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1 **Morphological dissection of behaviour: thoracic musculature clarifies**
2 **independent development of jumping mechanisms between sister groups,**
3 **planthoppers and leafhoppers (Insecta: Hemiptera: Auchenorrhyncha)**
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1 **Abstract** Morphological and behavioural characters are frequently examined for comparative
2 studies. Unlike morphology, a single behavioural trait is difficult to subdivide as multiple
3 characters, even when achieved by many evolutionary changes. Therefore, when similar
4 behavioural traits evolved independently among closely related taxa, their distinction is
5 difficult. Almost all members of the suborder Auchenorrhyncha (Insecta: Hemiptera) possess
6 a jumping ability that uses metathoracic muscles, and this behavioural trait has been regarded
7 as a synapomorphy. In this study, the anatomical observations of metathoracic muscles
8 revealed that highly elaborated jumping ability was gained independently within the suborder,
9 although the evolution of jumping ability might have been initiated at their common ancestor.
10 Our results provide an example of identifying a true evolutionary pathway by dissecting a
11 behavioural character into mechanical elements.
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23 **Key words** functional morphology • behavior • character evolution • evolutionary novelty
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Introduction

For morphology-based phylogenetic analyses and/or studies of morphological evolution, a single structure is usually subdivided into several smaller elements. For example, the insect mandible is composed of a single sclerite, but molar, incisor, and anterior and posterior articulations, among others, are recognized as mandibular elements and coded separately for phylogenetic and/or evolutionary analyses. By contrast, such a subdivision is usually difficult for behavioural characters. Therefore, when a behavioural trait is the subject of phylogenetic comparative analyses, the trait is generally treated as a single character (eg. "eusociality" in Carpenter 1982; "parasitism" in Johnson et al. 2004; "maternal child care" in Tsai et al. 2015), although a single behavioural change almost always involves multiple morphological, physiological, and/or neural changes.

"Jumping ability" is such an example, and when this trait has been the focus of study, it is treated as a single character (Hennig 1981). However, this ability was actually achieved by a combination of many structural modifications, including those of muscles, muscle attachments, and associated sclerites and those for energy storage and the locking system, among others (Gorb 2004). Therefore, the jumping behaviour can be separated into many functional elements morphologically that can clarify the evolutionary pathway of jumping ability. In some simple cases, the independent origins of these functional elements are obvious. For example, locusts jump using muscles in their hind femur, whereas fleas use extrinsic leg muscles (Bennet-Clark and Lucey 1967; Brown 1967), and the independent origins are easily recognizable. By contrast, both locusts and jumping cockroaches use hind femur muscles for jumping (Picker, Colville, and Burrows 2011); however, distant phylogenetic affinity indicates independent origins of jumping ability. When similar mechanisms evolved independently in closely related taxa, however, their distinction is far more difficult.

The suborder Auchenorrhyncha (Insecta: Hemiptera) is composed of planthoppers (infraorder Fulgoromorpha) and leafhoppers, treehoppers, froghoppers (or spittle bugs) and cicadas (infraorder Cicadomorpha). Monophyly of Auchenorrhyncha was once debated (Bourgoin and Campbell 2002; Forero 2008), but subsequent morphological (Yoshizawa and Saigusa 2001) and molecular (Cryan and Urban 2012; Misof et al. 2014) analyses converged to support its monophyly. The suborder is well known for jumping ability, with the exception

1 of cicadas. The jumping is very fast and strong, and the suborder includes champions among
2 all jumping insects with take-off velocities that reach up to 5.5 m s⁻¹ and 719g in kicking force
3 (Fulgoroidea: Issidae) (Burrows 2009a). All auchenorrhynchous insects use the metathoracic
4 muscles for jumping. Therefore, by focusing only on this behavioural character, the most
5 parsimonious interpretation for the evolution of their jumping ability is that it evolved once in
6 their common ancestor and then the ability was lost secondarily in cicadas (Fig. 1A), as
7 generally assumed (Hennig 1981; Kristensen 1975; Shcherbakov and Popov 1997). However,
8 the condition of the principal jumping muscle (i.e., trochanter depressor muscle) is different
9 between Cicadomorpha and Fulgoromorpha (Burrows and Bräunig, 2010). In addition,
10 froghoppers (Cicadomorpha: Cercopoidea) have protrusions on the hind coxa and femur that
11 are engaged when the hindleg is cocked for jumping preparation (Burrows 2006), whereas the
12 femoral protrusion is completely reduced in planthoppers (Fulgoromorpha) (Burrows
13 2009). Because of these morphological and mechanical differences, jumping ability might
14 have evolved independently in these sister infraorders, which is a less parsimonious
15 interpretation based on the behavioural trait (Fig. 1B). Furthermore, when we accept the
16 independent origins of jumping ability, then independent origins of jumping ability within
17 Cicadomorpha (Fig. 1C) or a more complicated evolutionary scenario (Fig. 1D) also become
18 equally parsimonious interpretations. To solve this question, detailed morphological
19 observations throughout the auchenorrhynchans and phylogenetic reconstruction of character
20 evolution are required.

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38 In this study, we verify these four alternative hypotheses by morphological
39 dissection and observation of auchenorrhynchan jumping muscles. Our examination
40 provides an example assessing the more likely evolutionary pathway by dissecting a
41 behavioural character into mechanical elements. The results also provide useful information
42 for understanding the ancestral traits of morphology and behaviour in Hemiptera.
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48 **Materials and Methods**

49 *Taxa examined*

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52 We selected Ricaniidae and Fulgoridae (Fulgoromorpha), Cicadellidae and
53 Membracidae (Membracoidea), Cercopidae, Machaerotidae, Clastopteridae and
54 Aphrophoridae (Cercopoidea) and Cicadidae and Tettigarctidae (Cicadoidea) for
55 examinations. *Stenopsocus nigricellus* (Psocodea: "Psocoptera") was selected as a close
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1 out-group, and the tree was rooted with Zorotypidae (Zoraptera: Friedrich and Beutel 2008).
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3 Jumping behavior does not occur in the selected out-groups. The taxa examined are listed in
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5 Table 1.
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8 *Specimen preparation and observation*

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10 Specimens fixed in FAA solution (formalin:alcohol:acetic acid = 6:16:1) and stored
11 in 80% ethanol were used. A specimen of Tettigarctidae (Cicadoidea) that had originally been
12 dried and later soaked was also examined as a supplemental specimen. Specimens were
13 dissected with a FH-20 razor blade (Feather Safety Razor Co., Ltd., Osaka, Japan) and forceps.
14 Some specimens were macerated in 10% KOH solution to facilitate observations of the
15 skeletons. SZ61 and SZX16 binocular microscopes (Olympus Corporation, Tokyo, Japan) and
16 a Zeiss Axiophoto light microscope (Carl Zeiss, Oberkochen, Germany) were used for
17 observations. The illustrations were drawn using a Cintiq 13HD graphics tablet (Wacom Co.,
18 Ltd., Saitama, Japan) and Clip Studio Paint Pro (Celsys, Inc., Tokyo, Japan) and modified in
19 Adobe Photoshop CC and Adobe Illustrator CC. The investigated muscles were homologized
20 based on their origin/insertion points and their positional relation to the circumjacent muscles.
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31 *Terminologies of Muscles*

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33 Terminologies of individual muscles followed Friedrich and Beutel (2008) because
34 of their systematic nomenclature. The thoracic segments were indicated by roman numerals
35 prefixed to the muscle name (e.g., IIIIdvm1: metathoracic dvm1). Correspondence to the
36 traditional nomenclature, abbreviations and their origin and insertion is given in Table 2.
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43 *Target muscles for observation*

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45 We focused on metathoracic indirect flight muscles and trochanter depressor
46 muscles. Meso- and metathoraces of neopteran insects are usually filled with large indirect
47 flight muscles (Fig. 2). Whereas some muscles are bifunctional and provide power for flight
48 and walking, the principal indirect flight muscles are usually monofunctional (Brodsky 1994).
49 They attach to robust sclerites, i.e., tergum, sternum and phragma, and they generate principle
50 flight power (Brodsky 1994). The indirect flight muscles were classified into three categories:
51 dorsal longitudinal indirect flight muscle (DLM), dorsoventral flight muscle (DVM) and
52 oblique dorsal flight muscle (ODM) (Brodsky 1994; Crossley 1978) (Fig. 2). DLM, DVM and
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1 ODM correspond to dlm1 (phragma-phragmalis muscle), dvm1 (noto-sternalis muscle), and
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3 dlm2/3 (noto-phragmalis muscle/scutello-scutellaris muscle), respectively.
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5 The trochanter depressor muscles generate principal power of auchenorrhynchan jumping,
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7 which can be subdivided into functional elements (Burrows and Bräunig 2010; Gorb 2004).
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9 Neopteran insects usually have four bundles of metathoracic trochanter depressor muscles,
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11 scm6 (from furca), pcm5 (from metanepisternum and basalare), and dvm7 (from notum)
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13 (Friedrich and Beutel 2008) (Fig. 2).
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16 *Phylogenetic hypothesis*

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18 Phylogenetic relationships of Auchenorrhyncha and out-groups were taken from
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20 Urban and Cryan (2007), Cryan and Urban (2012) and Misof et al. (2014). Most parsimonious
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22 reconstruction of the ancestral character states (jumping behaviour and conditions of
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24 jumping/flight muscles) was performed using Mesquite 3.04 (Maddison and Maddison 2015).
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27 **Results**

28 29 30 *Metathoracic musculature of Fulgoroidea (Fulgoromorpha)*

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32 Metathoracic musculature in the Fulgoromorpha is highly modified and rearranged
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34 (Fig. 3A, B). The lower part of the metathorax is filled with a cylinder-shaped jumping
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36 muscle (Fig. 3A, B). The jumping muscle originates from a well-developed basalare and
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38 small metanepisternum (Character 2:0; 3:1) (Fig. 5A), and is inserted into the dorsal region of
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40 the robust tendon (Figs 3A, B; 4A). The attachment point of the tendon has the form of a
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42 funnel (Character 10:0) (Fig. 4A). The jumping muscle is homologous to IIIpcm5 (Character
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44 1:1). Completely absent are other trochanter depressor muscles, IIIscm6 and IIIdvm7
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46 (Character 4:1). The DLM and ODM are well developed (Character 7:0; 9:0; 11:0), but the
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48 DVM is completely absent (Character 6:1) (Fig. 3A, B).
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51 *Metathoracic musculature of Membracoidea (Cicadomorpha)*

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53 As in the Fulgoroidea, the Membracoidea also have jumping muscles in the
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55 metathorax. However, their metathoracic musculature differs significantly from that of the
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57 fulgoromorphans, as also noted by Burrows and Bräunig (2010) and Burrows (2013) (Fig. 3C,
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Most flight muscles are reduced, and most of the metathoracic space is filled with the jumping muscles composed of two trochanter depressor muscles (Fig. 3D) (Burrows 2007; Gorb 2004; Maki 1938). In Membracidae, the tendon is shaped as a shingle sheet with a sclerotized stem. The tendon of Cicadellidae is similar, but the tendon forks basally (Fig. 4B) (Character 10:1). Both jumping muscles are inserted on the ventral side of the tendon. The muscle inserted on the ventroproximal side is homologous to IIIIdvm7 (Character 4:0; 5:1), and its origin occupies most parts of the metanotum and the entire posterior surface of the mesophragma (Character 11:1). The muscle inserted on the ventrolateral side of the tendon (including the small branch in Cicadellidae) is IIIpcm5 (Character 1:1), originating from the anterolateral bulged metanepisternum and the tiny basalare (Character 2:1; 3:0) (Fig. 3D). IIIscm6 is absent. Due to the expansion of the attached area of IIIIdvm7, DLM is strongly reduced and changes its origin/insertion points to a very narrow area of the dorsal margin of the meso-/metaphragma, respectively (Character 7:1). The DVM is also greatly reduced but retained in all taxa (Character 6:0). The ODM is remained in Cicadellidae, but was completely absent in Membracidae (Character 9:1).

Metathoracic musculature of Cercopoidea (Cicadomorpha)

The metathoracic musculature of Cercopoidea is also highly modified and rearranged (Fig. 3E, F). Although the external morphology of the hind leg base is quite different between Cercopoidea and Membracoidea (with narrow and conical hind coxae in Cercopoidea whereas broadly transverse hind coxae in Membracoidea: Burrows 2006; 2007), the metathoracic musculature of cercopoids is very similar to that of membracoids.

The jumping muscles also comprise two bundles, IIIpcm5 and IIIIdvm7 (Fig. 3F) (Character 1:1; 4:0; 5:1). The tendon clearly forks basally, and each branch is composed of robust stem and membranous field (Character 10:1), and both surfaces are used for muscle attachment (Fig. 4C). The muscle inserted on the inner fork is homologous to IIIIdvm7. The muscle is broadly expanded dorsally, and its attachment occupies most area of the metanotum and the entire posterior surface of the mesophragma (Character 11:1). The muscle inserted into the lateral fork is IIIpcm5, originating from anterolateral bulged metanepisternum and small basalare (Character 2:1; 3:0) (Gorb 2004; Savinov 1990) (Fig. 4F). Absent was IIIscm6. According to the expansion of the attached area of IIIIdvm7, DLM is strongly reduced and changed its origin/insertion points to a very narrow area of the dorsal margin of the

1 meso-/metaphragma, respectively. The right and left bundles of DLM are separated by
2 internal branch of IIIIdvm7 (Character 8:1). DLM of Cercopidae and Clastopteridae is
3 completely absent, although that of Aphrophoridae and Machaerotidae remains (Character
4 7:1). DVM is also greatly reduced but is retained in all taxa (Character 6:0). The ODM is also
5 reduced but is relatively well retained (Fig. 3E, F) (Character 9:1).
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10 11 12 *Metathoracic musculature of Cicadoidea (Cicadomorpha)*

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14 The arrangement of the metathoracic muscles in Cicadoidea is distinctly different
15 from the condition observed in the other groups (Snodgrass 1935; Maki 1938: Fig. 3G, H).
16 DLM is retained but distinctly reduced and placed at the dorsolateral crack formed by the
17 shortened and strongly arched metanotum (Character 7:1). DVM is also reduced in size but
18 retained (Character 6:0). *Graptopsaltria* and *Huechys* (Maki 1938) retain a reduced ODM,
19 whereas ODM is completely absent in *Meimuna* (Cicadidae) (Character 9:1). The tendon
20 forms a less-sclerotized and expanded dorsal sheet with a small lateral fork (Fig. 3B)
21 (Character 10:1). The muscles homologous to the jumping muscles in the other
22 cicadomorphans (IIIIdvm7 and IIIpcm5) are weakly developed and composed of three subunits.
23 The lateral subunit originating from the ventral metanepisternum which is homologous to the
24 IIIpcm5 of the jumping cicadomorphans (Character 1:0; 2:0), is inserted on the small fork of
25 the trochanteral tendon (Figs 3H; 4D). The other two subunits are both inserted on the
26 sheet-like dorsal expansion of the trochanteral tendon (Figs 3H; 4D) (Character 10:1). One
27 originates from the anterolateral lobe of the scutum along the antecoxal suture (Figs 3H; 4D)
28 and the other from the ventral region of the mesophragma (* in Figs 3G, H; 4D). Together,
29 these two subunits correspond to the IIIIdvm7 in the jumping cicadomorphans (Character 4:0;
30 5:0). IIIscm6 is also absent. In Cicadidae, a wide empty area is present on the posterodorsal
31 surface of the mesophragma (Fig. 3H) (Character 11:2), unlike the mesophragma of the
32 jumping cicadomorphans, which is completely occupied by IIIIdvm7 (Character 11:1) (Fig.
33 3C-F), or unlike the ordinal pterothorax, which is completely occupied by DLM (Character
34 11:0) (Fig. 1). This condition was also observed in the *Tettigarcta* (Tettigarctidae). The
35 specimen was originally dried, and the thoracic musculature was not well preserved, but the
36 condition of the IIIIdvm7 and the empty area on the mesophragma were clearly visible.
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57 58 *Parsimony analysis*

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1 The ancestral condition of the metathoracic structures potentially associated with
2 the evolution of jumping behaviour was reconstructed parsimoniously using previously
3 estimated trees (Fig. 6: characters listed in Appendix 1). The infraorder Fulgoromorpha was
4 implied to share the following states in the common ancestor: enlarged apodeme developed
5 from basalare (Character 3:1), loss of III_{dvm}7 (Character 4:1), and loss of DVM (Character
6 6:1). Expansion of metanepisternum (Character 2:1), development of III_{dvm}7 as a jumping
7 muscle (Character 5:1), reduction of DLM (Character 7:1), reduction of ODM (9:1), the
8 sheet-like trochanter tendon (10:1), and occupation of the mesophragma by III_{dvm}7 (11:1)
9 were considered to have evolved in the common ancestor of the infraorder Cicadomorpha.
10 The III_{pcm}5 develops as a jumping muscle (Character 1:1) in both Cicadomorpha and
11 Fulgoromorpha. The empty area on the mesophragma (Character 11:2) related to the
12 reduction of the jumping muscle III_{dvm}7 (Character 5:0) was regarded as an autapomorphy
13 of the Cicadoidea. Jumping function of III_{pcm}5 was secondarily reduced in Cicadoidea
14 (Character 1:0).
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29 Discussion

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32 All jumping species of Auchenorrhyncha possess large metathoracic jumping
33 muscles transformed from the trochanter depressors. However, the condition of the jumping
34 muscles is very distinctly different between the two infraorders. Fulgoromorpha have very
35 large jumping muscles developed from only III_{pcm}5, which is inserted to the funnel shaped
36 trochanteral tendon and is originated from the expanded basalare (Figs 3A, B; 4A) (Character
37 1:1; 2:0; 3:1; 10:0). In contrast, two superfamilies of Cicadomorpha (Membracoidea and
38 Cicadoidea) possess very large jumping muscles composed of modified and enlarged III_{dvm}7
39 and III_{pcm}5 inserted on an enlarged trochanteral tendon (Figs 3C-F; 4B, C) (Character 1:1;
40 5:1; 10:1). In Cicadoidea, the trochanter depressor muscles originate from the pleura, notum
41 and phragma and are inserted on the trochanteral tendon (Figs 3G, H; 4D).
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51 The most parsimonious reconstruction of the metathoracic muscular characters
52 suggests that almost all apomorphic conditions associated with the jumping ability evolved
53 independently in Cicadomorpha and Fulgoromorpha (Fig. 6). The development of III_{pcm}5 as
54 a jumping muscle is shared by Cicadomorpha and Fulgoromorpha (Character 1:1), but its
55 origin (Character 2; Fig. 5) and insertion points (Character 3; Fig. 4) considerably. Therefore,
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1 although the development of jumping ability may have originated in their common ancestor
2 (Hennig 1981; Kristensen 1975), it is evident that the highly elaborate jumping ability and
3 mechanism as observed in extant groups of Auchenorrhyncha has been achieved
4 independently between two infraorders, as suggested by Burrows and Bräunig (2010) and
5 Burrows (2013) (Fig. 1B, C).
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10 From the present morphological analyses, the evolution of the auchenorrhynchan
11 jumping ability can be explained as follows. In Fulgoromorpha, the muscle originating from
12 the metanepisternum and basalare (IIIpcm5) were transformed into jumping muscles
13 (Character 1:1). The enlarged attachment point was formed by the strong expanded basalare
14 (Character 3:1). The tendon was also modified as an enlarged funnel-shaped structure for
15 expanding the attachment point, which was also strengthened to support the huge contracting
16 power of the jumping muscle. Absence of IIIIdvm7 (Character 4:1) and IIIscm6 might be the
17 result of constraint in attachment area in the notum (with the flight muscles) and tendon (with
18 enlarged IIIpcm5), respectively. Because the jumping muscles occupied only the lower half of
19 the metathorax, adequate room for storing the flight muscles could be retained in the upper
20 part. In the jumping Cicadomorpha (Membracoidea and Cercopoidea), IIIpcm5 and IIIIdvm7
21 transformed to the jumping muscles (Character 1:1; 5:1). Attachment points of the jumping
22 muscles were expanded: IIIIdvm7 was attached into mesophragma (Character 11:1), in
23 addition to the notum. Reductions of flight muscles and the absence of IIIscm6 (both muscles
24 attached to the notum and phragma) were most likely the result of competition for attachment
25 space for jumping muscles. Whereas the shape of the tendon (a single sheet in Membracoidea
26 vs. birurcated in Cercopoidea), muscle attachment manner on tendon (ventral side vs. both
27 sides), and location of DLM (Character 8) differ between the two superfamilies, their jumping
28 muscles and related morphologies were considered to be gained in the common ancestor
29 because of the fundamental similarities.
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47 Additionally, under the assumption of independent evolution of the jumping ability
48 in Fulgoromorpha and Cicadomorpha, two equally parsimonious scenarios are also possible,
49 i.e., a secondarily reduced jumping ability in Cicadoidea (Fig. 1B) or independent origins of
50 jumping ability in Cicadomorpha (Fig. 1C). Of the two scenarios, the arrangements of the
51 jumping musculatures of cicadomorphans indicates that the secondary reduction hypothesis is
52 more likely. Expansion of the original position of the IIIIdvm7 from the notum to
53 notum+mesophragma (Character 11:1) and the reduction of the DLM (Character 7:1) are
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1 estimated to have evolved in the common ancestor of Cicadomorpha. Reduction of the DLM
2 is strongly associated with the development of the IIIIdvm7 because, in ordinal flying insects,
3 DLM occupies almost the entire surface of the posterior mesophragma (Character 11:0).
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5 Although a wide empty space is on the mesophragma of the Cicadoidea (Character 11:2), the
6 cicadoidean DLM occupies only a very narrow dorsal margin of the phragma (Fig. 3H), as
7 also observed in the Membracoidea and Cercopoidea (Fig. 3D, F). This strongly suggests that
8 the expansion of the jumping muscle to the anterior phragma occurred in the common
9 ancestor of Cicadomorpha, and that the poorly developed jumping muscle in the Cicadoidea
10 represents a secondary reduction. Additionally, the presence of phragma-trochanteralis muscle
11 in Cicadoidea (* in Fig. 3G, H) also supports the secondary reduction interpretation. The
12 muscle is never present in insects other than jumping Auchenorrhyncha. Therefore, this
13 muscle in Cicadoidea can be interpreted as a vestige of the jumping muscle after secondary
14 reduction of expanded IIIIdvm7 and its absence from the notum.
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25 In summary, the muscle morphology suggests that some fundamental aspects of
26 jumping ability originated in the common ancestor of Auchenorrhyncha, several details of the
27 jumping mechanisms of Cicadomorpha and Fulgoromorpha evolved independently. The lack
28 of the jumping ability in the Cicadoidea represents a secondarily reduced condition. This
29 more complicated evolutionary scenario could not be extracted from a simple maximum
30 parsimony reconstruction of the behavioural character (Fig. 1A), and observation of the
31 muscles associated with the jumping ability was required to reach this conclusion. Our results
32 provide an example that the morphological dissection of a behavioural trait is valid for
33 implicating a more likely evolutionary pathway. Shcherbakov and Popov (1997) claimed that
34 the jumping ability is a synapomorphic trait in the order. However, the implication was
35 proposed based on a fossilized exoskeleton without considering internal morphology. To
36 understand the origins and evolution of the jumping ability in all of groups of Hemiptera,
37 detailed morphological and functional investigations are obligatory.
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7 Fig. 1. Phylogeny of Auchenorrhyncha and four possible evolutionary scenarios for the
8 evolution of jumping ability. The tree was summarized from Cryan & Urban
9 (2012). The black and white rectangles/squares indicate presence and absence of
10 jumping ability, respectively. A, The most parsimonious interpretation implied
11 from jumping behaviour (2 steps). B, The independent origins hypothesis as
12 suggested by Burrows & Bräunig (2010) and Burrows (2013) (3 steps). C–D,
13 Two additional possibilities with evolutionary steps = 3.
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21 Fig. 2. Flight and jumping musculatures of the bark louse genus *Stenopsocus* (Psocodea:
22 “Psocoptera”: Stenopsocidae), lateral view. Redrawn and modified from
23 Badonnel (1934) and Maki (1938). Indirect flight muscles were colored blue:
24 DLM, dorsal longitudinal indirect flight muscle (dlm1); DVM, dorsoventral
25 flight muscle (dvm1); ODM, oblique dorsal flight muscle (dlm2/3). Trochanter
26 depressor muscles were colored by respective muscles. Terminology followed
27 Crossley (1978), Brodsky (1994) and Beutel et al. (2014). The border of
28 mesophragma is highlighted by green line.
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38 Fig. 3. Flight and jumping muscles of Auchenorrhyncha, lateral (left) and posterior
39 (right) views. A, *Ricania japonica* (Fulgoromorpha: Fulgoroidea: Ricaniidae); B,
40 *Cicadella viridis* (Cicadomorpha: Membracoidea: Cicadellidae); C, *Aphrophora*
41 *pectoralis* (Cercopoidea: Aphrophoridae); D, *Graptopsaltria nigrofuscata*
42 (Cicadidae: Cicadoidea). See Fig. 2 for terminology, colours and abbreviations.
43 The right side of posterior images shows muscles (colored shadows) and muscle
44 attachment regions (black dots). The border of mesophragma is highlighted by
45 green line.
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54 Fig. 4. Enlarged view of left metatrocanteral tendons and attachments point of muscles.
55 A, *Ricania japonica* (Fulgoromorpha: Fulgoroidea: Ricaniidae); B, *Cicadella*
56 *viridis* (Cicadomorpha: Membracoidea: Cicadellidae); C, *Aphrophora pectoralis*
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1 (Cercopoidea: Aphrophoridae); D, *Graptopsaltria nigrofuscata* (Cicadoidea:
2 Cicadidae). See Fig. 2 for terminology and abbreviations. The painted regions
3 indicate the muscle attachment areas. Deep and light gray indicate the attached
4 area of IIIIdvm7 and IIIIpcm5, respectively. Arrows with a spot represent muscle
5 bundles. Dashed lines indicate concealed muscles or sclerite borders.
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12 Fig. 5. Metathoracic endoskeletons and attachment regions of IIIIpcm5, lateral view. See
13 Fig. 2 for terminology and abbreviations. A, *Ricania japonica* (Fulgoromorpha:
14 Fulgoroidea: Ricaniidae); B, *Cicadella viridis* (Cicadomorpha: Membracoidea:
15 Cicadellidae). IIIIpcm5 is indicated by gray shadow. Dotted areas indicate
16 muscle attachment regions.
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25 Fig. 6. Most parsimonious reconstruction of character states scored in this study
26 (Appendix 1) onto the phylogeny of Auchenorrhyncha estimated by Misof et al.
27 (2014), Cryan and Urban (2012) and Urban and Cryan (2007). Outgroups are
28 omitted. Character and character state changes reconstructed on the branches are
29 indicated by black (gain) and white bars (reversal). For some characters (e.g.,
30 Character 5), an alternative interpretation for character evolution may be
31 possible but, based on the present morphological observation (see text), the
32 interpretation given in the figure is considered to be likely. The result indicated
33 common origin of the jumping ability in Auchenorrhyncha (1:0 → 1 at the root),
34 but independent evolution of jumping mechanisms between Cicadomorpha and
35 Fulgoromorpha.
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3 Appendix 1. Characters and their states reconstructed in this study.
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7 Character 1. IIIpcm5: not developed as jumping muscle (0) developed as major jumping
8 muscle (1). State 0 was observed in out-groups and Cicadoidea. State 1 was
9 observed in all jumping Auchenorrhyncha (Fig. 3A-F).
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14 Character 2: Origin of IIIpcm5: restricted to dorsal episternum and basalare (0);
15 expanded to ventral metanepisternum (1). State 0 was observed in out-groups and
16 Fulgoromorpha. State 1 was observed throughout Cicadomorpha including
17 Cicadoidea.
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23 Character 3: Apodeme of basalare: not enlarged (0); enlarged (1). State 1 was only
24 observed in Fulgoromorpha.
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29 Character 4. IIIdvm7: present (0); absent (1). State 1 was only observed in
30 Fulgoromorpha. (Fig. 3A, B).
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34 Character 5. Jumping function in IIIdvm7: not developed as jumping muscle (0);
35 developed as jumping muscle (1). State 1 was only observed in jumping
36 Cicadomorphans. State of Fulgoromorpha was treated as unknown.
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41 Character 6. DVM (IIIIdvm1): present (0); absent (1). State 1 was only observed in
42 Fulgoromorpha (Fig. 3A, B). DVM of the other examined taxa was present (State
43 0).
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49 Character 7. DLM (IIIIdlm1): developed (0); reduced or absent (1). State 1 was observed
50 in all cicadomorphans (Fig. 3C-H). Fulgoromorpha and out-groups possessed
51 developed DLM (State 0)
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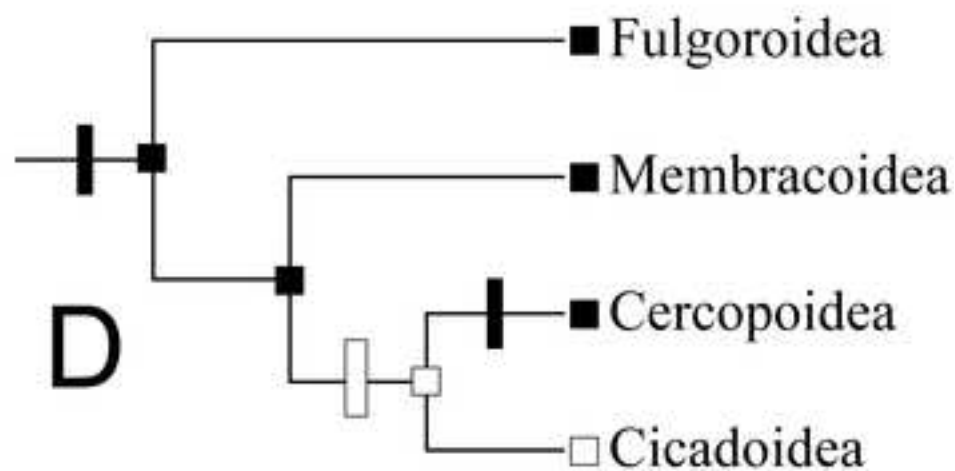
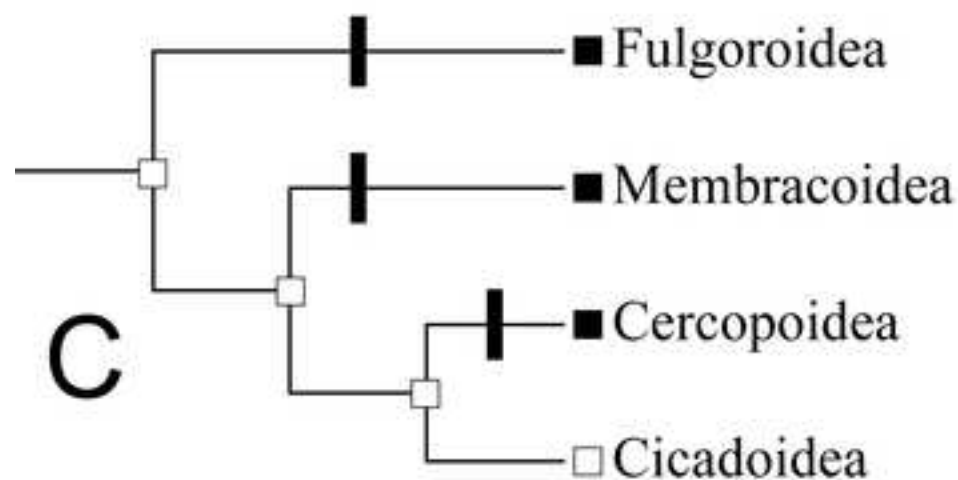
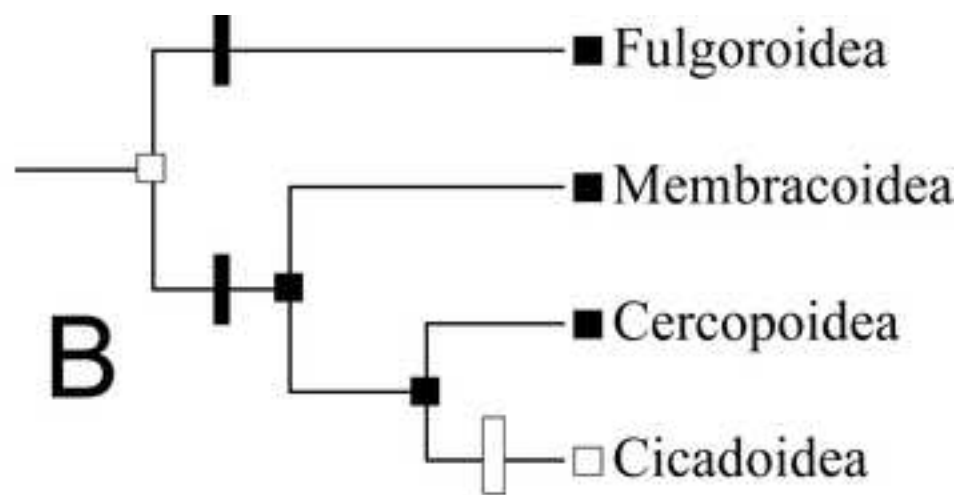
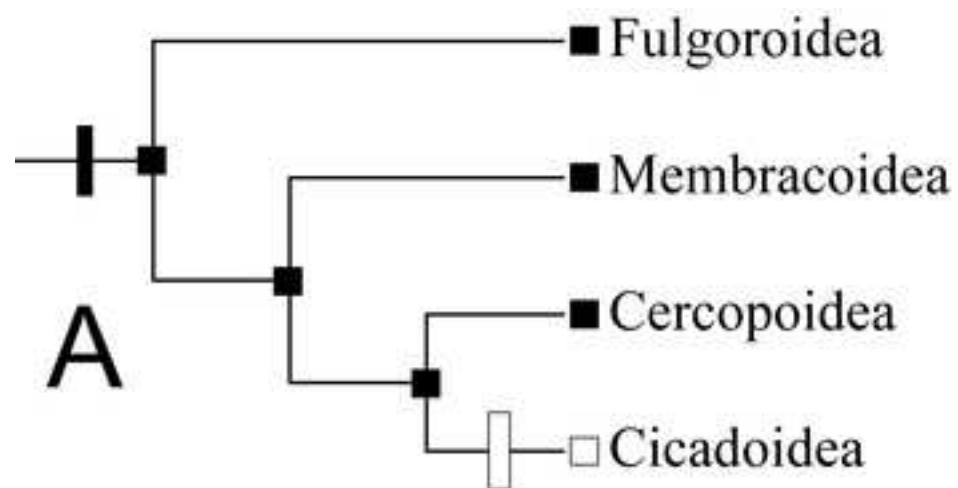
54 Character 8. DLM (IIIIdvm1): independent from IIIIdvm7 (0); surrounded by IIIIdvm7 (1).
55 Almost examined taxa have two bundles of DLM (Figs 2; 3A, B, E, F; Friedrich &
56 Beutel 2008) (State 0). In Aphrophoridae (Fig. 3C, D) and Machaerotidae
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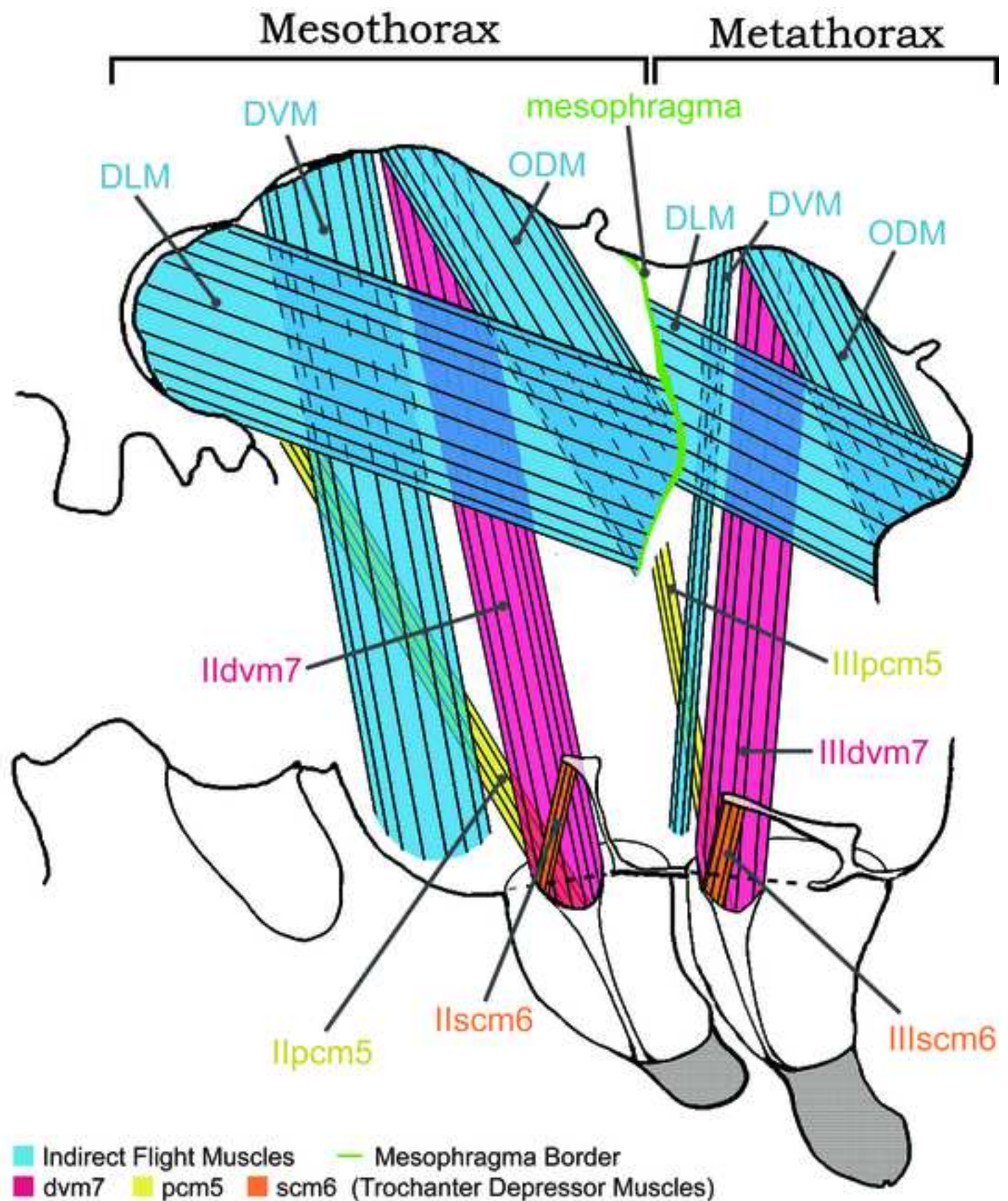
1 (Cercopoidea), small DLM was surrounded by huge IIIIdvm7 (State 1).
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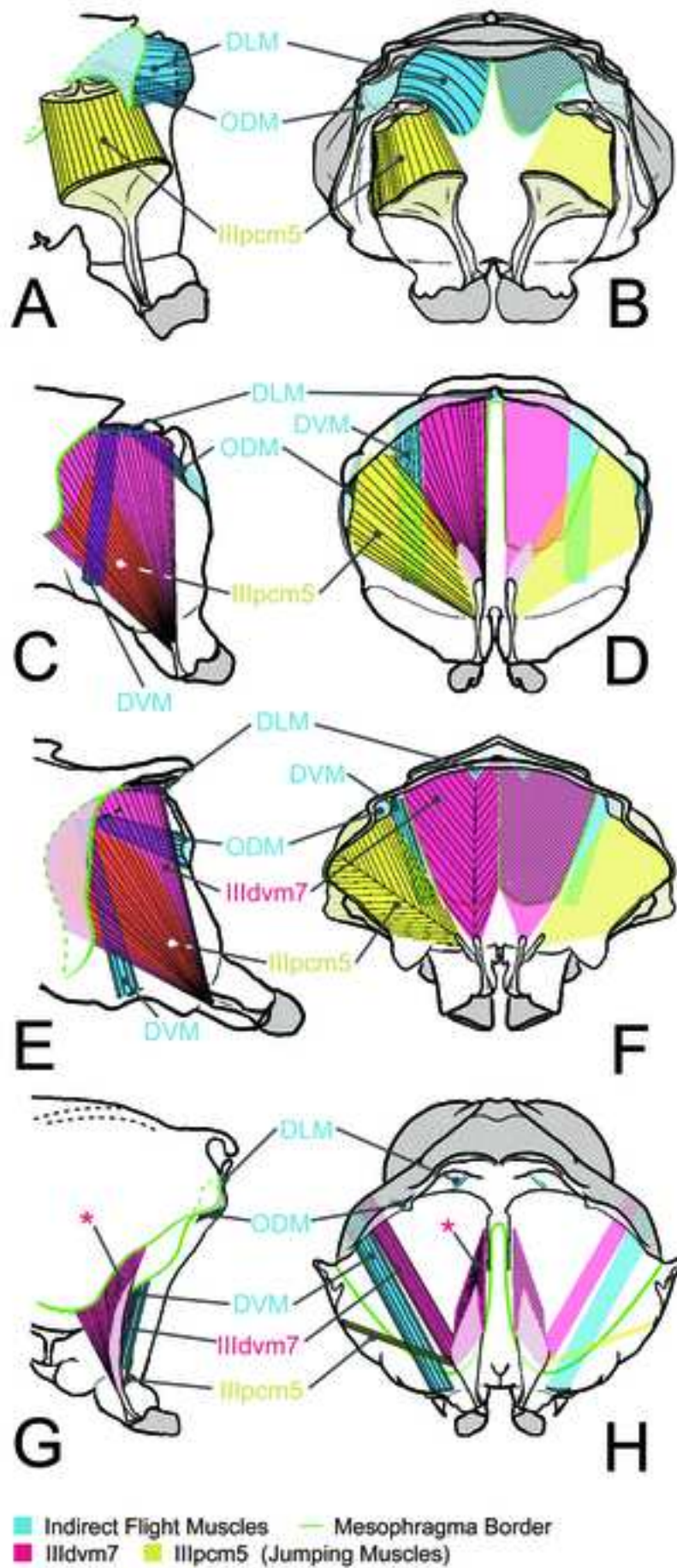
3 Character 9. ODM (IIIIdlm2/3): developed (0); reduced or absent (1). In almost all
4 Cicadomorphans, ODM was reduced (Fig. 3C, E, G) (State 1). Fulgoromorpha and
5 out-groups possessed developed ODM (State 0).
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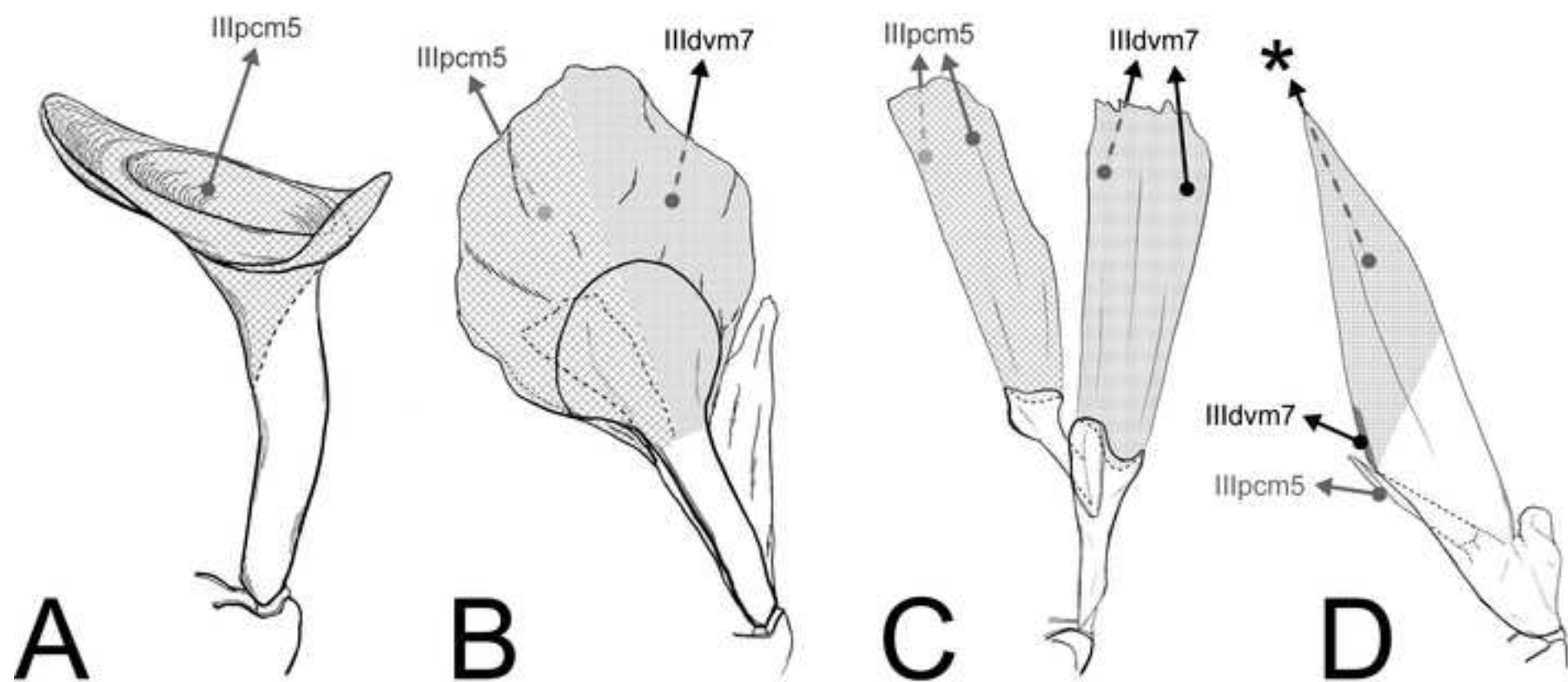
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10 Character 10. Hind trochanteral tendon: not sheet shaped (0); sheet-shaped (1).
11 Sheet-shaped tendon (state 1) was observed in Cicadomorphans, although
12 morphologies were more or less different (Fig. 4B-D). Fulgoromorpha and
13 Stenopsocidae had a non-sheet-shaped tendon.
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19 Character 11. Mesophragma: occupied by DLM (0); occupied by IIIIdvm7 (1); with
20 large empty space (2). The mesophragma of Fulgoromorpha was occupied by
21 DLM (State0: Fig. 3A, B). State 1 was observed in jumping Cicadomorpha (Fig.
22 3D, F), and State 2 was only observed in Cicadoidea (Fig. 3H).
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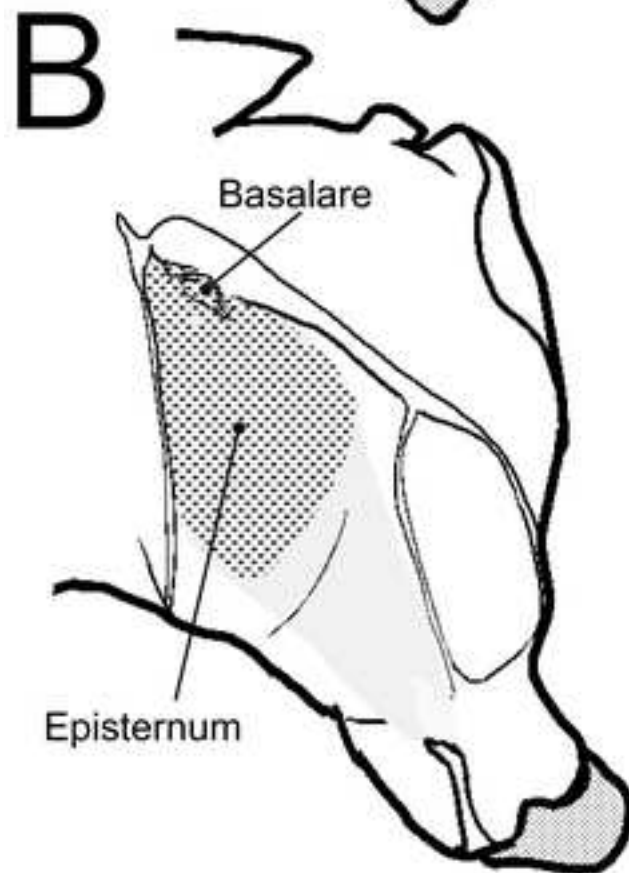


Figure 6

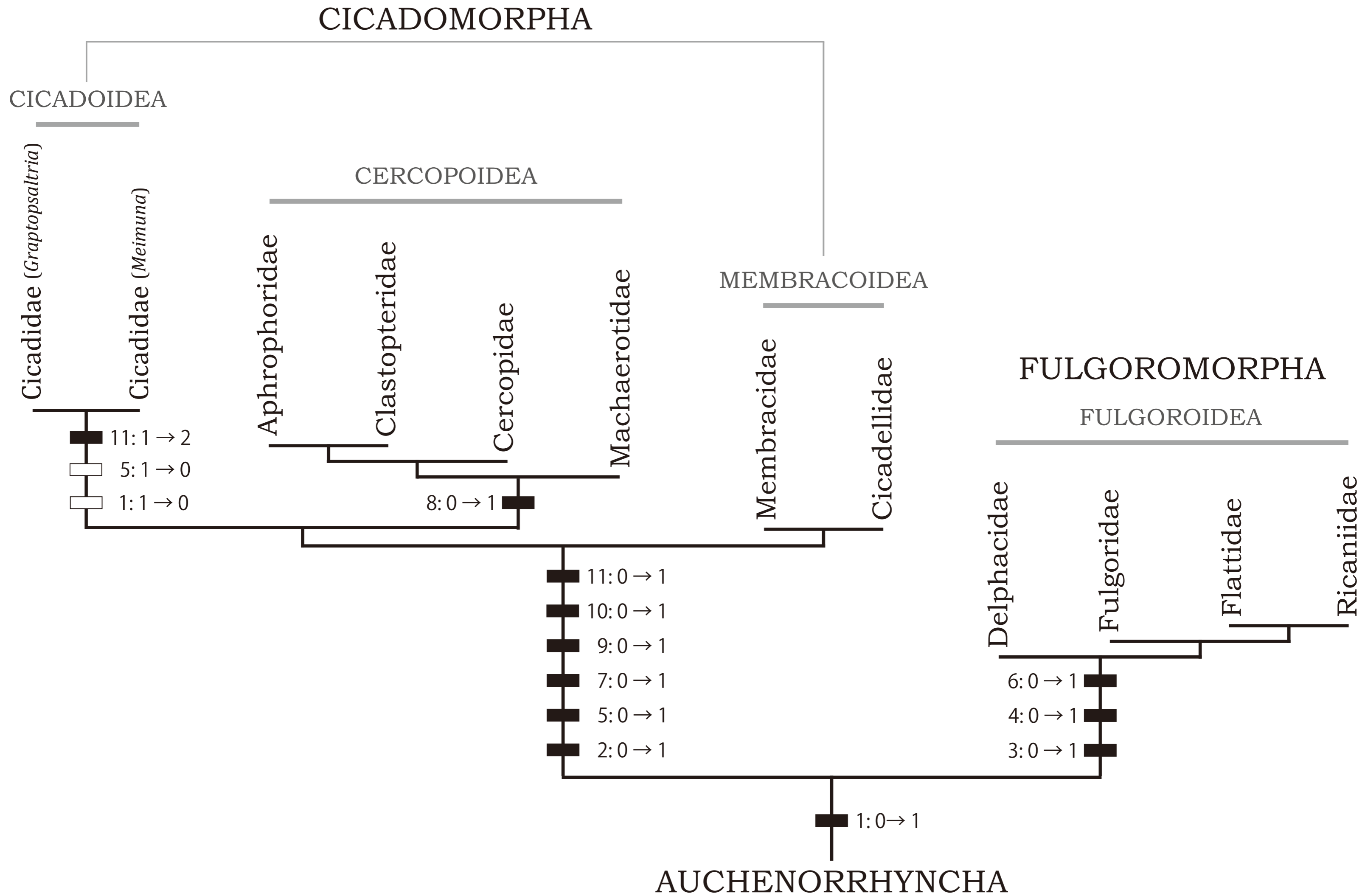


Table 1. Taxa examined for this study. The specimens examined are stored at Systematic Entomology, Hokkaido University (SEHU).

HEMIPTERA: AUCHENORRHYNCHA

CICADOMORPHA

CERCOPOIDEA

Aphrophiridae

Aphrophora pectoralis Matsumura

Clastopteridae

Clastoptera obtusa (Say)

Cercopidae

Euscartopsis assimilis (Uhler)

Cosmoscarta sp.

Machaerotidae

Machaerota takeuchii (Kato)

MEMBRACOIDEA

Membracoidae

Anthianthe sp.

Archasia sp.

Ophiderma salamandra Fairmaire

Cicadellidae

Cicadella viridis (Linnaeus)

CICADOIDEA

Tettigarctidae

Tettigarcta crinite White

Cicadidae

Graptopsaltria nigrofuscata (Motschulsky)

Meimuna iwasaki (Matsumura)

FURGOROMORPHA

Delphacidae

Tropidocephala brunneipennis Signoret

Fulgoridae

Pyrops candelania (Linnaeus)

Lycorma delicatula (White)

Flattidae

Geisha distinctissima (Walker)

Ricaniidae

Ricania japonica Melichar

ZORAPTERA

Zorotypidae

Zorotypus hubbardi Caudell (scored from Friedrich & Beutel (2008))

PSOCODEA

Stenopsocidae

Stenopsocus nigricellus Okamoto

Table 2. Correspondence between the generalized thoracic muscle nomenclature and abbreviation (from Friedrich & Beutel 2008, modified).

Category		Abbrev.	Name	Origin	Insertion
Trochanter depressor muscle		scm6	M. furca-trochanteralis	furca	trochanter
		pcm5	M. episterno-trochanteralis	basalare or episternum	
		dvm7	M. noto-trochanteralis	Notum	
Indirect flight muscle	DLM	d1m1	M. phragma-phragmalis	anterior phragma	posterior phragma
	DVM	dvm1	M. noto-sternalis	notum	sternum
	ODM	d1m2	M. noto-phragmalis	notum	phragma
		d1m3	M. scutello-phragmalis	scutal rim	scutellum

Table 3. Data matrix used for the parsimonious reconstruction. See text for characters and their states. *Zorotypus hubbardi* were scored from Friedrich and Beutel (2008).

Character No.	5					10						
ZORAPTERA (<i>Zorotypus hubbardi</i>)	0	0	0	0	0	0	0	0	0	0	?	0
PSOCOPTERA (<i>Stenopsocus nigricellus</i>)	0	0	0	0	0	0	0	0	0	0	0	0
Cicadidae (<i>Graptosaltria nigrofuscata</i>)	0	1	0	0	0	0	0	1	0	1	1	2
Cicadidae (<i>Meimuna iwasakii</i>)	0	1	0	0	0	0	0	1	0	1	1	2
Aphrophoridae (<i>Aphrophora pectoralis</i>)	1	1	0	0	1	0	1	1	1	1	1	1
Clastopteridae (<i>Clastoptera obtusa</i>)	1	1	0	0	1	0	1	?	1	1	1	1
Cercopoidae (<i>Euscartopsis assimilis</i>)	1	1	0	0	1	0	1	?	1	1	1	1
Machaerotidae (<i>Machaerota takeuchii</i>)	1	1	0	0	1	0	1	1	1	1	1	1
Membracidae (<i>Anthianthe</i> sp.)	1	1	0	0	1	0	1	0	1	0	1	1
Cicadellidae (<i>Cicadella viridis</i>)	1	1	0	0	1	0	1	0	1	1	1	1
Delphacidae (<i>Tropidocephala brunneipennis</i>)	1	0	1	1	?	1	0	0	0	0	0	0
Fulgoridae (<i>Lycorma delicatula</i>)	1	0	1	1	?	1	0	0	0	0	0	0
Flattidae (<i>Geisha distinctissima</i>)	1	0	1	1	?	1	0	0	0	0	0	0
Ricaniidae (<i>Ricania japonica</i>)	1	0	1	1	?	1	0	0	0	0	0	0

?, not applicable.