _                   | root                   |                           | _                | Ax1                          | Ax2              | Ax3               | -           | _                   |
| Sípek et al. (2016: fig. 2)                | c et al. (2016: fig. 2) Scarabaeidae – elytral root |                     | al root                | Ax2-Root connection       | _                | Ax2                          | Ax3              | -                 | _           |                     |
| El-Kifl (1953: fig. 25)                    | Tenebrionidae                                       | _                   | basal process          |                           | _                | lateral plate of mesonotum ? | 1Ax              | 2Ax               | 3Ax?        | _                   |
| Doyen (1966: fig. 38)                      | Tenebrionidae                                       | _                   | basal process          |                           | _                | _                            | axillary 2       | axillary 3        | _           | axillary 1          |
| Tremblay (1958: figs 1–2)                  | Cleridae  | 1M<br>(mesopterale) | PBA (joint process)    |                           | AR-2M (part)     | 2M (part)                    | 2M (part) (2Ax)  | ЗМ                | -           | _                   |
| Rivnay (1928: fig. 15)                     | fig. 15) Chrysomelidae – apophysis                  |                     | _                      | _                         | _                | _                            | _                | _                 |             |                     |













Figure 7



