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Morphological dissection of behaviour: thoracic musculature clarifies independent development of jumping mechanisms between sister groups, planthoppers and leafhoppers (Insecta: Hemiptera: Auchenorrhyncha)

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Abstract Morphological and behavioural characters are frequently examined for comparative studies. Unlike morphology, a single behavioural trait is difficult to subdivide as multiple characters, even when achieved by many evolutionary changes. Therefore, when similar behavioural traits evolved independently among closely retaled taxa, their distinction is difficult. Almost all members of the suborder Auchenorrhyncha (Insecta: Hemiptera) possess a jumping ability that uses metathoracic muscles, and this behavioural trait has been regarded as a synapomorphy. In this study, the anatomical observations of metathoracic muscles revealed that highly elaborated jumping ability was gained independently within the suborder, although the evolution of jumping ability might have been initiated at their common ancestor. Our results provide an example of identifying a true evolutionary pathway by dissecting a behavioural character into mechanical elements.

Key words functional morphology • behavior • character evolution • evolutionary novelty

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

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

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

Materials and Methods

Taxa examined

We selected Ricaniidae and Fulgoridae (Fulgoromorpha), Cicadellidae and Membracidae (Membracoidea), Cercopidae, Machaerotidae, Clastopteridae and Aphrophoridae (Cercopoidea) and Cicadidae and Tettigarctidae (Cicadoidea) for examinations. *Stenopsocus nigricellus* (Psocodea: "Psocoptera") was selected as a close

out-group, and the tree was rooted with Zorotypidae (Zoraptera: Friedrich and Beutel 2008). Jumping behavior does not occur in the selected out-groups. The taxa examined are listed in Table 1.

Specimen preparation and observation

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

Terminologies of Muscles

Terminologies of individual muscles followed Friedrich and Beutel (2008) because of their systematic nomenclature. The thoracic segments were indicated by roman numerals prefixed to the muscle name (e.g., IIIdvm1: metathoracic dvm1). Correspondence to the traditional nomenclature, abbreviations and their origin and insertion is given in Table 2.

Target muscles for observation

We focused on metathoracic indirect flight muscles and trochanter depressor muscles. Meso- and metathoraces of neopteran insects are usually filled with large indirect flight muscles (Fig. 2). Whereas some muscles are bifunctional and provide power for flight and walking, the principal indirect flight muscles are usually monofunctional (Brodsky 1994). They attach to robust sclerites, i.e., tergum, sternum and phragma, and they generate principle flight power (Brodsky 1994). The indirect flight muscles were classified into three categories: dorsal longitudinal indirect flight muscle (DLM), dorsoventral flight muscle (DVM) and oblique dorsal flight muscle (ODM) (Brodsky 1994; Crossley 1978) (Fig. 2). DLM, DVM and

ODM correspond to dlm1 (phragma-phragmalis muscle), dvm1 (noto-sternalis muscle), and dlm2/3 (noto-phragmalis muscle/scutello-scutellaris muscle), respectively.
The trochanter depressor muscles generate principal power of auchenorrhynchan jumping, which can be subdivided into functional elements (Burrows and Bräunig 2010; Gorb 2004). Neopteran insects usually have four bundles of metathoracic trochanter depressor muscles, scm6 (from furca), pcm5 (from metanepisternum and basalare), and dvm7 (from notum) (Friedrich and Beutel 2008) (Fig. 2).

Phylogenetic hypothesis

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

Results

Metathoracic musculature of Fulgoroidea (Fulgoromorpha)

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

Metathoracic musculature of Membracoidea (Cicadomorpha)

As in the Fulgoroidea, the Membracoidea also have jumping muscles in the metathorax. However, their metathoracic musculature differs significantly from that of the fulgoromorphans, as also noted by Burrows and Bräunig (2010) and Burrows (2013) (Fig. 3C, D).

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 IIIdvm7 (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 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 IIIdvm7, 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 broadely 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 IIIdvm7 (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 IIIdvm7. 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 IIIdvm7, DLM is strongly reduced and changed its origin/insertion points to a very narrow area of the dorsal margin of the

meso-/metaphragma, respectively. The right and left bundles of DLM are separated by internal branch of IIIdvm7 (Character 8:1). DLM of Cercopidae and Clastopteridae is completely absent, although that of Aphrophoridae and Machaerotidae remains (Character 7:1). DVM is also greatly reduced but is retained in all taxa (Character 6:0). The ODM is also reduced but is relatively well retained (Fig. 3E, F) (Character 9:1).

Metathoracic musculature of Cicadoidea (Cicadomorpha)

The arrangement of the metathoracic muscles in Cicadoidea is distinctly different from the condition observed in the other groups (Snodgrass 1935; Maki 1938: Fig. 3G, H). DLM is retained but distinctly reduced and placed at the dorsolateral crack formed by the shortened and strongly arched metanotum (Character 7:1). DVM is also reduced in size but retained (Character 6:0). *Graptopsaltria* and *Huechys* (Maki 1938) retain a reduced ODM, whereas ODM is completely absent in *Meimuna* (Cicadidae) (Character 9:1). The tendon forms a less-sclerotized and expanded dorsal sheet with a small lateral fork (Fig. 3B) (Character 10:1). The muscles homologous to the jumping muscles in the other cicadomorphans (IIIdvm7 and IIIpcm5) are weakly developed and composed of three subunits. The lateral subunit originating from the ventral metanepisternum which is homologous to the IIIpcm5 of the jumping cicadomorphans (Character 1:0; 2:0), is inserted on the small fork of the trochanteral tendon (Figs 3H; 4D). The other two subunits are both inserted on the sheet-like dorsal expansion of the trochanteral tendon (Figs 3H; 4D) (Character 10:1). One originates from the anterolateral lobe of the scutum along the antecoxal suture (Figs 3H; 4D) and the other from the ventral region of the mesophragma (* in Figs 3G, H; 4D). Together, these two subunits correspond to the IIIdvm7 in the jumping cicadomorphans (Character 4:0; 5:0). IIIscm6 is also absent. In Cicadidae, a wide empty area is present on the posterodorsal surface of the mesophragma (Fig. 3H) (Character 11:2), unlike the mesophragma of the jumping cicadomorphans, which is completely occupied by IIIdvm7 (Character 11:1) (Fig. 3C-F), or unlike the ordinal pterothorax, which is completely occupied by DLM (Character 11:0) (Fig. 1). This condition was also observed in the *Tettigarcta* (Tettigarctidae). The specimen was originally dried, and the thoracic musculature was not well preserved, but the condition of the IIIdvm7 and the empty area on the mesophragma were clearly visible.

Parsimony analysis

The ancestral condition of the metathoracic structures potentially associated with the evolution of jumping behaviour was reconstructed parsimoniously using previously estimated trees (Fig. 6: characters listed in Appendix 1). The infraorder Fulgoromorpha was implied to share the following states in the common ancestor: enlarged apodeme developed from basalare (Character 3:1), loss of IIIdvm7 (Character 4:1), and loss of DVM (Character 6:1). Expansion of metanepisternum (Character 2:1), development of IIIdvm7 as a jumping muscle (Character 5:1), reduction of DLM (Character 7:1), reduction of ODM (9:1), the sheet-like trochanter tendon (10:1), and occupation of the mesophragma by IIIdvm7 (11:1) were considered to have evolved in the common ancestor of the infraorder Cicadomorpha. The IIIpcm5 develops as a jumping muscle (Character 1:1) in both Cicadomorpha and Fulgoromoprha. The empty area on the mesophragma (Character 11:2) related to the reduction of the jumping muscle IIIdvm7 (Character 5:0) was regarded as an autapomorphy of the Cicadoidea. Jumping function of IIIpcm5 was secondarily reduced in Cicadoidea (Character 1:0).

Discussion

All jumping species of Auchenorrhyncha possess large metathoracic jumping muscles transformed from the trochanter depressors. However, the condition of the jumping muscles is very distinctly different between the two infraorders. Fulgoromorpha have very large jumping muscles developed from only IIIpcm5, which is inserted to the funnel shaped trochanteral tendon and is originated from the expanded basalare (Figs 3A, B; 4A) (Character 1:1; 2:0; 3:1; 10:0). In contrast, two superfamilies of Cicadomorpha (Membracoidea and Cicadoidea) possess very large jumping muscles composed of modified and enlarged IIIdvm7 and IIIpcm5 inserted on an enlarged trochanteral tendon (Figs 3C-F; 4B, C) (Character 1:1; 5:1; 10:1). In Cicadoidea, the trochanter depressor muscles originate from the pleura, notum and phragma and are inserted on the trochanteral tendon (Figs 3G, H; 4D).

The most parsimonious reconstruction of the metathoracic muscular characters suggests that almost all apomorphic conditions associated with the jumping ability evolved independently in Cicadomorpha and Fulgoromorpha (Fig. 6). The development of IIIpcm5 as a jumping muscle is shared by Cicadomorpha and Fulgoromorpha (Character 1:1), but its origin (Character 2; Fig. 5) and insertion points (Character 3: Fig. 4) considerably. Therefore,

although the development of jumping ability may have originated in their common ancestor (Hennig 1981; Kristensen 1975), it is evident that the highly elaborate jumping ability and mechanism as observed in extant groups of Auchenorrhyncha has been achieved independently between two infraorders, as suggested by Burrows and Bräunig (2010) and Burrows (2013) (Fig. 1B, C).

From the present morphological analyses, the evolution of the auchenorrhynchan jumping ability can be explained as follows. In Fulgoromorpha, the muscle originating from the metanepisternum and basalare (IIIpcm5) were transformed into jumping muscles (Character 1:1). The enlarged attachment point was formed by the strong expanded basalare (Character 3:1). The tendon was also modified as an enlarged funnel-shaped structure for expanding the attachment point, which was also strengthened to support the huge contracting power of the jumping muscle. Absence of IIIdvm7 (Character 4:1) and IIIscm6 might be the result of constraint in attachment area in the notum (with the flight muscles) and tendon (with enlarged IIIpcm5), respectively. Because the jumping muscles occupied only the lower half of the metathorax, adequate room for storing the flight muscles could be retained in the upper part. In the jumping Cicadomorpha (Membracoidea and Cercopoidea), IIIpcm5 and IIIdvm7 transformed to the jumping muscles (Character 1:1; 5:1). Attachment points of the jumping muscles were expanded: IIIdvm7 was attached into mesophragma (Character 11:1), in addition to the notum. Reductions of flight muscles and the absence of IIIscm6 (both muscles attached to the notum and phragma) were most likely the result of competition for attachment space for jumping muscles. Whereas the shape of the tendon (a single sheet in Membracoidea vs. birurcated in Cercopoidea), muscle attachiment manner on tendon (ventral side vs. both sides), and location of DLM (Character 8) differ betweenthe two superfamilies, their jumping muscles and related morphologies were considered to be gained in the common ancestor because of the fundamental similarities.

Additionally, under the assumption of independent evolution of the jumping ability in Fulgoromorpha and Cicadomorpha, two equally parsimonious scenarios are also possible, i.e., a secondarily reducted jumping ability in Cicadoidea (Fig. 1B) or independent origins of jumping ability in Cicadomorpha (Fig. 1C). Of the two scenarios, the arrangements of the jumping musculatures of cicadomorphans indicates that the secondary reduction hypothesis is more likely. Expansion of the original position of the IIIdvm7 from the notum to notum+mesophragma (Character 11:1) and the reduction of the DLM (Character 7:1) are

estimated to have evolved in the common ancestor of Cicadomorpha. Reduction of the DLM is strongly associated with the development of the IIIdvm7 because, in ordinal flying insects, DLM occupies almost the entire surface of the posterior mesophragma (Character 11:0). Although a wide empty space is on the mesophragma of the Cicadoidea (Character 11:2), the cicadoidean DLM occupies only a very narrow dorsal margin of the phragma (Fig. 3H), as also observed in the Membracoidea and Cercopoidea (Fig. 3D, F). This strongly suggests that the expansion of the jumping muscle to the anterior phragma occurred in the common ancestor of Cicadomorpha, and that the poorly developed jumping muscle in the Cicadoidea represents a secondary reduction. Additionally, the presence of phragma-trochanteralis muscle in Cicadoidea (* in Fig. 3G, H) also supports the secondary reduction interpretation. The muscle is never present in insects other than jumping Auchenorrhyncha. Therefore, this muscle in Cicadoidea can be interpreted as a vestige of the jumping muscle after secondary reduction of expanded IIIdvm7 and its absence from the notum.

In summary, the muscle morphology suggests that some fundamental aspects of jumping ability originated in the common ancestor of Auchenorrhyncha, several details of the jumping mechanisms of Cicadomorpha and Fulgoromorpha evolved independently. The lack of the jumping ability in the Cicadoidea represents a secondarily reduced condition. This more complicated evolutionary scenario could not be extracted from a simple maximum parsimony reconstruction of the behavioural character (Fig. 1A), and observation of the muscles associated with the jumping ability was required to reach this conclusion. Our results provide an example that the morphological dissection of a behavioural trait is valid for implicating a more likely evolutionary pathway. Shcherbakov and Popov (1997) claimed that the jumping ability is a synapomorphic trait in the order. However, the implication was proposed based on a fossilized exoskeleton without considering internal morphology. To understand the origins and evolution of the jumping ability in all of groups of Hemiptera, detailed morphological and functional investigations are obligatory.

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Figure captions

Fig. 1. Phylogeny of Auchenorrhyncha and four possible evolutionary scenarios for the evolution of jumping ability. The tree was summarized from Cryan & Urban (2012). The black and white rectangles/squares indicate presence and absence of jumping ability, respectively. A, The most parsimonious interpretation implied from jumping behaviour (2 steps). B. The independent origins hypothesis as suggested by Burrows & Bräunig (2010) and Burrows (2013) (3 steps). C–D, Two additional possibilities with evolutionary steps = 3.

Fig. 2. Flight and jumping musculatures of the bark louse genus *Stenopsocus* (Psocodea: "Psocoptera": Stenopsocidae), lateral view. Redrawn and modified from Badonnel (1934) and Maki (1938). Indirect flight muscles were colored blue: DLM, dorsal longitudinal indirect flight muscle (dlm1); DVM, dorsoventral flight muscle (dvm1); ODM, oblique dorsal flight muscle (dlm2/3). Trochanter depressor muscles were colored by respective muscles. Terminology followed Crossley (1978), Brodsky (1994) and Beutel et al. (2014). The border of mesophragma is highlighted by green line.

Fig. 3. Flight and jumping muscles of Auchenorrhyncha, lateral (left) and posterior (right) views. A, *Ricania japonica* (Fulgoromorpha: Fulgoroidea: Ricaniidae); B, *Cicadella viridis* (Cicadomorpha: Membracoidea: Cicadellidae); C, *Aphrophora pectoralis* (Cercopoidea: Aphrophoridae); D, *Graptopsaltria nigrofuscata* (Cicadidae: Cicadoidea). See Fig. 2 for terminology, colours and abbreviations. The right side of posterior images shows muscles (colored shadows) and muscle attachment regions (black dots). The border of mesophragma is highlighted by green line.

Fig. 4. Enlarged view of left metatrocanteral tendons and attachments point of muscles. A, *Ricania japonica* (Fulgoromorpha: Fulgoroidea: Ricaniidae); B, *Cicadella viridis* (Cicadomorpha: Membracoidea: Cicadellidae); C, *Aphrophora pectoralis*

(Cercopoidea: Aphrophoridae); D, *Graptopsaltria nigrofuscata* (Cicadoidea: Cicadidae). See Fig. 2 for terminology and abbreviations. The painted regions indicate the muscle attachment areas. Deep and light gray indicate the attached area of IIIdvm7 and IIIpcm5, respectively. Arrows with a spot represent muscle bundles. Dashed lines indicate concealed muscles or sclerite borders.

Fig. 5. Metathoracic endoskeletons and attachment regions of IIIpcm5, lateral view. See Fig. 2 for terminology and abbreviations. A, *Ricania japonica* (Fulgoromorpha: Fulgoroidea: Ricaniidae); B, *Cicadella viridis* (Cicadomorpha: Membracoidea: Cicadellidae). IIIpcm5 is indicated by gray shadow. Dotted areas indicate muscle attachment regions.

Fig. 6. Most parsimonious reconstruction of character states scored in this study (Appendix 1) onto the phylogeny of Auchenorrhyncha estimated by Misof et al. (2014), Cryan and Urban (2012) and Urban and Cryan (2007). Outgroups are omitted. Character and character state changes reconstructed on the branches are indicated by black (gain) and white bars (reversal). For some characters (e.g., Character 5), an alternative interpretation for character evolution may be possible but, based on the present morphological observation (see text), the interpretation given in the figure is considered to be likely. The result indicated common origin of the jumping ability in Auchenorrhyncha (1:0 –> 1 at the root), but independent evolutionof jumping mechanisms between Cicadomorpha and Fulgoromorpha.

Appendix 1. Characters and their states reconstructed in this study.

Character 1. IIIpcm5: not developed as jumping muscle (0) developed as major jumping muscle (1). State 0 was observed in out-groups and Cicadoidea. State 1 was observed in all jumping Auchenorrhyncha (Fig. 3A-F).

Character 2: Origin of IIIpcm5: restricted to dorsal episternam and basalare (0); expanded to ventral metanepisternum (1). State 0 was observed in out-groups and Fulgoromorpha. State 1 was observed throughout Cicadomorpha including Cicadoidea.

Character 3: Apodeme of basalare: not enlarged (0); enlarged (1). State 1 was only observed in Fulgoromorpha.

Character 4. IIIdvm7: present (0); absent (1). State 1 was only observed in Fulgoromorpha. (Fig. 3A, B).

Character 5. Jumping function in IIIdvm7: not developed as jumping muscle (0); developed as jumping muscle (1). State 1 was only observed in jumping Cicadomorphans. State of Fulgoromorpha was treated as unknown.

Character 6. DVM (IIIdvm1): present (0); absent (1). State 1 was only observed in Fulgoromorpha (Fig. 3A, B). DVM of the other examined taxa was present (State 0).

Character 7. DLM (IIIdlm1): developed (0); reduced or absent (1). State 1 was observed in all cicadomorphans (Fig. 3C-H). Fulgoromorpha and out-groups possessed developed DLM (State 0)

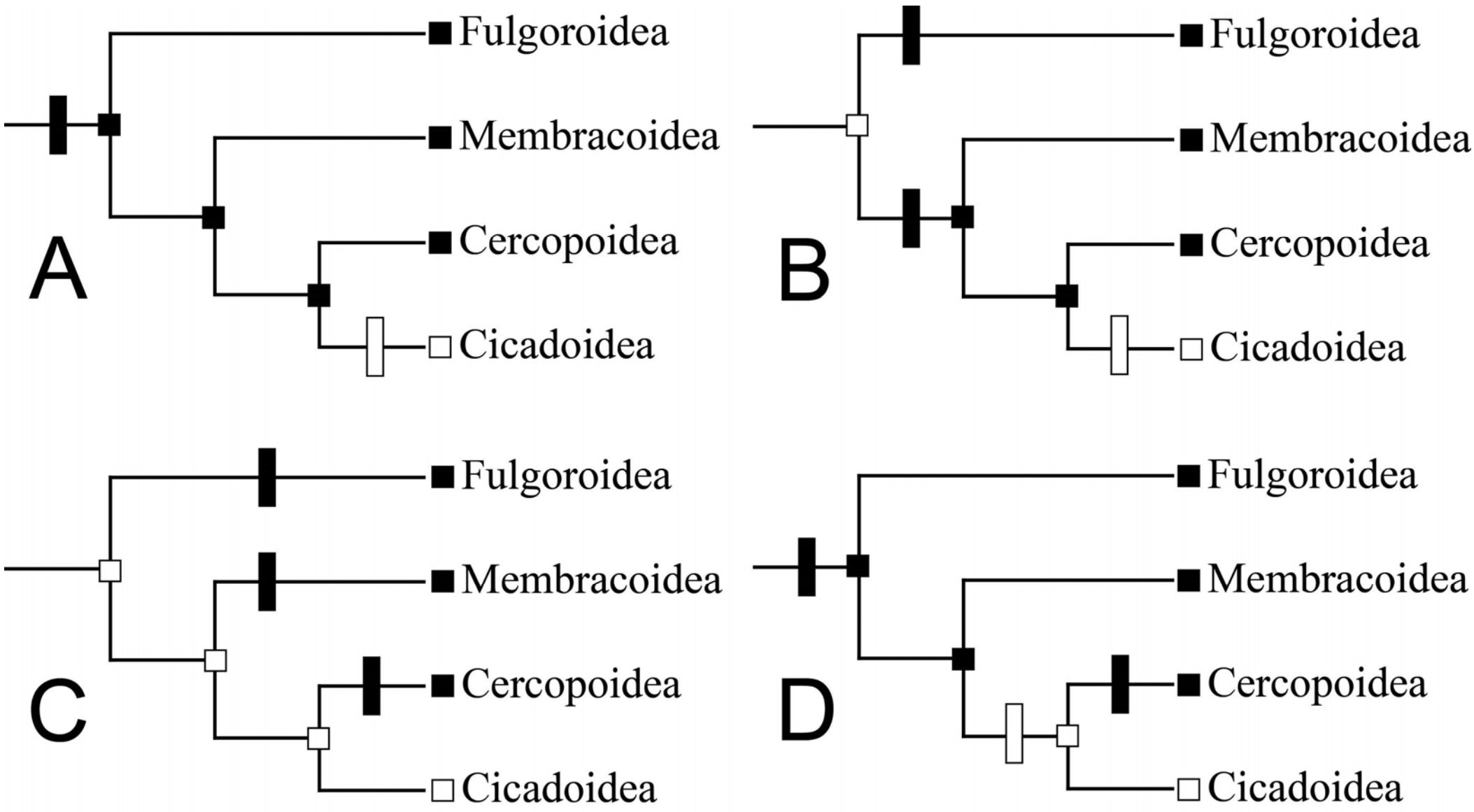
Character 8. DLM (IIIdvm1): independent from IIIdvm7 (0); surrounded by IIIdvm7 (1). Almost examined taxa have two bundles of DLM (Figs 2; 3A, B, E, F; Friedrich & Beutel 2008) (State 0). In Aphrophoridae (Fig. 3C, D) and Machaerotidae

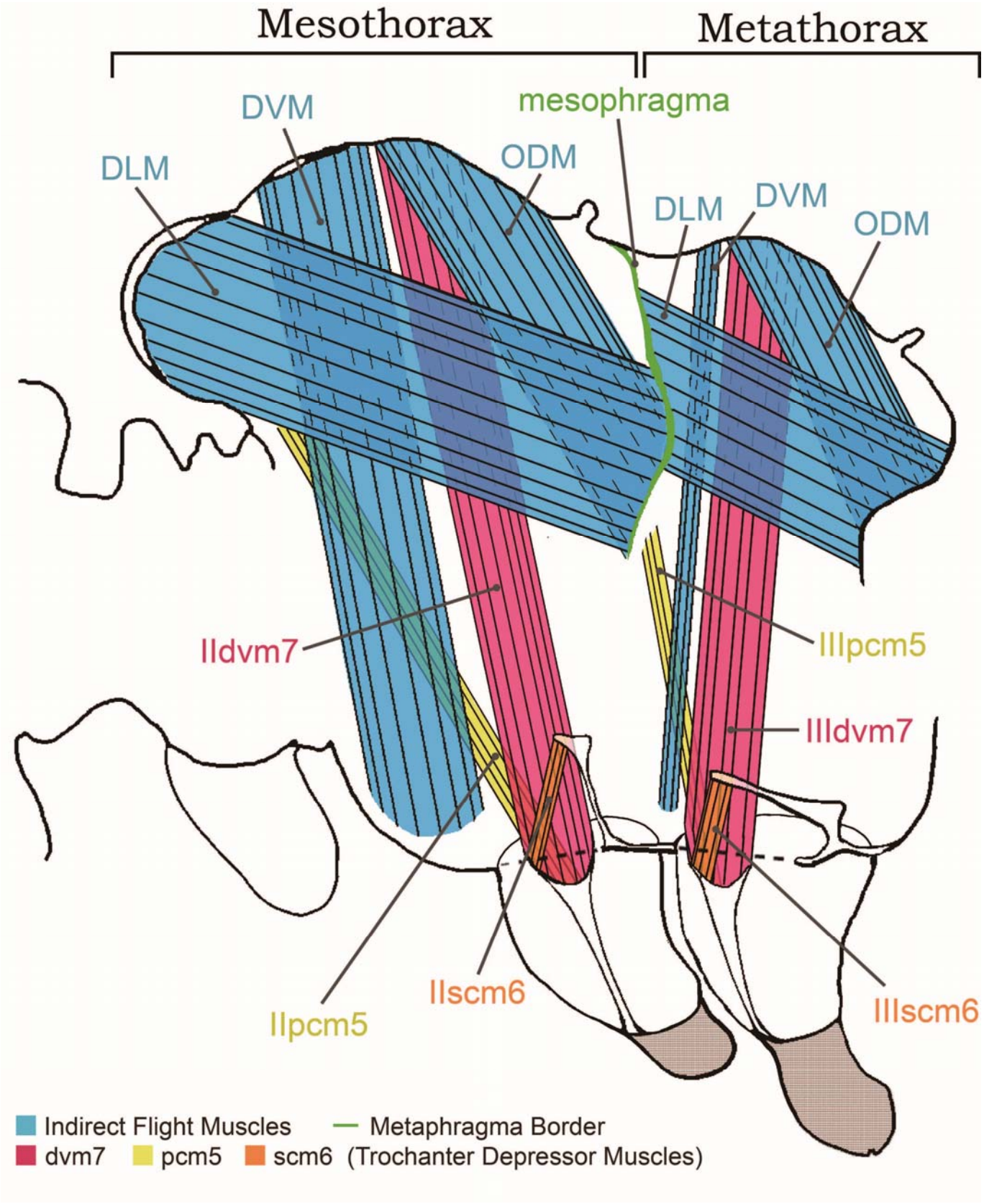
(Cercopoidea), small DLM was surrounded by huge IIIdvm7 (State 1).

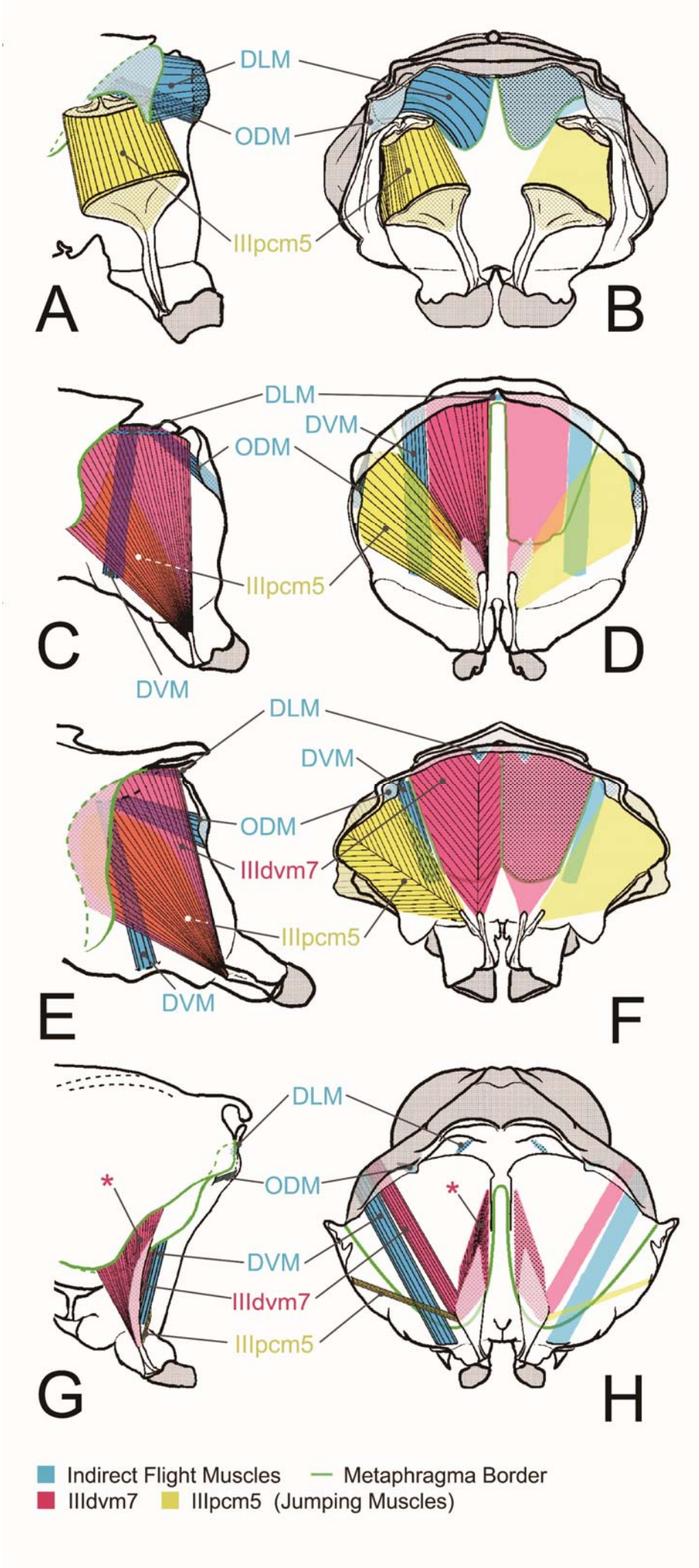
Character 9. ODM (IIIdlm2/3): developed (0); reduced or absent (1). In almost all Cicadomorphans, ODM was reduced (Fig. 3C, E, G) (State 1). Fulgoromorpha and out-groups possessed developed ODM (State 0).

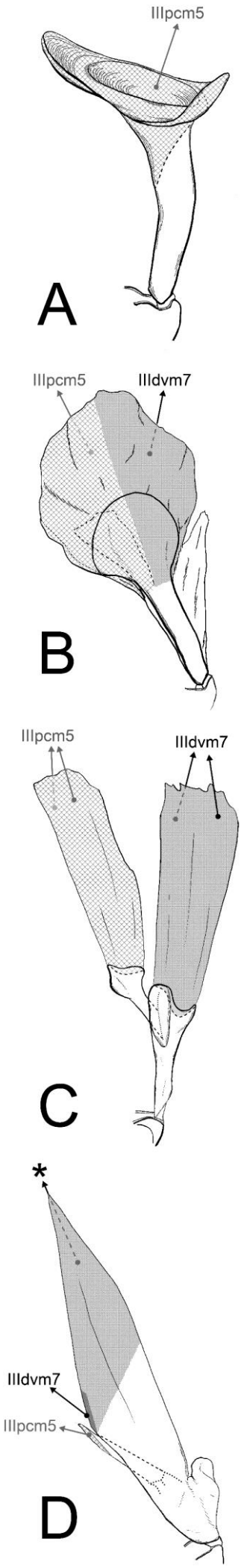
Character 10. Hind trochanteral tendon: not sheet shaped (0); sheet-shaped (1). Sheet-shaped tendon (state 1) was observed in Cicadomorphans, although morphologies were more or less different (Fig. 4B-D). Fulgoromorpha and Stenopsocidae had a non-sheet-shaped tendon.

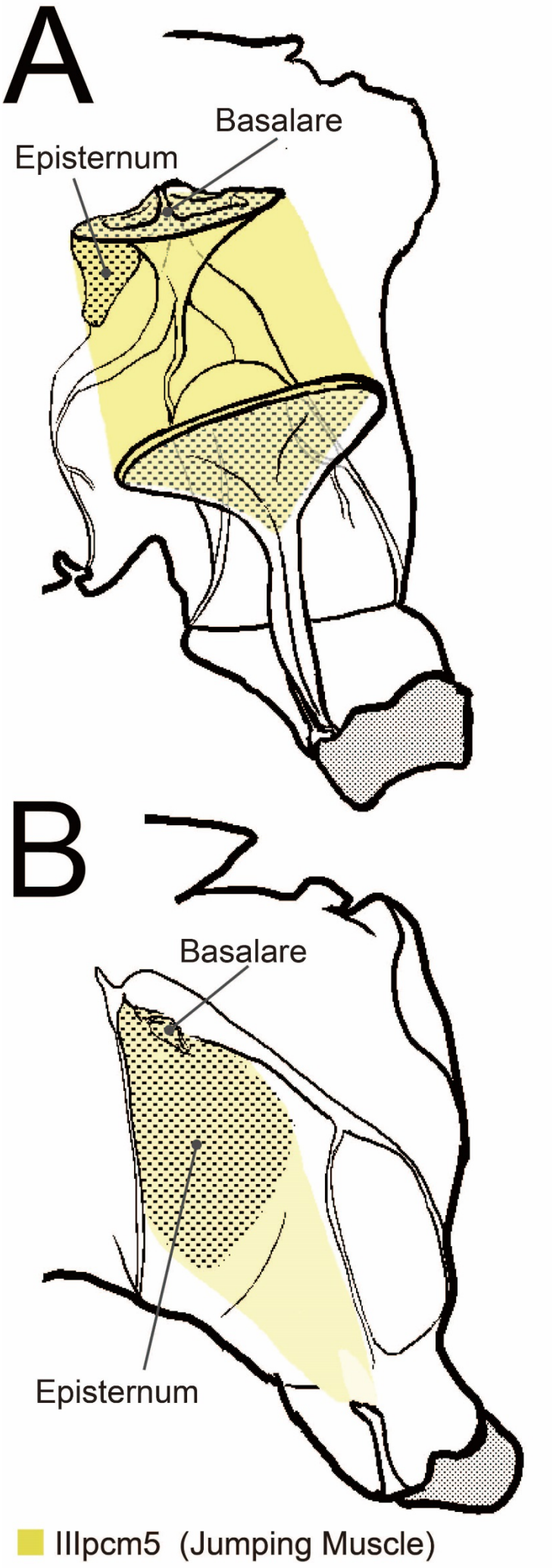
Character 11. Mesophragma: occupied by DLM (0); occupied by IIIdvm7 (1); with large empty space (2). The mesophragma of Fulgoromorpha was occupied by DLM (State0: Fig. 3A, B). State 1 was observed in jumping Cicadomorpha (Fig. 3D, F), and State 2 was only observed in Cicadoidea (Fig. 3H).


A
Fulgoroidea
Membracoidea
Cercopoidea
Cicadoidea
B
Fulgoroidea
Membracoidea
Cercopoidea
Cicadoidea
C
Fulgoroidea
Membracoidea
Cercopoidea
Cicadoidea
D
Fulgoroidea
Membracoidea
Cercopoidea
Cicadoidea


Mesothorax
Metathorax
mesophragma
DVM
DLM
ODM
DLM
DVM
ODM
IIdvm7
IIIpcm5
IIIdvm7
IIpcm5
IIscm6
IIIscm6
Indirect Flight Muscles
Metaphragma Border
dvm7
pcm5
scm6 (Trochanter Depressor Muscles)


DLM
ODM
IIIpcm5
A
B
DLM
DVM
ODM
IIIpcm5
C
D
DVM
DLM
DVM
ODM
IIIdvm7
IIIpcm5
E
F
DVM
DLM
ODM
*
*
DVM
IIIdvm7
IIIpcm5
G
H
Indirect Flight Muscles
Metaphragma Border
IIIdvm7
IIIpcm5 (Jumping Muscles)


IIIpcm5
A
IIIpcm5
IIIdvm7
B
IIIpcm5
IIIdvm7
C
*
IIIdvm7
IIIpcm5
D


A
Basalare
Episternum
B
Basalare
Episternum
IIIpcm5 (Jumping Muscle)

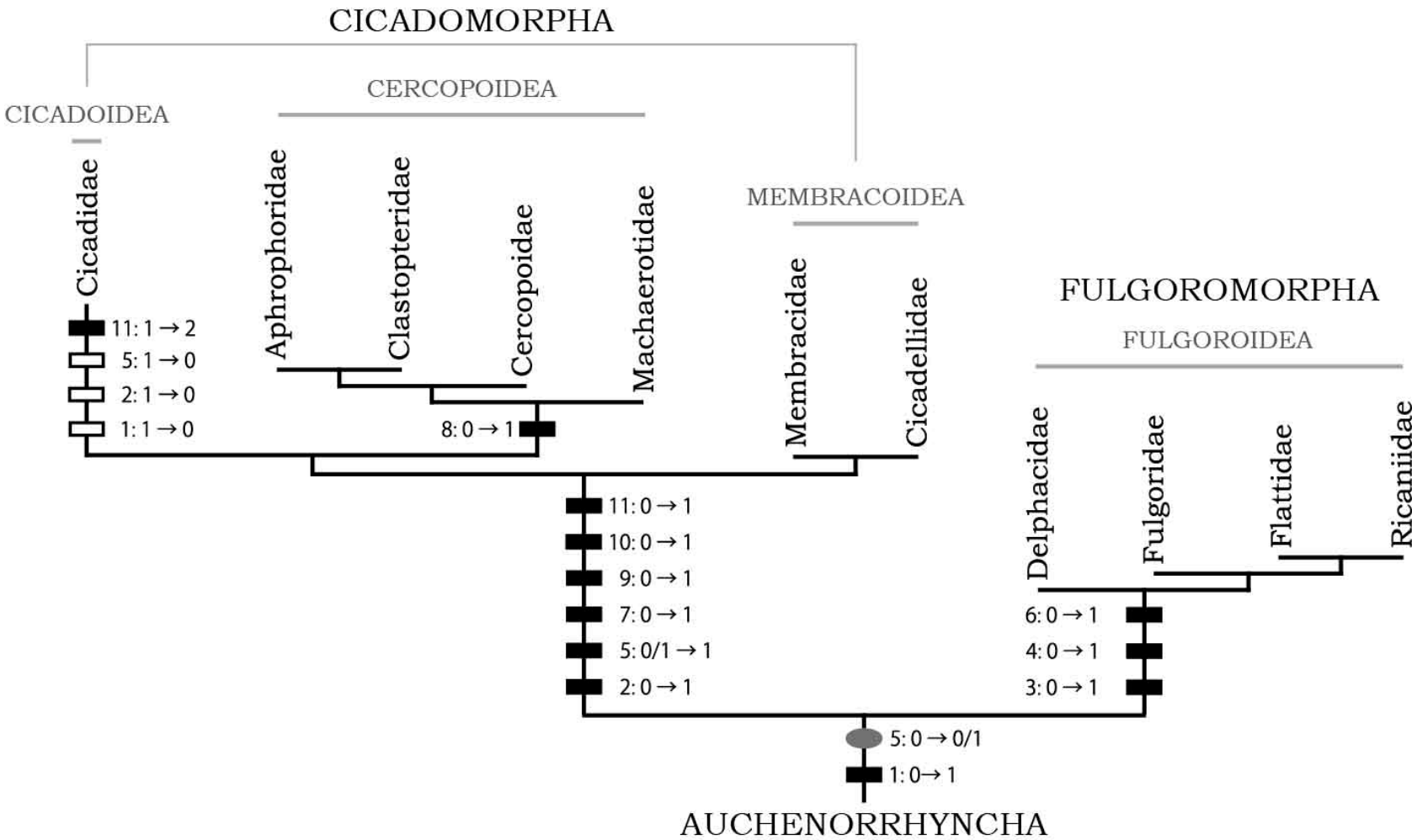

CICADOMORPHA
CICADOIDEA
CERCOPOIDEA
MEMBRACOIDEA
Cicadidae
Aphrophoridae
Clastopteridae
Cercopoidae
Machaerotidae
Membracidae
Cicadellidae
FULGOROMORPHA
FULGOROIDEA
Delphacidae
Fulgoridae
Flattidae
Ricaniidae
11: 1 → 2
5: 1 → 0
2: 1 → 0
1: 1 → 0
8: 0 → 1
11: 0 → 1
10: 0 → 1
9: 0 → 1
7: 0 → 1
5: 0/1 → 1
2: 0 → 1
6: 0 → 1
4: 0 → 1
3: 0 → 1
5: 0 → 0/1
1: 0→ 1
AUCHENORRHYNCHA

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
    - Tettigardtidae
      - *Tettigarcta crinite* White
    - Cicadidae
      - *Graptopsaltria nigrofuscata* (Motschulsky)
      - *Meimuna iwasakii* (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	dlm1	M. phragma-phragmalis	anterior phragma	posterior phragma
	DVM	dvm1	M. noto-sternalis	notum	sternum
	ODM	dlm2	M. noto-phragmalis	notum	phragma
		dlm3	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 (*Zorotypus hubbardi*)	0	0	0	0	0	0	0	0	0	?	0
PSOCOPTERA (*Stenopsocus nigricellus*)	0	0	0	0	0	0	0	0	0	0	0
Cicadidae (*Graptopsaltria nigrofuscata*)	0	1	0	0	0	0	1	0	1	1	2
Cicadidae (*Meimuna iwasakii*)	0	1	0	0	0	0	1	0	1	1	2
Aphrophoridae (*Aphrophora pectoralis*)	1	1	0	0	1	0	1	1	1	1	1
Clastopteridae (*Clastoptera obtusa*)	1	1	0	0	1	0	1	?	1	1	1
Cercopoidae (*Euscartopsis assimilis*)	1	1	0	0	1	0	1	?	1	1	1
Machaerotidae (*Machaerota takeuchii*)	1	1	0	0	1	0	1	1	1	1	1
Membracidae (*Anthianthe* sp.)	1	1	0	0	1	0	1	0	1	0	1
Cicadellidae (*Cicadella viridis*)	1	1	0	0	1	0	1	0	1	1	1
Delphacidae (*Tropidocephala brunneipennis*)	1	0	1	1	?	1	0	0	0	0	0
Fulgoridae (*Lycorma delicatula*)	1	0	1	1	?	1	0	0	0	0	0
Flattidae (*Geisha distinctissima*)	1	0	1	1	?	1	0	0	0	0	0
Ricaniidae (*Ricania japonica*)	1	0	1	1	?	1	0	0	0	0	0

?, not applicable.