

Comparative Morphology of the Orthopteran Thorax With a Discussion of Phylogenetically Relevant Characters

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Abstract

Orthoptera, or Saltatoria, represents the most diverse insect group among the lower neopterans or Polyneoptera. The present study provides a detailed comparative investigation of the skeletal and muscular thoracic morphology of 23 orthopteran species. For the first time, we investigate unstudied ensiferan key taxa including Gryllacrididae (raspy crickets), Stenopelmatidae (Jerusalem crickets), and Prophalangopsidae (hump-winged crickets). We identify novel thoracic characters that might represent apomorphies of Orthoptera: the connection of propleura and prosternum as pleurosternal bridge, the pterothoracic furcae that enclose the respective pleural arm from the ventral side, the mesofurca and mesospina that are situated in a single line along the sternacosta, and a stalked mesospina with a delimited dorsal plate. In particular, the morphology of the sternal apophyses turned out to show major differences between the two major subgroups of Orthoptera: Caelifera (short-horned grasshoppers) and Ensifera (long-horned grasshoppers). For example, the profurca bears a single arm in Caelifera and is branched in the majority of Ensifera. A number of thoracic muscles, like the *Musculus mesofurca-propleuralis* (Ilspm9), could be identified and defined for Orthoptera, muscles that have never been described before to be present in other neopteran insects. Additionally, the obtained data set is used to reconstruct the orthopteran ground pattern of the thoracic skeletomuscular complex. Moreover, all characters potentially containing phylogenetic information are discussed and compiled in a morphological character matrix in order to be accessible for future phylogenetic studies.

Key words: Caelifera, Ensifera, skeleton, musculature, μ CT.

With more than 27,500 described extant species, Orthoptera (or Saltatoria) forms the most species-rich lineage among the lower neopteran insects (Grimaldi and Engel 2005, Cigliano et al. 2017). Apart from the polar regions, orthopterans inhabit all continents with an overwhelming abundance in diversity and the range of occupied terrestrial habitats (Beier 1972, Kevan 1982). Although sometimes doubted (Sharov 1968, Xiao et al. 2012), the monophyly of Orthoptera is well supported by various morphological characters, such as the large saddle-shaped pronotum, an internal cryptopleura, and the saltatorial hind legs that exhibit a straightened femur-tibia articulation in combination with a conceivable reduction of the trochanter (Kristensen 1991, Grimaldi and Engel 2005, Kluge 2016). Orthoptera is subdivided into two major lineages: Caelifera (short-horned grasshoppers: locusts, grasshoppers, and allies) and Ensifera (long-horned grasshoppers: crickets, katydids, wetas, and allies). In contrast to this basal dichotomy, the phylogenetic relationships

among orthopterans, especially those of Ensifera, appear to be largely unresolved (Legendre et al. 2010).

With large-scale cladistic studies available based on morphology (Gwynne 1995, Desutter-Grandcolas 2003), mitochondrial genomes (Zhou et al. 2017), various single genes and ribosomal DNA (Song et al. 2015, Vandergast et al. 2017), the proposed phylogenetic relationships of Ensifera have been tested more recently based on a much wider spectrum of character systems. Nevertheless, almost every possible scheme of internal relationships of Ensifera was proposed in often drastically different phylogenetic hypotheses. Thereof, generating more data of phylogenetic significance is necessary to re-evaluate all those existing contradicting hypotheses.

The outstanding work of Ander (1939) was the first to combine different morphological character systems for a vast number of ensiferan taxa. In light of recent phylogenetic studies, Ander's work is surprisingly up-to-date and was truly ahead of its time as his

phylogenetic conclusions were exclusively based on shared derived (= synapomorphic) characters, which is remarkable since his work was published roughly 10 yr before Hennig (1950) formulated his fundamentals in phylogenetic systematics.

Kjell Ander already found that skeletal and muscular features of the ensiferan thorax are highly informative for understanding phylogenetic relationships of this diverse taxon. Besides characters such as the prothoracic cryptopleura, the form of the first thoracic spiracle, certain muscle characters of the prothorax as well as the external shape and structure of the sternites, Ander considered the internal sternal skeleton to ‘offer excellent anatomical characters’ (*‘Das sternale innere Skelett bietet ebenfalls vortreffliche Merkmale.’* Ander 1939). Nonetheless, aside from little fragmentary information on the specific structure of the internal apophyses of the sternites (furcae) of crickets and Jerusalem crickets, Ander abstained from a detailed and comprehensive description in other ensiferan taxa. Until today, the thoracic morphology of ensiferans is hitherto insufficiently studied in a comparative approach, with publications that either give only a scarce description of the thoracic skeleton (Carpentier 1921a, Richards 1955) or merely include only a small part of the thoracic musculature (Carpentier 1923, O’Brien and Field 2001). Until now, comprehensive descriptions of skeletal structures in addition to a complete portrayal of the muscular equipment are published for only a few ensiferan species: the house cricket *Acheta domesticus* (L.) (Gryllidae) (Voss 1905a,b,c,d, 1912), the cave cricket *Troglophilus neglectus* Krauss (Rhaphidophoridae) (Leubner et al. 2016), and the dune cricket *Comicus calcaris* Irish (Schizodactylidae) (Leubner et al. 2017).

With the emergence of innovative and noninvasive techniques, like confocal laser scanning microscopy and micro-computed tomography (μ CT), the investigation and documentation of morphological structures of animals became more simplified and astonishingly detailed (Metscher 2009, Friedrich et al. 2013). Being established in insect morphology about 15 yr ago (Hörnschemeyer et al. 2002), μ CT is now one of the most commonly used techniques in studying the anatomy of small and medium sized insects (Friedrich et al. 2013). In contrast to a series of histological sections, whose quality and alignment depends on the mechanical skills of the researcher, μ CT scans provide perfectly aligned image stacks that represent the ideal source for precise three-dimensional reconstructions of skeletal elements and the musculature (Friedrich et al. 2013).

Many anatomical studies dealt with a precise description of the thoracic musculature in Caelifera (e.g., Snodgrass 1929, de Zolessi 1968) and other polyneopteran insects (e.g. Maki 1938, Rähle 1970, Bharadwaj and Chadwick 1974a), but only a few authors applied the nomenclature of preceding studies to their own results. As a consequence, a disastrous chaos was generated in terming and homologizing thoracic muscles of insects. To rectify this situation, Friedrich and Beutel (2008) established a new and consistent nomenclature for the muscles that can be present in neopteran insects. Hence, this study represented a main requirement for further more detailed investigations on the musculature of insect thoraces allowing for facilitated descriptions, a transparent presentation of new results and comparisons to descriptions of other authors. Based on the achievements of Friedrich and Beutel (2008), characters of the thoracic musculature of neopteran insects could subsequently be considered in an extensive phylogenetic analysis of morphological characters of the thorax (Wipfler et al. 2015). Regarding the Orthoptera, Wipfler et al. (2015) only included data on the thoracic morphology of a single caeliferan representative, a grasshopper (Snodgrass 1929), and a single ensiferan representative, the house cricket (Voss 1905a,b). As outlined above, this taxon sampling is not an ideal choice from a phylogenetic

point of view and still far from reflecting the phylogenetic and morphological diversity of Orthoptera.

Hence, the main objective of the present study lies in the examination and documentation of this yet neglected morphological character system in a wide spectrum of orthopteran representatives including yet unstudied caeliferan and ensiferan key taxa. This comprehensive comparative morphological approach is used to reconstruct a ground pattern regarding the thoracic skeletomuscular system of Orthoptera. Characters of the skeletal and muscular system of the thorax that were used in a previous cladistic analysis of major neopteran lineages (Wipfler et al. 2015) are discussed, re-evaluated, and complemented by novel orthopteran-specific characters. In addition, all of these characters potentially useful for a cladistic analysis are compiled in a data matrix in order to be considered and combined in subsequent phylogenetic studies based on different morphological character systems.

Material and Methods

Taxon Sampling

The sampling of Orthoptera represents 23 taxa covering the phylogenetic diversity of the group as currently recognized (Song et al. 2015), whereby data on the thoracic morphology available from previously published studies are also considered. In total, these represent 16 ensiferan representatives (14 investigated herein, two described in literature) and seven caeliferan representatives (two investigated herein, five described in literature). Extant representatives of all major ensiferan lineages, crickets (Gryllidae), mole crickets (Gryllotalpidae), katydids (Tettigoniidae), raspy crickets (Gryllacrididae), dune crickets (Schizodactylidae), Jerusalem crickets (Stenopematidae), cave crickets (Rhaphidophoridae), hump-winged crickets (Prophalangopsidae), and king crickets (Anostostomatidae) were included. Naming of the orthopteran species as well as their taxonomical affiliation follows the current classification of Cigliano et al. (2017). Since the phylogenetic affinities of Orthoptera within the Polyneoptera are still unknown, as is the basal branching event within Polyneoptera (e.g., Yoshizawa 2011, Letsch and Simon 2013, Misof et al. 2014, Song et al. 2016), the outgroup consulted for reconstructing the potential ground plan of the thoracic skeletomuscular complex in Orthoptera is represented by at least one representative of each polyneopteran subgroup. Furthermore, a number of representatives of the Paraneoptera, Holometabola, and the palaeopteran taxon Ephemeroptera (Matsuda 1956a) are included. The outgroup selection was based on a previous study of the insect thorax (Wipfler et al. 2015). For convenience, only the generic names of the investigated taxa are used in the following. A list of the 39 taxa studied in total and additional literature used for character coding, is provided in Table 1. Illustrations of the skeleton and musculature of the orthopteran representatives examined in the present study are compiled in Supp File 1 (online only).

Examination of Specimens, μ CT, and 3D-Reconstruction

The ingroup taxa that were investigated by μ CT in the present study are adult females, with the exception of *Cyphoderris* (Prophalangopsidae), for which only an adult male was available (Table 1). Where appropriate, the 70% ethanol-fixed specimens were stored in alcoholic Bouin’s fixative or stained in an iodine solution over night to gain more contrast of soft tissues and muscles during the μ CT (Metscher 2009). Samples were dehydrated in a graded ethanol series, critical-point dried (Balzer CPD 030), and mounted on a specimen holder (aluminium stub). The scans were either performed at

Table 1. List of examined species including information on taxonomy, distribution (collection site), µCT scan, sex, and (additional) literature used for coding characters

Taxon	Species	Distribution (collection site)	CT-scan	Sex	Skeleton	Musculature	
Caelifera	Tridactylidae Brullé, 1835						
		<i>Xya</i> sp. Latreille, 1809	Eurasia, Africa, Southeast Asia, Australia (Germany)	SRµCT BESSY Berlin, 11/2011	♀	Carpentier 1936	Carpentier 1936
	Eumastacoidea Burr, 1899						
	Morabinae Rehn, 1948						
	Proscopiidae Serville, 1838						
		<i>Orienscopia angustirostris</i> (Brunner von Wattenwyl, 1890)	Uruguay, Argentina	–	?	Blackith and Blackith 1966, 1969	Blackith and Blackith 1966, 1969
		synonym: <i>Cephalocoema albrechti</i> (de Zollessi, 1968)		–	?	de Zollessi 1968	de Zollessi 1968
	Acrididae McLeay, 1821	<i>Dissosteira carolina</i> (Linnaeus, 1758)	Northern America, Southeastern United States.	–	?	Snodgrass 1929	Snodgrass 1929
	Acrididae McLeay, 1821	<i>Locusta migratoria</i> (Linnaeus, 1758)	Europe, Southern Africa, Southeast Asia	–	?	Albrecht 1953	Albrecht 1953
	Acrididae McLeay, 1821	<i>Schistocerca gregaria</i> (Forskål, 1775)	Northern Africa	–	?	Misra 1946, 1947	Misra 1946, 1947
	Acrididae McLeay, 1821	<i>Stenobothrus lineatus</i> (Panzet, 1796)	Middle Europe (Germany)	µCT Kiel, 08/2014	♀	–	–
	Gryllidae Laicharting, 1781	<i>Acheta domestica</i> (Linnaeus, 1758)	Europe	–	?	Voss 1905a, 1905d	Voss 1905b, 1912
	Gryllidae Laicharting, 1781	<i>Gryllus bimaculatus</i> De Geer, 1773	Southern Europe, Northern Africa	SRµCT DESY Hamburg, 2012	♀	–	–
	Ensifera	Gryllotalpidae Leach, 1815					
		<i>Gryllotalpa gryllotalpa</i> (Linnaeus, 1758)	(breeding in Germany) Europe	µCT Greifswald, 02/2014	?	Carpentier 1921b, 1936, La Greca 1938	La Greca 1938
Rhaphidophoridae Walker, 1869		<i>Troglophilus (Paratroglophilus) neglectus</i> Krauss, 1879	Southeastern Europe (Slovenia)	SRµCT BESSY Berlin, 2011	♀	–	–
Gryllacrididae Blanchard, 1845		<i>Prosopogryllacris</i> sp. Karny, 1937	Southeast Asia, Philippines, Japan, Papua New Guinea	SRµCT DESY Hamburg, 07/2014	♀	–	–
Stenopelmatidae Burmeister, 1838		<i>Stenopelmatus</i> sp. Burmeister, 1838	Western North America	SRµCT DESY Hamburg, 07/2014	♀	–	–
Anostomatidae Saussure, 1859		<i>Papuastus</i> sp. Griffini, 1911	Asia-Tropical (Papua New Guinea)	µCT Kiel, 08/2014	♀	–	–
Anostomatidae Saussure, 1859		<i>Hemideina crassidens</i> (Blanchard, 1851)	Southeastern Australia, New Zealand (New Zealand)	µCT Kiel, 08/2014	♀	Maskell 1927, O'Brien and Field 2001	–
Prophalangopsidae Kirby, 1906		<i>Cyphoderris monstrosa</i> Uhler, 1864	Northern America (Northwestern United States)	SRµCT DESY Hamburg, 07/2014	♂	Naskrecki 2000	–
Schizodactylidae Blanchard, 1845		<i>Comicus calcaris</i> Irish 1986	Southern Africa (Namibia)	SRµCT DESY Hamburg, 2012	♀	Irish 1986	–
Schizodactylidae Blanchard, 1845		<i>Schizodactylus monstrosus</i> (Drury, 1770)	Asia-Tropical, Indian Subcontinent, Bengal	–	?	Khattar 1960, 1972, Khattar and Srivastava 1962	–
Tettigoniidae Krauss, 1902		<i>Tettigonia viridissima</i> (Linnaeus, 1758)	Europe (Germany)	µCT Kiel, 08/2014	♀	Naskrecki 2000	–
Tettigoniidae Krauss, 1902		<i>Conocephalus (Anisoptera) dorsalis</i> (Latreille, 1804)	Southwestern Europe (Germany)	µCT Greifswald, 02/2014	♀	Naskrecki 2000	Maki 1938
Tettigoniidae Krauss, 1902		<i>Pholidoptera griseocaptera</i> (De Geer, 1773)	Northern Europe (Germany)	µCT Kiel, 08/2014	♀	Naskrecki 2000	–

(Additional) literature

Table 1. Continued

							(Additional) literature		
Taxon	Species	Distribution (collection site)	CT-scan	Sex	Skeleton	Musculature			
Tettigoniidae	Krauss, 1902	<i>Meconema meridionale</i> Costa, 1860	Southeastern Europe (Germany)	♀	Naskrecki 2000	–			
Tettigoniidae	Krauss, 1902	<i>Meconema thalassinum</i> (De Geer, 1773)	Middle Europe (Germany)	♀	Naskrecki 2000	–			
Phasmatodea		<i>Megacrania tsudai</i> Shiraki, 1932	Taiwan	?	Maki 1935, Klug 2008, Bradler 2009	Maki 1935			
Phasmatodea		<i>Timema nevadense</i> Strohecker, 1966	Western United States	?	Tilgner et al. 1999, Tilgner 2002, Klug 2008	Klug 2008			
Embioptera		<i>Embia surcouffi</i> Navas, 1933	Eastern Africa, Mozambique	?	Rähle 1970, Barlet 1985a	Rähle 1970, Barlet 1985b, Klug 2008			
Zoraptera		<i>Zorotypus hubbardi</i> Caudell, 1916	North America, United States	?	Friedrich and Beutel 2008	Friedrich and Beutel 2008			
Dermaptera		<i>Euborellia annulipes</i> (Lucas, 1847)	North America, South America, Europe, India, China	?	Bharadwaj and Chadwick 1974b	Bharadwaj and Chadwick 1974a			
Mantodea		<i>Stagmomantis carolina</i> (Johansson, 1763)	North America, Central America, Southern South America	?	Leverreault 1938, Wieland 2006, 2013	Leverreault 1938			
Blattodea		<i>Periplaneta americana</i> (Linnaeus, 1758)	Southern North America, Middle Europe, Asia	?	Carbonell 1947, Matsuda 1956a	Carbonell 1947			
Mantophasmatodea		<i>Austrophasma caledonensis</i> Klass et al., 2003	Western South Africa, South Africa	?	Wipfler et al. 2015	Wipfler et al. 2015			
Grylloblattodea		<i>Grylloblatta campodeiformis</i> Walker, 1914	North America	?	Walker 1938	Walker 1938			
Plecoptera		<i>Perla abdominalis</i> Burmeister, 1839	Middle Europe, Southern Europe	?	Wittig 1955	Wittig 1955			
Psocoptera		<i>Stenopsocus stigmaticus</i> (Imhoff & Labram, 1842)	Middle Europe	?	Badonell 1934	Badonell 1934			
Thysanoptera		<i>Phloeothrips coriaceus</i> Haliday, 1836	Northern Europe, California	?	Mickoleit 1979	Mickoleit 1979			
Neuroptera		<i>Palpares libelluloides</i> (Linnaeus, 1764)	Southern Europe	?	Czihak 1954	Czihak 1954			
Hymenoptera		<i>Macroxylela ferruginea</i> (Say, 1824)	Northern America, United States	?	Vilhelmsen 2000, Vilhelmsen et al. 2010	Vilhelmsen 2000, Vilhelmsen et al. 2010			
Archostemata		<i>Tetrapteralerus bruchi</i> Heller, 1913	Argentina	?	Friedrich et al. 2009	Friedrich et al. 2009			
Ephemeroptera		<i>Siphonurus columbianus</i> McDunnough, 1925	North America, Northern United States, Canada	?	Matsuda 1956a	Matsuda 1956a			

synchrotron radiation facilities or at μ CT X-ray tomographs (details given in Table 1). The three-dimensional models of the thoraces were created using AMIRA (version 5.4.3 and 6.0.0.), and the skeletomuscular system was analyzed based on virtual sections. Images taken in AMIRA were thereafter edited to adjust contrast, brightness, and color using Adobe Photoshop CS3. Figures, plates, and schematic drawings were arranged in Adobe Illustrator CS4. Illustrations of the skeleton and musculature of the orthopteran representatives examined in the present study are compiled in Supp File 1 (Online only).

Terminology and Character Selection

The terminology of the thoracic skeleton largely follows Snodgrass (1935). The thoracic musculature of all examined specimens is homologized after the terminology of Friedrich and Beutel (2008). The homologization of thoracic muscles by Wipfler et al. (2015) concerning the outgroup taxa of the present study was thoroughly reviewed and revised (see Supp Table 1 [Online only]). In addition to the 23 orthopteran species considered in the character matrix, a proposed homologization for the musculature of another 10 orthopteran species extracted from literature is given in Supp Table 1 (Online only). A list of characters including detailed descriptions and literature sources is given in Supp File 2 (Online only). The skeleton complex comprises 47 characters in total. Of those, 26 characters were previously used for a cladistic analysis by Wipfler et al. (2015), 4 characters were modified from Wipfler et al. (2015), and 17 novel characters were coded. The musculature complex comprises 55 characters in total, of which 24 were used in Wipfler et al. (2015). The complete character matrix is presented in the appendix (Supp Table 2 [Online only]). The majority of entries into the data matrix for the skeleton and musculature are based on observations of a single specimen for each species representing certain supraspecific terminal taxa (Table 1). In a few cases, additional information on the morphology of the skeleton was extracted from previous studies containing more general descriptions of the genus or traditional family (e.g., Carpentier 1936, Maki 1938, Matsuda 1970) (see Table 1). Entries for the musculature of terminal supraspecific taxa were based on the present investigation or literature data of a single species with two exceptions. In the genus *Embia*, the thoracic musculature is a chimera combining two different species: prothoracic muscles of *Embia ramburi* Rimsky-Korsakow (Rähle 1970) and pterothoracic muscles of *Embia surcoufi* Navas (Barlet 1985a). Likewise, the musculature of Morabinae (Caelifera) is partly described for three different specimens (Blackith and Blackith 1967, see Supp Table 1 [Online only] for details).

Results

The character system studied herein is composed of two different but nonetheless closely related components: skeletal elements and musculature. As much as bones in the human body, the chitinous sclerites of the insect's external skeleton serve as attachment points for musculature and thereby enable a variety of complex movements, like running, jumping, or even flying. Besides the mere investigation and documentation of the thoracic skeletomuscular complex of Orthoptera in a comparative approach, another aim of the present study lies in translating these novel results into a morphological data matrix. The character selection is thereby based on the initial data matrix on the thoracic morphology of neopteran insects (Wipfler et al. 2015). Incorrect or missing entries of this initial matrix are fixed, some characters are modified due to different character states occurring within Orthoptera, and a number of orthopteran-specific characters are coded (see detailed list and discussion of characters in Supp File 2

[Online only]). In particular, the morphology of the sternal skeleton of Orthoptera and Ensifera provides a number of anatomical characteristics that might be useful in a phylogenetic reconstruction. Especially, the morphology of the sternal apophyses, the furcae, and spinae, has a much more complex appearance in Orthoptera than in other representatives of Polyneoptera which is amplified in the following:

Comparative Morphology of the Sternal Skeleton in Orthoptera

Profurca

In the wide range of Polyneoptera, the prothoracic furca of each body side consists of a single undivided extension, the profurcal arm, which projects in an anterior (*Timema*: Kristensen 1975, Tilgner et al. 1999; Zoraptera: Friedrich and Beutel 2008), posterior (Embioptera: Rähle 1970, *Xya* sp.: Supp File 1), or lateral direction (most Caelifera: Fig. 1F, Snodgrass 1929, Albrecht 1953, Blackith and Blackith 1966, de Zolessi 1968; Blattodea incl. Isoptera: Matsuda 1956b, 1970; Plecoptera: Wittig 1955; Dermaptera: Günther and Herter 1974; Mantodea: Matsuda 1970). Within the Ensifera, only the cave cricket *Troglophilus* (Leubner et al. 2016) and further representatives of the Rhaphidophoridae (Gurney 1935, Richards 1955) have a furca with a single furcal arm in the prothorax. The remaining representatives of Ensifera are characterized by a branched profurca that has an anterior arm-like branch and a posterior branch, which occurs in varying forms (Fig. 1). In Gryllidae (Voss 1905a) and Tettigoniidae (e.g., *Mecconema*: Fig. 1E), the profurca has a short slender stem that distally splits in an anterior tapered arm-like processus and a posterior bulbous or knob-like extension. Schizodactylidae (*Comicus*: Leubner et al. 2017, *Schizodactylus*: Khattar 1960), Anostomatidae (*Hemideina* and *Papuastus*: Fig. 1A and C), Stenopelmatidae (*Stenopelmatus*: Fig. 1B), Gryllacrididae (*Prosopogryllacris*: Fig. 1D), and Prophalangopsidae (*Cyphoderris*: Supp File 1 [Online only]) are characterized by a branched profurca with a pronounced arm-like processus extending into a posterior direction. An elongated posterior arm-like metafurcal processus is also found in mole crickets (Carpentier 1921a,b).

Prospina

In the vast majority of insects, the prospina is a stick-like tapered internal protrusion (Matsuda 1970). In most representatives of the Caelifera, the prospina appears as a flat median extension (Fig. 1F, Snodgrass 1929, Misra 1946, Blackith and Blackith 1966, de Zolessi 1968). Only in the caeliferan *Xya* sp. Latreille, the prospina is a long and massive structure, extending into the mesothorax (Fig. 2F). In contrast, all examined ensiferans are characterized by a prospina that always bears a slim stalk and a distal expansion, formed as a distal plate that bear lateral, anterior, and/or posterior processi serving as attachment points for the well-developed ventral longitudinal musculature (Fig. 2). In representatives of Gryllidae (Voss 1905a), Prophalangopsidae (Fig. 2C), Gryllotalpidae (Carpentier 1921b), and all representatives of the Tettigoniidae (Fig. 2A and B), the posterior processus is a single protrusion. In contrast, Anostomatidae (*Hemideina*: Fig. 2D), Gryllacrididae (*Prosopogryllacris*: Fig. 2E), Stenopelmatidae (not illustrated), Rhaphidophoridae (Richards 1955, Leubner et al. 2016), and Schizodactylidae (Khattar 1960, Leubner et al. 2017) have a prospina that bears a paired posterior processus, each pointing to a more posterolateral direction.

Mesofurca

In the vast majority of Polyneoptera, the mesofurcal arm of each body side is an unfurcated elongated apophysis that extends in a lateral

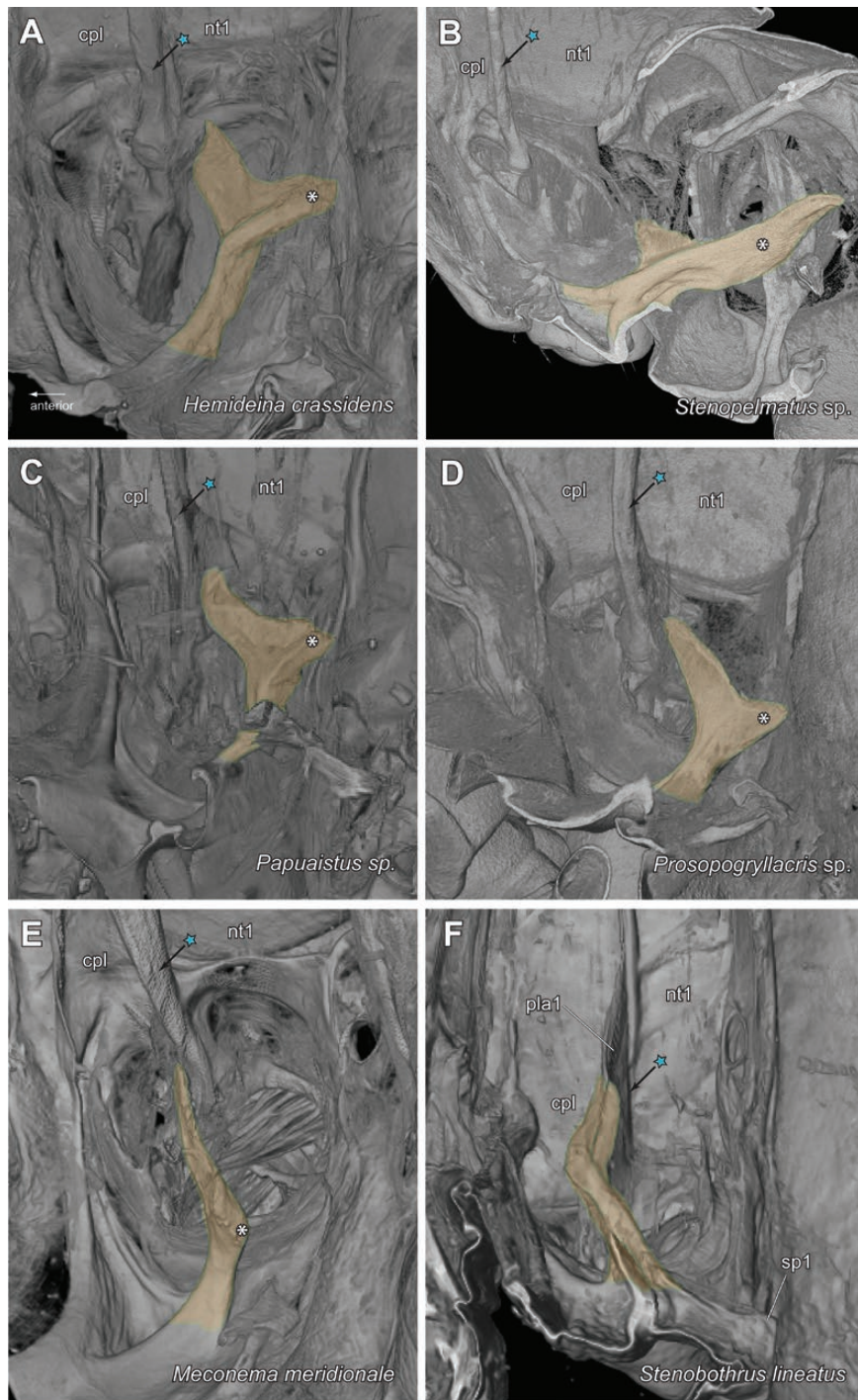


Fig. 1. Morphology of the prothoracic furca in representatives of Ensifera (A–E) and Caelifera (F). Lateral view. Profurca is highlighted in transparent orange. The white asterisk * marks the posterior arm-like or bulbous extension of the profurca. Blue asterisks mark the pleural ridge of cryptopleura. In contrast to (A–E), caeliferan representative in (F) has strikingly marked prothoracic pleural arm. *cpl* (cryptopleura), *nt1* (pronotum), *pla1* (prothoracic pleural arm), *sp1* (prospina).

direction, as it is documented for Grylloblattodea (Walker 1938), Embioptera (Barlet 1985b, Klug 2008), Phasmatodea (Tilgner et al. 1999, Klug 2008), Mantodea (Matsuda 1970), Blattodea (Matsuda 1956b), and Plecoptera (Matsuda 1970). Correspondingly, the mesofurcal arm of Ensifera appears as a lateral projection that bears no anterior process (Fig. 3). In contrast, the mesofurcal arm of Caelifera is characterized by an anteriorly directed process (Fig. 3C and F, Snodgrass 1929, Misra 1947, de Zolessi 1968).

An additional characteristic of the anterior mesofurcal process in Caelifera is that it serves as an insertion point for the ventral longitudinal muscles Ivlm7 (*Musculus profurca-mesofurcalis*) and Ivlm9 (*Musculus prospina-mesofurcalis*). In Ensifera, where the anterior process is absent, both muscles insert at the anterior edge of the mesofurcal arm (Fig. 3A and B). An anterior mesofurcal process serving as an insertion point for Ivlm7 (Ivlm9 is absent) is also reported for Mantophasmatodea (Wipfler et al. 2015). The state of

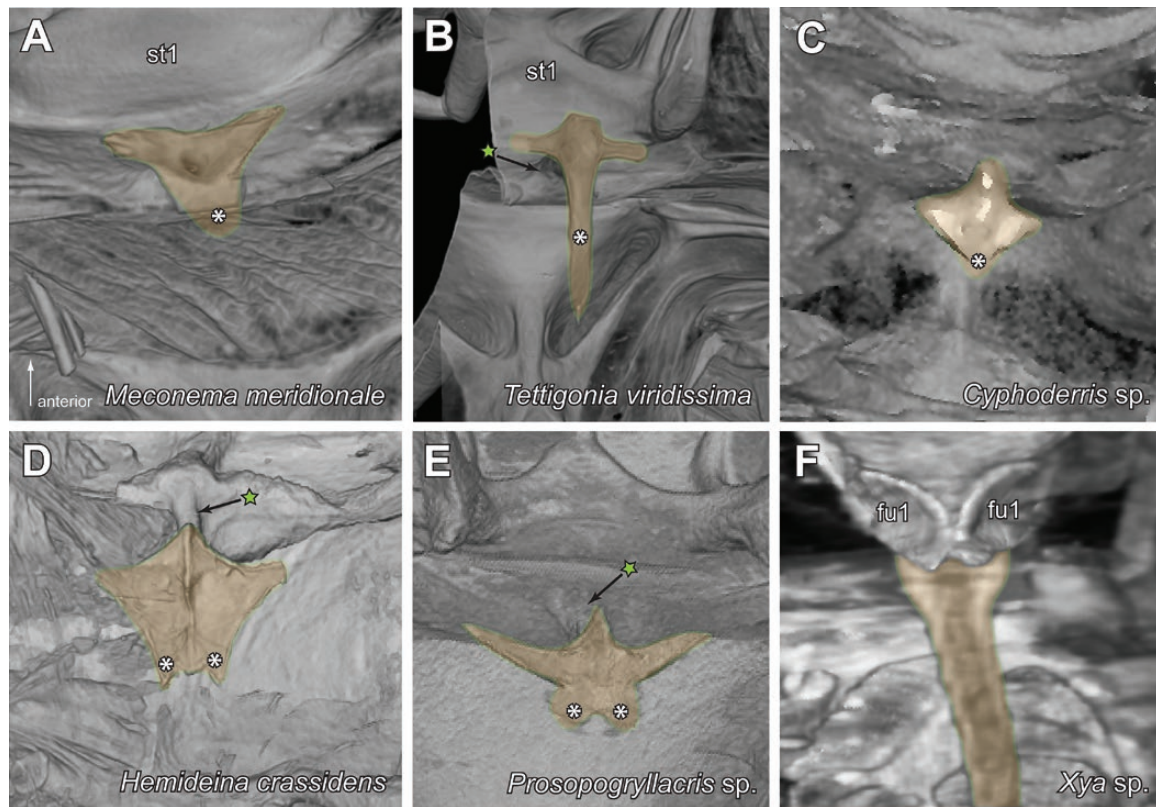


Fig. 2. Morphology of the prothoracic spina in representatives of Ensifera (A–E), and Caelifera (F). Dorsal view. Prospina is highlighted in transparent orange. The white asterisk * marks the single or paired posterior processus of the prospina. Green asterisks mark visible prospinal stalk. In contrast to (A–E), the prospina of the caeliferan representative (F) has a broad basis and is nonstalked. *fu1* (profurca).

this character in Zoraptera and Dermaptera is unknown. Whereas no concrete description is available for the morphology of the mesofurca, an anterior protrusion is recognizable in the illustrations of Zoraptera (Fig. 6C in Friedrich and Beutel 2008) and Dermaptera (Fig. 14b in Kleinow 1966).

Mesospina

In Polyneoptera, the unpaired median protrusion of the mesothorax, the mesospina, is mainly of simple, spine-like, tapered, or knob-like shape, without bearing any processi (e.g., Dermaptera: Barlet 1985c; Mantophasmatodea: Wipfler et al. 2015; Blattodea and Isoptera: Matsuda 1956b, 1970; Zoraptera: Friedrich and Beutel 2008).

In contrast, members of both subtaxa of Orthoptera have a stalked mesospina bearing a more complex overall morphology. In Caelifera, the distal part of the mesospina is flattened, fin-shaped, and oriented along the longitudinal axis (Fig. 4M, Misra 1947, Blackith and Blackith 1966, de Zolessi 1968). The mesospina of Ensifera has an even more complex structure with several processi (Fig. 4A–L). In addition to paired ventrolateral and paired dorsolateral processi occurring, e.g., in Tettigoniidae (Fig. 4A, B, D), Gryllacrididae (Fig. 4I), Stenopelmatidae (Fig. 4J), or Prophalangopsidae (Fig. 4K), an unpaired posterior processus is present in some ensiferan representatives (Anostomatidae: Fig. 4C, Rhaphidophoridae: Fig. 4H). The mesospina of mole crickets (Gryllotalpidae) was reported to be a massive, rod-shaped structure that reaches far into the metathorax (Carpentier 1936). In contrast, by investigating μ CT data, it could be figured out that the mesospina of *Gryllotalpa* bears a short stalk, ventrally oriented lateral processi and a single elongated posterior processus (Fig. 4L). Members of the Schizodactylidae, namely

Comicus (Fig. 4F) and *Schizodactylus* (Khattar and Srivastava 1962) have a mesospina with a single lateral processus, thereby having a T-shaped appearance.

Metafurca

Like in other representatives of the Polyneoptera (Matsuda 1970), the metafurca of Orthoptera is composed of an obligate lateral processus (Fig. 5). With the exception of Gryllidae (Fig. 5A) and Tridactylidae (Fig. 5N), an additional anterior metafurcal processus is present in Orthoptera. Such an anteriorly oriented processus that serves as an attachment point for ventral longitudinal musculature is also described for other polyneopteran taxa, such as Mantophasmatodea (Wipfler et al. 2015) or Dermaptera (Bharadwaj and Chadwick 1974b). Only a few subordinate ensiferan taxa have an additional dorsal metafurcal processus. This triramous appearance of the metafurca is found in Prophalangopsidae (*Cyphoderris*: Fig. 5E), Anostomatidae (*Hemideina*: Fig. 5F; *Papuaistus*: Fig. 5H), Stenopelmatidae (*Stenopelmatus*: Fig. 5G), and Rhaphidophoridae (*Troglophilus*: Fig. 5I).

Thoracic Musculature in Orthoptera

Following Friedrich and Beutel (2008), each thoracic muscle can be assigned to one of eight different muscles groups, which are exemplarily shown in the tettigoniid *Meconema meridionale* Costa: dorsal longitudinal (Fig. 6), dorsoventral (Fig. 7A), tergopleural (Fig. 8), pleuropleural (Fig. 8A), sternopleural (Fig. 8A), pleurocoxal (Fig. 6), ventral longitudinal (Fig. 8A), or sternocoxal (Fig. 7). Additionally, the three-dimensional reconstruction of the thoracic musculature of all herein investigated taxa of Orthoptera is figured in the electronic supplement

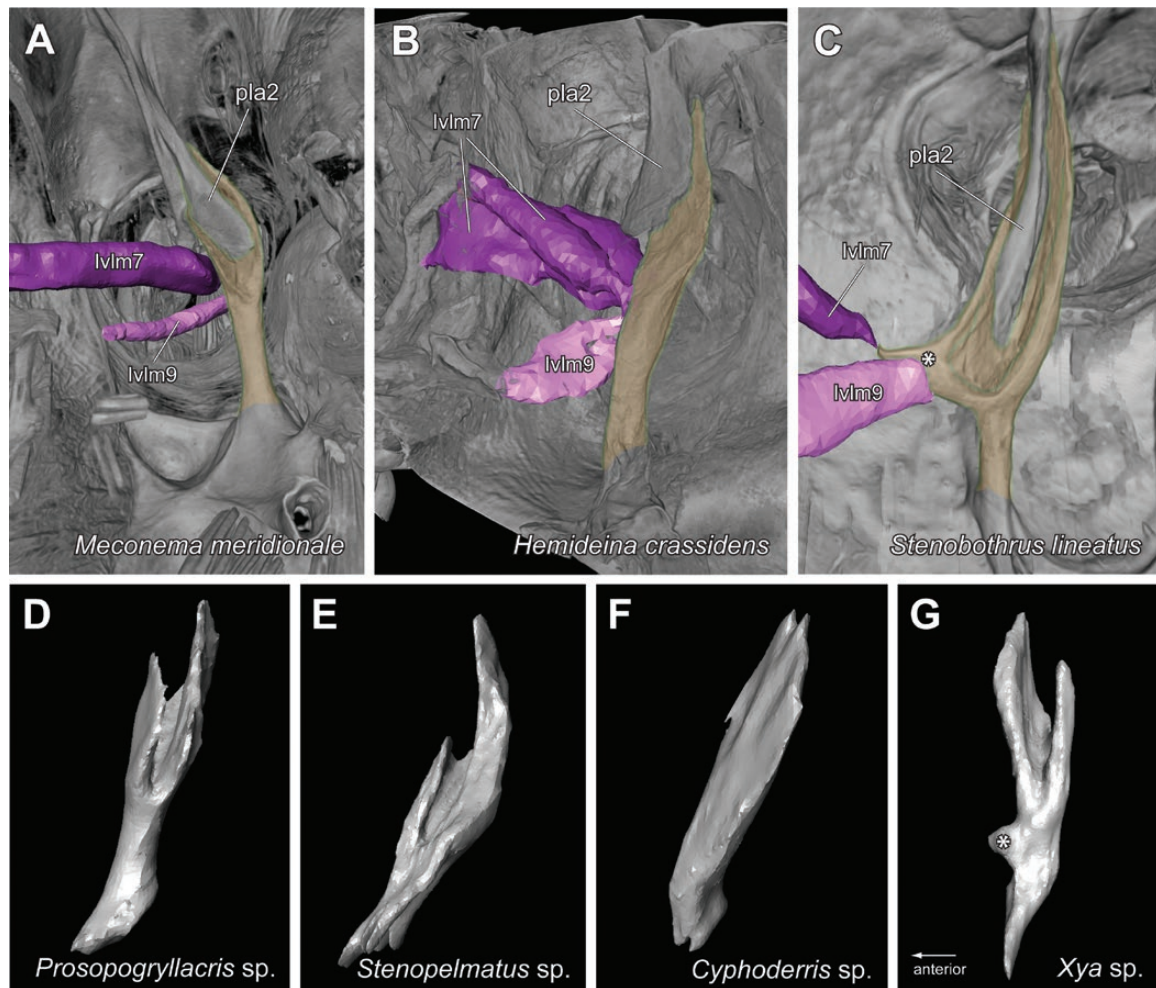


Fig. 3. Morphology of the mesothoracic furca in representatives of Ensifera (A, B, D–F) and Caelifera (C and G). (A–C) Volume rendering of mesothorax showing ventral longitudinal muscles inserting at anterior process * or anterior edge of mesofurca. Mesofurca is enclosing the pleural arm from ventral side. (D–G) 3D reconstruction of mesofurcae. In contrast to ensiferan representatives, the mesofurca of the caeliferan *Xya* sp. (G) bears an anterior process *. The muscles lvm7 (*M. profurca-mesofurcalis*) and lvm9 (*M. prospina-mesofurcalis*) insert at anterior processus or homologous area. *pla2* (mesothoracic pleural arm).

(Supp File 1). A detailed table compiling the thoracic musculature of all examined orthopteran representatives, a homologization according to the nomenclature of Friedrich and Beutel (2008), which also includes previous publications that describe the complete or partial set of thoracic muscles in other representatives of the Orthoptera, is given in the electronic supplement (Supp Table 1 [Online only]).

Discussion

The present study significantly expands the knowledge on the thoracic morphology of Neoptera by providing data on further, previously neglected groups and additional characters. By including yet unstudied ensiferan taxa such as Gryllacrididae and Stenopelmatidae, the herein presented comparative investigation of the thoracic skeletomuscular system of Orthoptera is the most comprehensive one conducted so far.

The Ground Pattern of Orthopterans' Thoracic Skeleton

The saddle-shaped pronotum that occurs in combination with an internally exposed and widened pleura supports the assumption of monophyletic Orthoptera (Wipfler et al. 2015; Fig. 9). The precoxal connection of this so-called cryptopleura to the prosternum

in Orthoptera is different from the vast majority other polyneopteran taxa (Matsuda 1970). Both elements are inflexibly connected through a pleurosternal bridge. As the cryptopleura of Orthoptera is exposed to high mechanical stress because of its function as an area of muscle origin, the pleurosternal bridge likely represents a stabilizing element that fixes the cryptopleura in its position. Within Polyneoptera and probably developed as a convergent trait, a pleurosternal bridge is only found in praying mantises and is likewise suggested to provide the required stability of the prothorax (Wieland 2002, 2013). Other characters that might represent apomorphies of Orthoptera are the pterothoracic furcae that enclose the respective pleural arm from the ventral side, the mesofurca and mesospina that are situated in one line at the sternacosta, and a stalked mesospina with a delimited dorsal plate (for detailed discussion see Supp File 2 [Online only]). The majority of the characters coded for the data matrix contain anatomical features of the sternal region of the thorax, a character system that already was suggested to contain phylogenetic information for Orthoptera before (Ander 1939, Naskrecki 2000). A number of these characters show different character states in Caelifera and Ensifera, respectively. In these cases, an unambiguous reconstruction of the orthopteran ground pattern is impeded (Table 2).

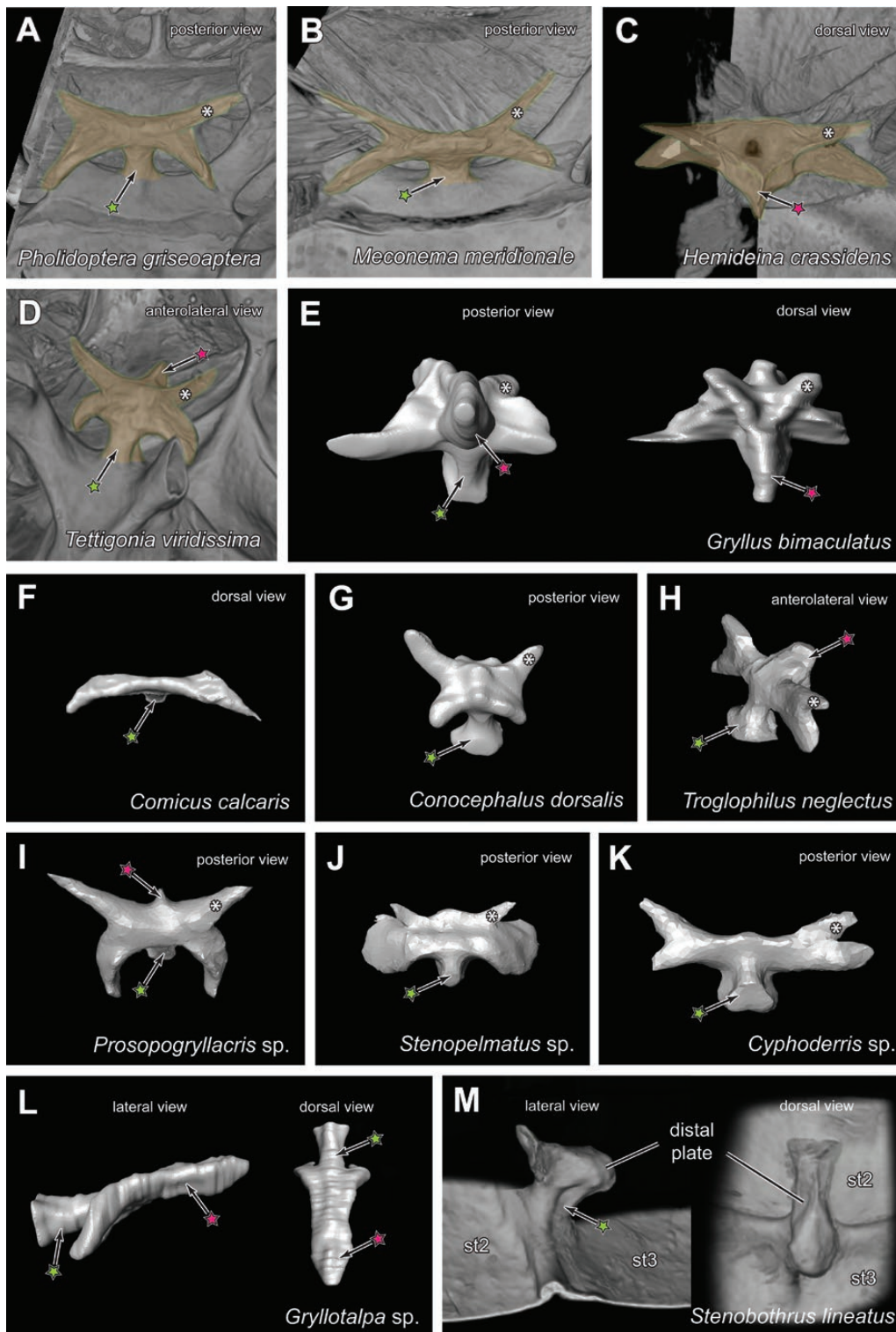


Fig. 4. Morphology of mesospina in representatives of Ensifera (A–L) and Caelifera (M). (A–D) Volume rendering. (E–M) 3D reconstruction. Orthoptera bear a stalked mesospina (green asterisk). The vast majority of Ensifera is characterized by a mesospina that bears paired dorsolateral* and ventrolateral processes, only *Comicus calcaris* has a single lateral process (F). Whereas the dorsolateral process* is tapered in most Ensifera, the dorsolateral process* in *Gryllus bimaculatus* is knob-like (E). Some taxa have an unpaired posterior process, marked by pink asterisk. The mesospina of *Stenobothrus lineatus* is characterized by a distal plate that lacks processi. st2 (mesosternum), st3 (metasternum).

The presence of detached lateral cervical sclerites is regarded as an apomorphic trait of Pterygota (Matsuda 1970, Wieland 2006). Nevertheless, there are different opinions about the polarization of

this character in pterygote insects. Either a single lateral cervical sclerite represents the plesiomorphic condition, with multiplied lateral cervical sclerites being the result of secondary partitions of

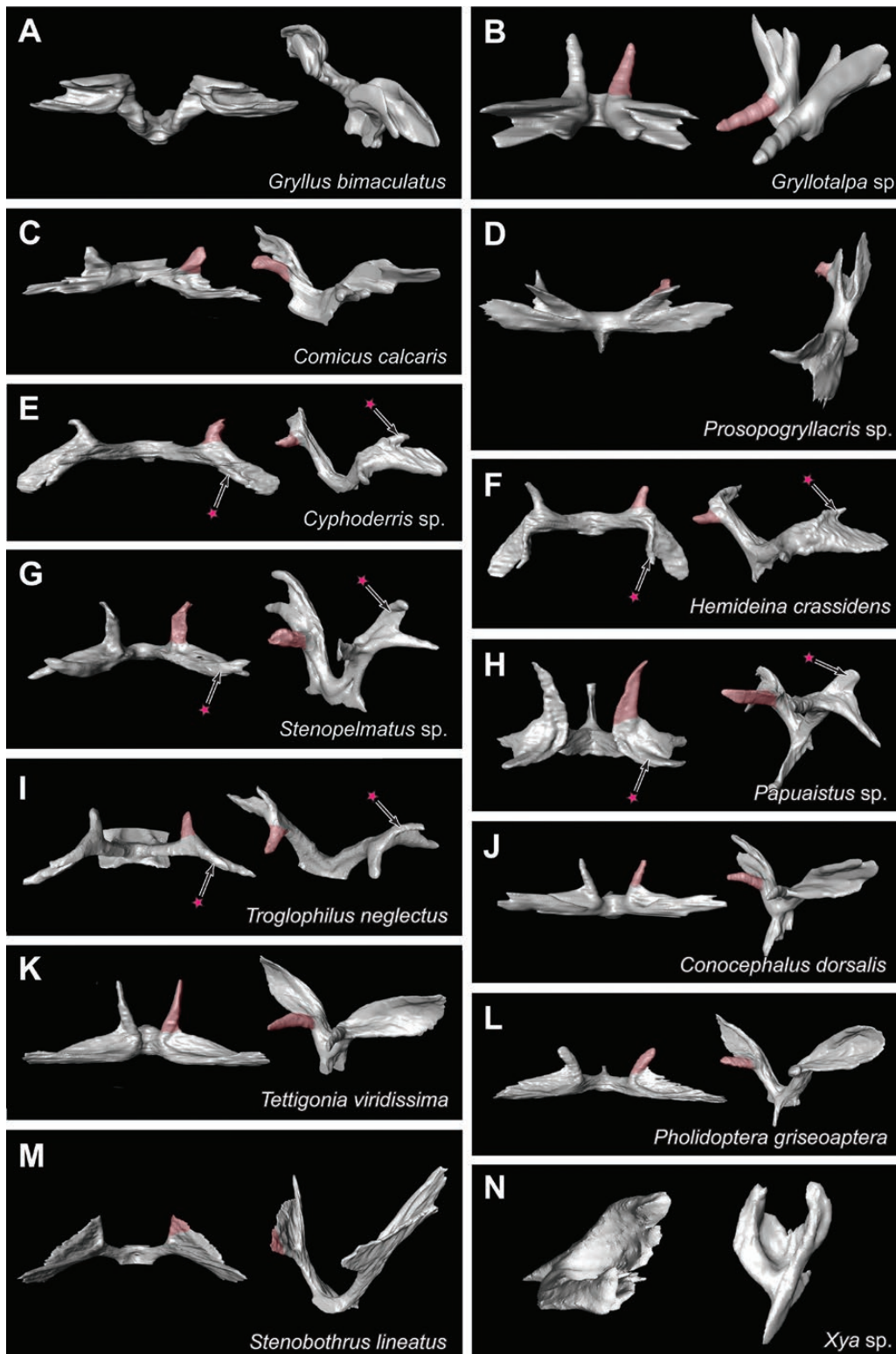


Fig. 5. Morphology of metafurca in Ensifera (A–L) and Caelifera (M and N). 3D reconstruction. Metafurca in dorsal and anterolateral view. An anterior furcal process, shaded in red, is present in the vast majority of Ensifera. Whereas the anterior furcal process is rod-shaped and tapered in representatives of the Ensifera, it forms a transition to the lateral furcal arm in the Caeliferan representative *Stenobothrus lineatus* (M). A dorsal furcal process, marked by pink asterisks, is present only in some ensiferan taxa (E–I).

this sclerite (Matsuda 1970, Whiting et al. 1997, Wieland 2006, Bradler 2009). Or alternatively, the presence of two separated lateral cervical sclerites is assumed to be plesiomorphic (Martin

1916, Crampton 1926, Snodgrass 1935). Hence, the occurrence of a single lateral sclerite is subsequently a consequence of the fusion of the two sclerites or the reduction of one of them. Even

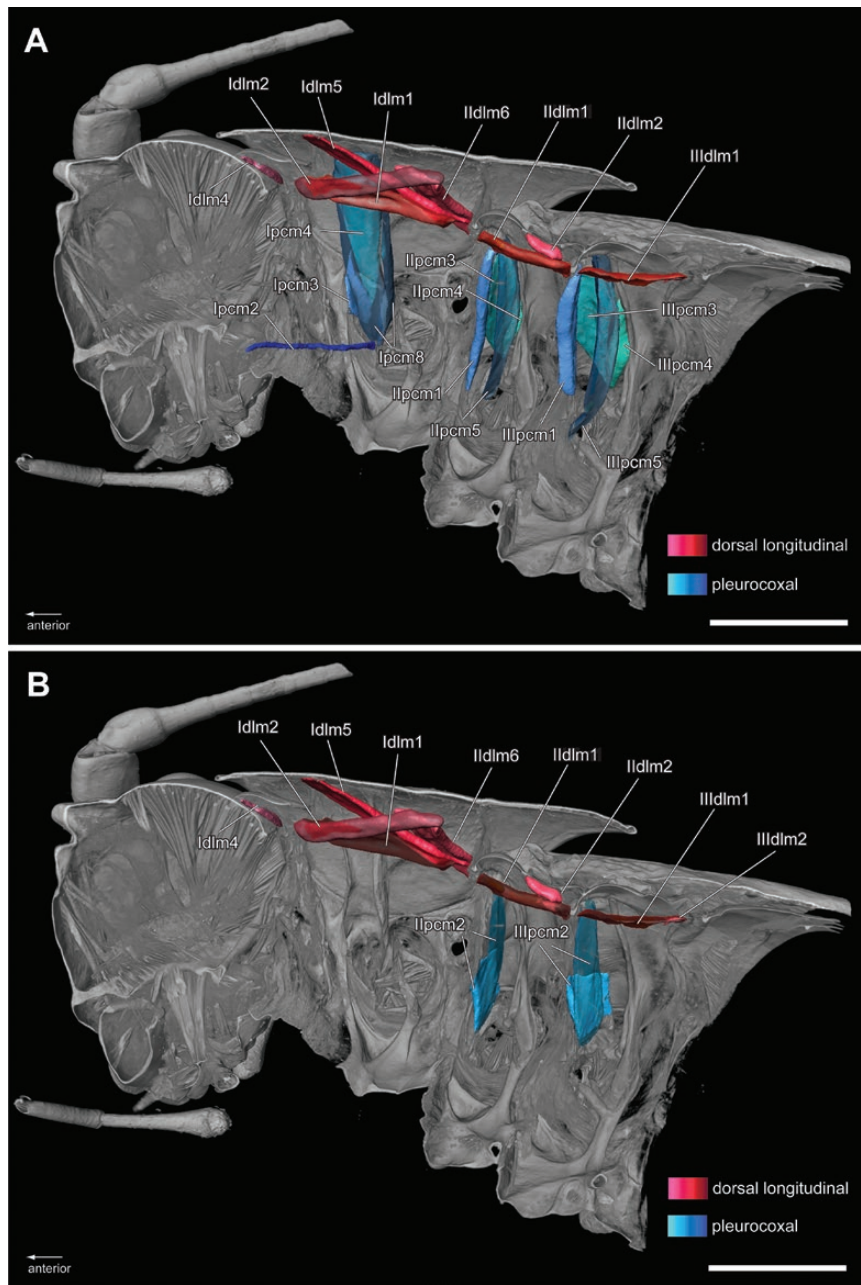


Fig. 6. Thoracic muscles of *Meconema meridionale*. Right body half. Interior lateral view. (A) Dorsal longitudinal and pleurocoxal musculature. (B) Dorsal longitudinal musculature and pterothoracic pcm2 (Mm. basalare-trochantinalis) composed of a long and a short bundle. Scale bars: 1 mm.

a convergent origin of the single lateral sclerite is possible. In the majority of Polyneoptera, two distinctly separated sclerites are present, namely in Embioptera (Rähle 1970), Phasmatodea (Bradler 2009), Dictyoptera (Wieland 2006), Mantophasmatodea (Wipfler et al. 2015), Grylloblattodea (Walker 1938), Zoraptera (Friedrich and Beutel 2008), and Dermaptera (Crampton 1926, Matsuda 1970). Only in Plecoptera, the lateral cervical sclerite appears as a single undivided plate, but it is separated in two parts in *Eusthenia* (Zwick 1980), likely representing the derived condition for this taxon (Matsuda 1970). Caelifera is characterized by the presence of a pair of lateral cervical sclerites. In contrast, in all Ensifera except Schizodactylidae only a single lateral cervical sclerite is present (see Supp File 2 [Online only]). In consequence, the presence of a single pair of lateral cervical sclerites might represent a

derived condition in Ensifera and is most likely a consequence of the fusion of the two cervical sclerites found in other Polyneoptera. This is supported by the musculature that is associated with the lateral cervical sclerite. All muscles that are found in association with the cervical sclerites in Caelifera (e.g. Idvm2, Idvm3, Idvm5, Idvm6) are likewise present in the Ensifera, albeit the respective muscles are here inserted on distant parts of the single lateral cervical sclerite. If the single lateral sclerite of Ensifera was the result of the reduction of one sclerite, the respective muscles would most likely have been lost as well.

The presence of dorsal cervical sclerites was considered to be a potential synapomorphy of Polyneoptera (Wipfler et al. 2015), although their absence in several subgroups would indicate multiple independent losses within the group (e.g., *Xenonomia*, Dermaptera).

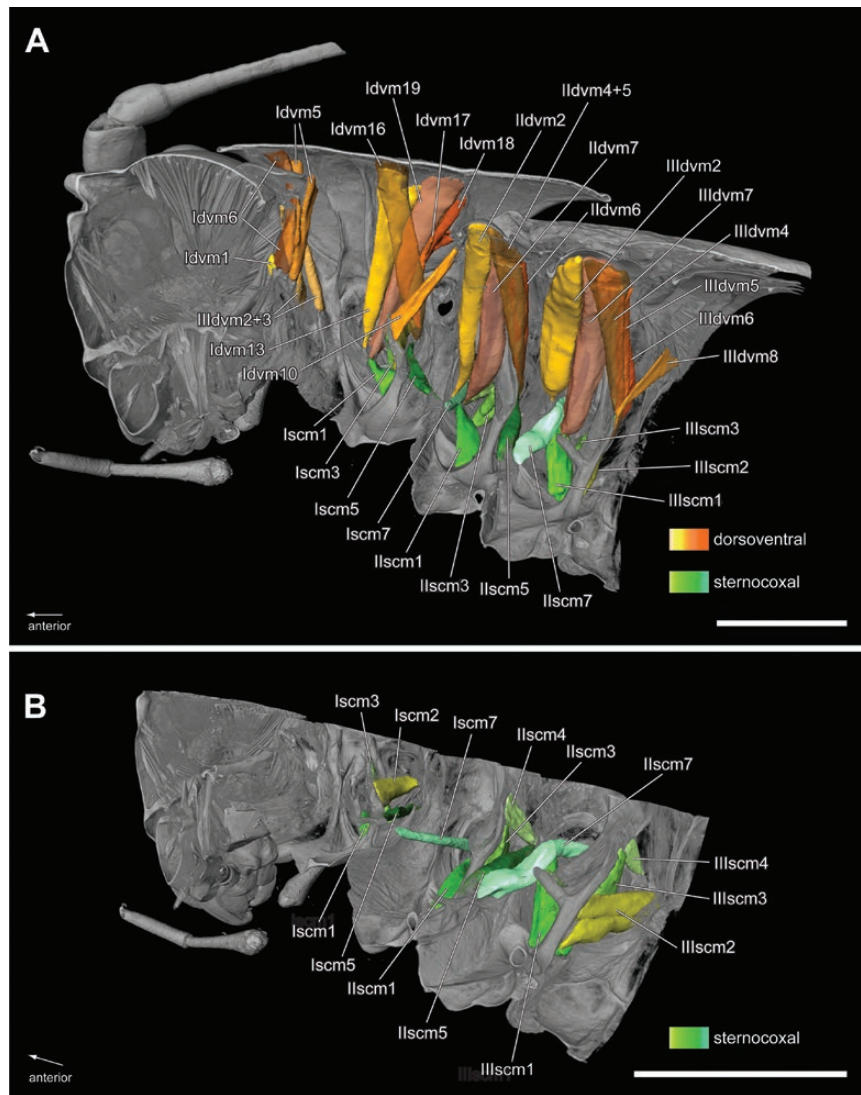


Fig. 7. Thoracic muscles of *Meconema meridionale*. Right body half. Interior lateral view. (A) Dorsoventral and sternocoxal musculature. (B) Slightly shifted dorsolateral view, dorsal body half clipped off. Sternocoxal muscles. Scale bars: 1 mm.

In that analysis, only the grasshopper *Dissosteira* (Caelifera) and the cricket *Acheta* are included. However, the extended taxon sampling of Orthoptera in the present study reveals a much higher variability of this character within Orthoptera. Within the investigated Caelifera, only *Xya* (Tridactylidae) lacks dorsal cervical sclerites. Besides, their presence is documented for another species of the Tridactyloidea, *Cylindrorhynchus spegazzinii* (Giglio-Tos) (Cylindrachetidae) (Carpentier 1936), and also for Tettigoniidae and Pamphagidae (Alicata 1962). Within the Ensifera, dorsal cervical sclerites are present in Gryllidae (Voss 1905a), Gryllotalpidae (Carpentier 1936), and in *Troglophilus* (Rhaphidophoridae). Nevertheless, in contrast to other representatives of the Orthoptera (Alicata 1962), the dorsal cervical sclerite in *Troglophilus* is unpaired, having a clip-like appearance (Leubner et al. 2016). The same morphology is described for the raphidophorid *Dolichopoda geniculata* (Costa) (Alicata 1962). However, only a small dorsal sclerite is present in *Ceuthophilus brevipes* Scudder (*precervicale* in Gurney 1935), and no dorsal cervical sclerite is described in *Macropathus filifer* Walker (Richards 1955). Therefore, it is not likely that this unpaired clip-like dorsal cervical sclerite is an autapomorphy of all

cave crickets (Rhaphidophoridae) but most probably represents a character that evolved within the group.

The Ground Pattern of Orthopterans' Thoracic Musculature

The total number of thoracic muscles in both subgroups of the Orthoptera is markedly different. In Caelifera it varies between 57 (muscles per each side of the body) (*Cephalocoema*), 59 (*Xya*), and 65–68 in Acrididae and Eumastacidae. In Ensifera, the vast majority of examined species exhibits around 80 thoracic muscles or even more. Here, the total number varies between 84–92 in Tettigoniidae, 89 or 95 in Gryllidae, 87–88 in Anostomatidae, 83 in *Gryllotalpa*, 79 in *Stenopelmatus*, and 92 in *Prosopogryllacris*. A decreased number of thoracic muscles is only found in *Comicus* (68) and *Troglophilus* (70). Generally, the number of thoracic muscles is reduced in wingless species in both Caelifera and Ensifera. The exceedingly small number of thoracic muscles in *Comicus* as compared to other ensiferans might be explained by some modifications in the skeletal anatomy characterized by several fused thoracic sclerites (Leubner et al. 2017).

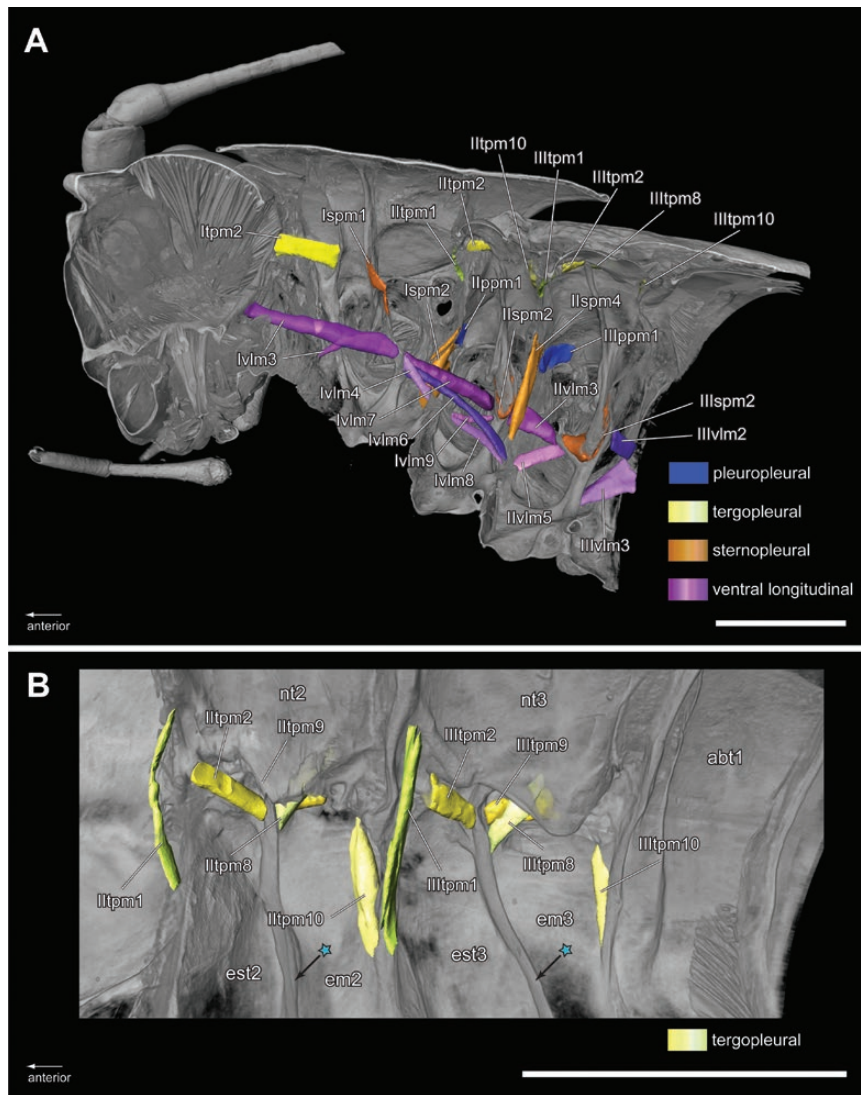


Fig. 8. Thoracic muscles of *Meconema meridionale*. Right body half. Interior lateral view. (A) Pleuropleural, tergopleural, sternopleural, and ventral longitudinal muscles. (B) Slightly shifted dorsolateral view of the pterothorax. Pterothoracic tergopleural muscles. Blue asterisks mark pleural ridge. *abt1* (first abdominal tergite), *em2/3* (meso-/metathoracic epimeron), *est2/3* (meso-/metathoracic episternum), *nt2/nt3* (meo-/metanotum). Scale bars: 1 mm.

The thoracic musculature of Orthoptera shows some peculiarities that might be useful for subsequent phylogenetic analyses including this character complex. Some thoracic muscles are only found in a single subgroup and thereby likely represent autapomorphies of a certain taxon, e.g., the *M. prospina-mesopleuralis* (*Ispm2*) for Tettigoniidae (Fig. 10C) or the *M. pronoto-apodemalis anterior* (*Itpm4*) for Gryllidae (Fig. 10B). In addition, a number of muscles are found in Orthoptera that were not described in the neopteran thorax before (Friedrich and Beutel 2008), e.g., the *M. mesofurca-propleuralis* (*IIspm9*, Fig. 10C). This muscle originates on the anterior edge of the mesofurcal arm and inserts at the pleural ridge of the prothoracic cryptopleura. It was only found in two representatives of Orthoptera, in the cave cricket *Troglophilus* (Ensifera) (Leubner et al. 2016) and the pygmy mole cricket *Xya* (Caelifera) (Supp File 1 [Online only]). As this muscle is hitherto only found in these distantly related orthopteran lineages (Song et al. 2015), the most likely explanation is a convergent formation of *IIspm9* in both representatives.

Without doubt, a large number of thoracic muscles were present in the orthopteran ground pattern (Figs. 10–12). Nevertheless, the

complete set of characteristic muscles differs exceedingly between the both major subgroups Caelifera and Ensifera. For example, the muscle *IIscm7* (*M. mesospina-metacoxalis*) is solely present in ensiferans (Fig. 10B), whereas the muscle *IIIvIm1* (*M. metafurca-spinalis*) could only be found in caeliferans (Fig. 10C).

Apart from the sheer reconstruction of the ground pattern concerning the thoracic musculature, characteristics of some thoracic muscles show interesting correlations between short-horned and long-horned grasshoppers that are elucidated in the following:

The muscle *M. procoxa-cervicalis transversalis* (*Ipcm2*) connects the prothoracic coxal rim with the lateral cervical sclerite of the opposite side of the body (Fig. 10A). Within the Orthoptera, this muscle is present in the majority of ensiferan representatives. In contrast, the muscle *Ipcm2* is absent in the majority of examined caeliferan species, although it was mistakenly stated to be present in *Dissosteira carolina* (Orthoptera: Acrididae) by Wipfler et al. (2015). This muscle of *Dissosteira* was originally described by Snodgrass (1929), therein initially termed *M. profurca-cervicalis transversalis* (*IvIm10*) (Fig. 10C), and runs from the profurcal arm to the cervical sclerite of the opposite side of the body. It is likewise found in all other examined

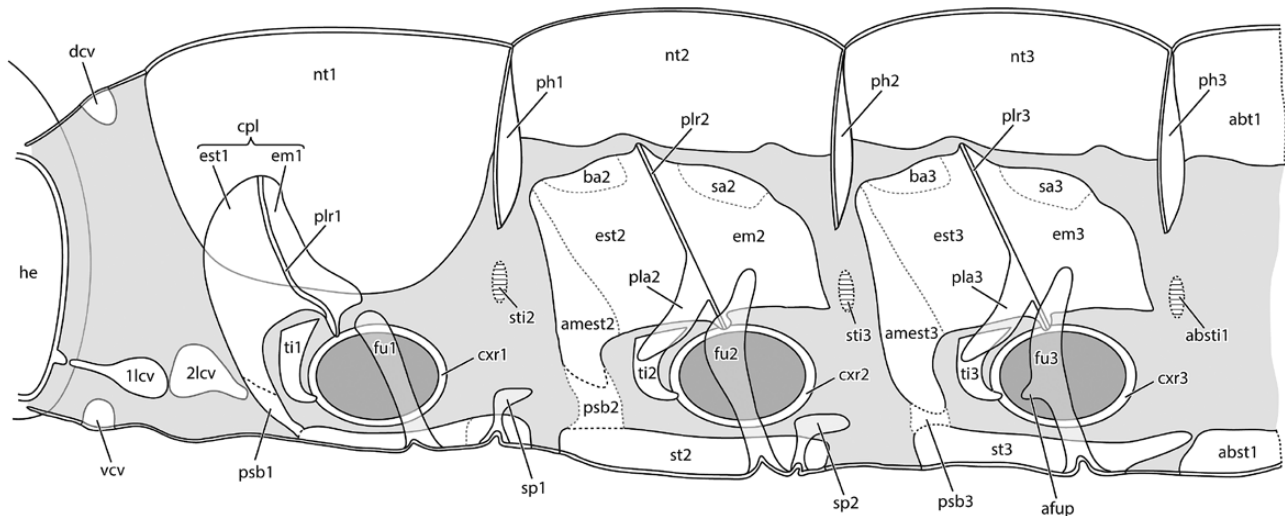


Fig. 9. Thoracic skeleton of Orthoptera. Structures in light gray are not present in all examined members of the Orthoptera. Wing base and sclerites (ba, sa) represent the unwinged condition. *1/2lcv* (first/second lateral cervical sclerite), *abst1* (first abdominal sternum), *abst1* (first abdominal stigma), *abt1* (first abdominal tergum), *afup* (anterior furcal process), *amest2/3* (anterior margin of mes-/metepisternum), *ba2/3* (basalare of meso-/metathorax), *cpl* (cryptopleura), *cxr1/2/3* (pro-/meso-/metacoxal rim), *dcv* (dorsal cervical sclerite), *est1/2/3* (pro-/mes-/metepisternum), *em1/2/3* (pro-/mes-/metepimeron), *fu1/2/3* (pro-/meso-/metafurca), *he* (head), *nt1/2/3* (pro-/meso-/metanotum), *ph1/2/3* (pro-/meso-/metaphragma), *pla2/3* (meso-/metapleural arm), *plr1/2/3* (pro-/meso-/metathoracic pleurosternal ridge), *psb1/2/3* (pro-/meso-/metathoracic pleurosterna bridge), *sa2/3* (subalare of meso-/metathorax), *sp1/2* (pro-/mesospina), *st1/2/3* (pro-/meso-/metasternum), *sti2/3* (meso-/metathoracic stigma), *ti1/2/3* (pro-/meso-/metatrochantin), *vcv* (ventral cervical sclerite).

Table 2. List of characters of the sternal skeleton whose character state differs between Ensifera and Caelifera

Character of the sternal skeleton	Last common ancestor of Orthoptera	Last common ancestor of Caelifera	Last common ancestor of Ensifera
Connection of profurcal arm and propleura	Uncertain	Profurcal arm and propleura firmly fused	Uncertain Firmly fused in <i>grylloid clade</i> ; connected by muscle in <i>tettigonioid clade</i> (muscle absent in <i>Troglophilus</i> , <i>Cyphoderris</i> , and <i>Stenopelmatus</i>)
Profurca	Uncertain	With single furcal arm	Branched
Prospina located	On distinct spinasternite between pro- and mesosternum	on posterior part of basisternum	–
Shape of prospina	Uncertain	Flat median extension? (different in <i>Xya</i>)	Stalked, with distal plate and processi
Anterior process of mesofurca	Absent	Present	–
Distal part of stalked mesospina	Uncertain	Without processi	With processi

The majority of characters has an uncertain state in the last common ancestor of Orthoptera, but a distinct state in the two subtaxa respectively

representatives of the Acrididae (Misra 1946, Albrecht 1953), in Eumastacidae (Blackith and Blackith 1967), and Pyrgomorphidae (Maki 1938, Blackith and Blackith 1967). In *Cephalocoema*, neither *Ipcm2* nor *Ivlm10* is present (de Zolessi 1968). As *Ivlm10* has never been described to be present simultaneously with *Ipcm2*, and both insert at the same point, it is likely that these muscles are homologous, albeit differing in the point of origin. Interestingly, among the investigated representatives of the Caelifera, the muscle *Ipcm2* is solely found in *Xya*. This taxon is a representative of the pygmy mole crickets (Tridactylidae), an early branch of short-horned grasshoppers that has been recovered as sister taxon to the remaining Caelifera in a number of phylogenetic analyses (Flook et al. 1999, Zhang et al. 2013, Song et al. 2015). Hence, the presence of *Ipcm2* in *Xya* might be supporting this hypothesis as a putative ground plan feature of all Orthoptera. Whether the replacement of *Ipcm2* by *Ivlm10* might represent an autapomorphy of the remaining Caelifera has to be elucidated by the investigation of additional caeliferans.

Ipcm8 (*M. propleuro-trochanteralis*) is a muscle running from the propleura to the trochanter of the fore leg that is present in all polyneopteran taxa. Yet, its characteristics differ between Orthoptera and most Polyneoptera. In Polyneoptera, it generally appears to be a single muscle (e.g., Bharadwaj and Chadwick 1974a, Wipfler et al. 2015). In Orthoptera, this muscle is composed at least of two bundles (Fig. 10A), with the exception of the gaudy grasshopper *Atractomorpha*, for which only a single muscle is described (Maki 1938). For the remaining Polyneoptera, a likewise two-bundled muscle *Ipcm8* is only reported for *Periplaneta* (Carbonell 1947). Both bundles of *Ipcm8* in *Periplaneta* originate from the pleural arm (Carbonell 1947). In all representatives of Caelifera, the respective muscle is consisting of a bundle originating from the undersurface of the pleural arm, in addition to a bundle that originates from the dorsal area of the episternum (e.g., Albrecht 1953, Blackith and Blackith 1967, de Zolessi 1968). Only in matchstick grasshoppers (Eumastacidae) (Blackith

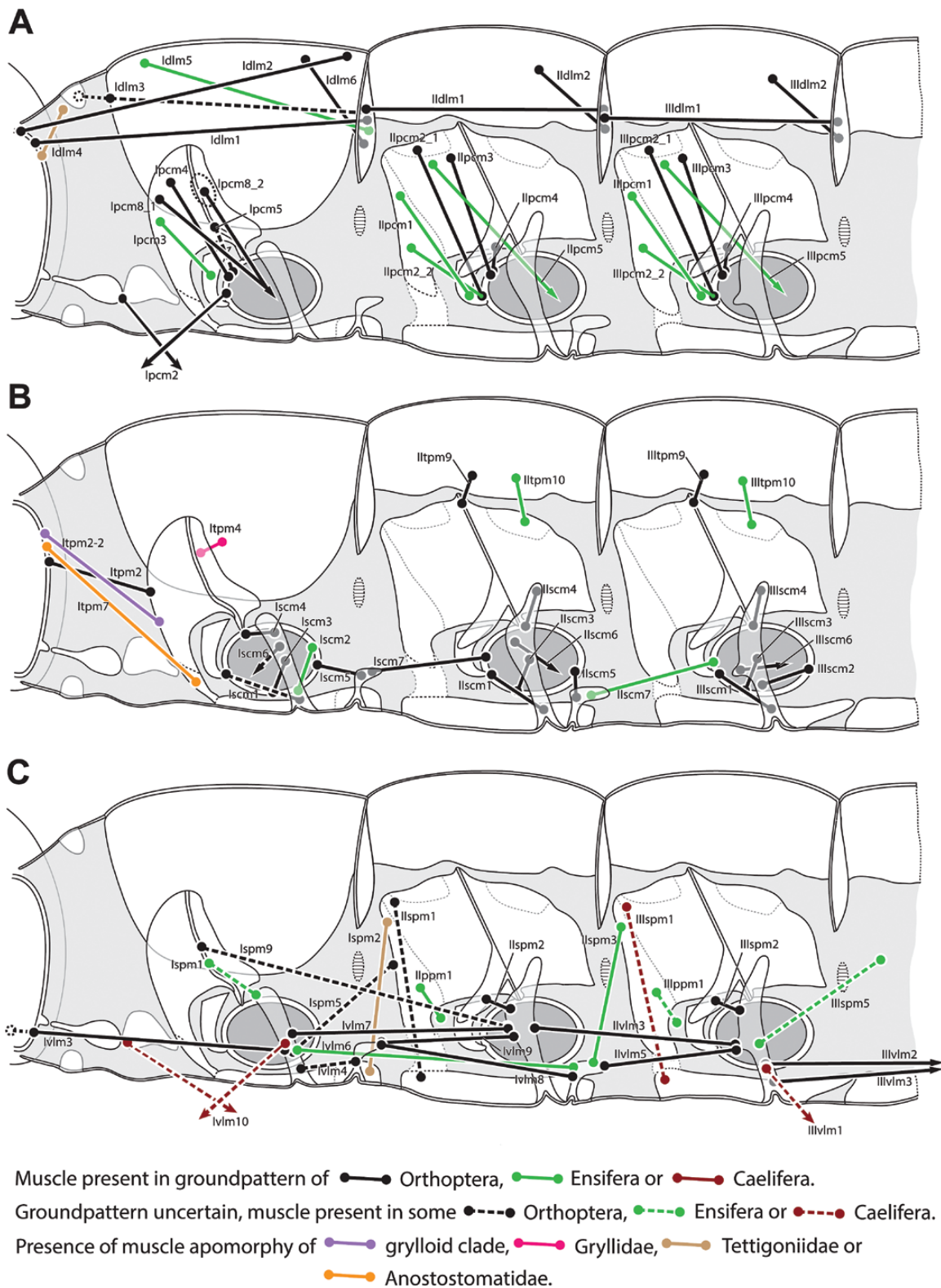


Fig. 10. Thoracic musculature of Orthoptera. (A) Dorsal longitudinal and pleurocoxal muscles. (B) Sternocoxal muscles. Tergopleural muscles that are present in unwinged Orthoptera. (C) Ventral longitudinal, sternopleural, and pleuropleural muscles.

and Blackith 1967) and in *Xya* (Tridactylidae), an additional bundle of Ipcm8 is present that originates from the pleural ridge (Supp File 1 [Online only]). All examined members of Ensifera are characterized by a two-bundled Ipcm8, whereby one bundle

originates dorsally from the episternal area of the cryptopleura, the other from the epimeral area or pleural ridge of the cryptopleura (Fig. 6). This common feature of Ensifera was regarded as a potential autapomorphy for this group by Ander (1939).

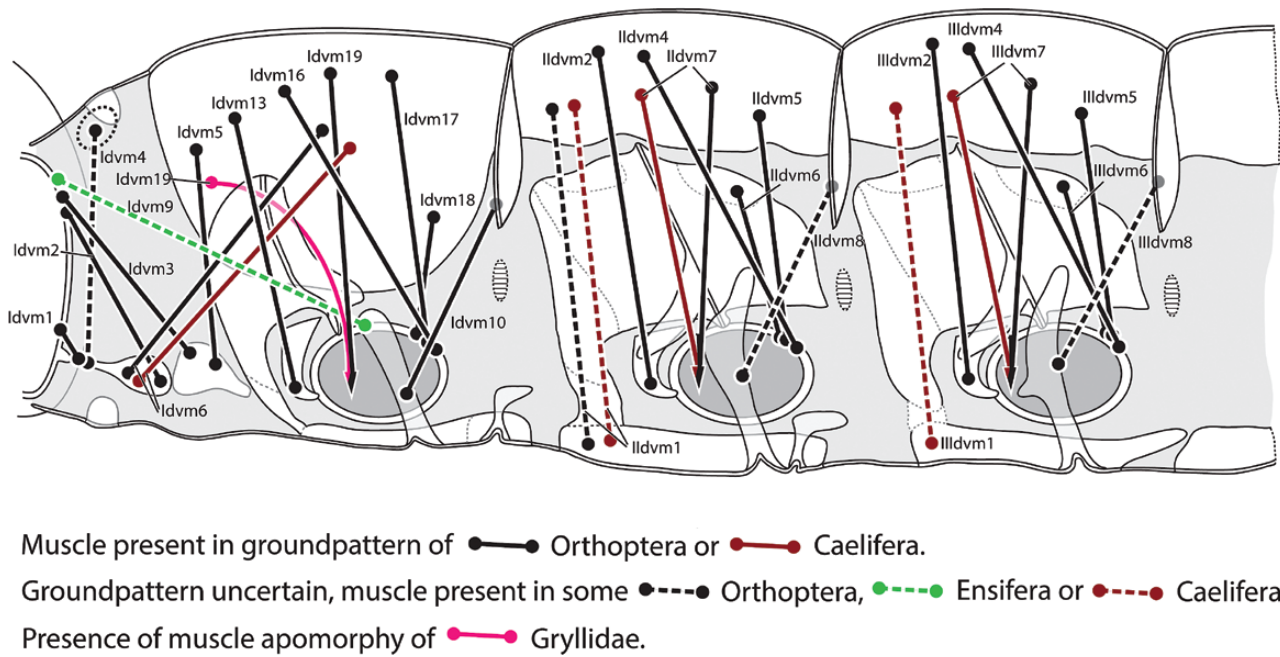


Fig. 11. Dorsoventral musculature in the thorax of Orthoptera.

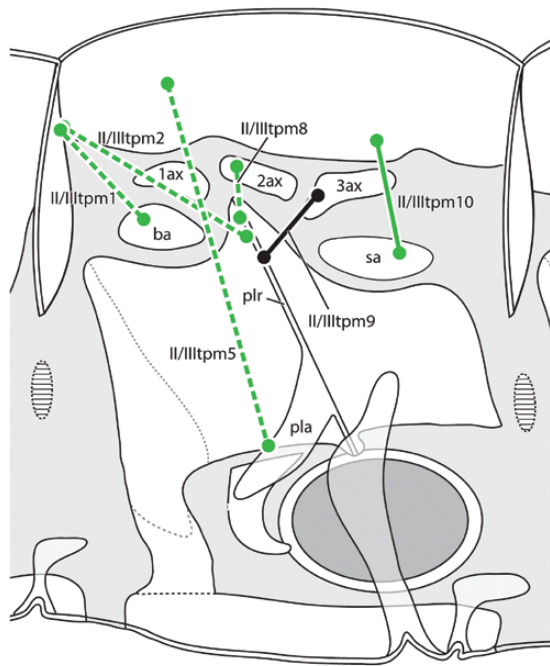
Nevertheless, the bundle of Ipcm8 that runs from the pleural arm found in Caelifera and the one in Ensifera originating from the epimeral area or pleural ridge might represent a homologous bundle since a pleural arm is lacking in Ensifera but present in Caelifera (e.g., Snodgrass 1929, Matsuda 1970).

All neopteran insects are characterized by specific thoracic muscles that are associated to the trochanter (Friedrich and Beutel 2008). These trochanteral muscles are composed of several bundles that originate from different parts of the thoracic skeleton running together into one tendon (Friedrich and Beutel 2008). Generally, three muscles are differentiated in the pterothorax: II/IIIIdvm7 (Mm. noto-trochanteralis), running from the notum of a pterothoracic segment (Fig. 11), II/IIIpcm5 (Mm. episterno-trochanteralis), originating from the episternum (Fig. 10A), and II/IIIscm6 (Mm. furca-trochanteralis), running from the furcal arm to the trochanter (Fig. 10B). Interestingly, the Mm. episterno-trochanteralis of the pterothorax is solely present in members of the Ensifera (Fig. 10A). In contrast, a second bundle of the Mm. noto-trochanteralis is present in the pterothorax of Caelifera (Fig. 11) that might represent the translocated bundle of the episternal muscle found in Ensifera. With the exception of *Cephalocoema* (Proscopiidae) (de Zollessi 1968), this second noto-trochanteral bundle is found in the remaining investigated caeliferan taxa (e.g., Snodgrass 1929, Misra 1947) and also in some further taxa that were not included in the present phylogenetic analyses (Maki 1938, Ewer 1958).

Some additional worthwhile findings are related to the characteristics of the indirect flight musculature occurring in Caelifera and Ensifera in particular. Orthoptera in general are considered to have a decreased flight ability and performance since they primarily move by jumping (Beier 1972). The wings are mainly used to control the direction and trajectory during the jumping process (Beier 1972). While there is no support for ensiferan representatives having an enhanced flight ability (Ander 1939, Beier 1972), the only caeliferan taxa, for which excellent and enduring flight abilities are reported, are the swarming grasshoppers (e.g., *Schistocerca*, *Locusta*) (Beier 1972). Two muscles that are indirectly involved in flying are the Mm. pleura-sternalis (II/IIIsp1) and Mm. noto-sternalis (II/

IIIIdvm1), with a supporting function in spreading and raising the wings (Voss 1905b). Both of these muscles are present in the mesothorax as well as in the metathorax of only certain caeliferan taxa: in short-horned grasshoppers and locusts (Acrididae) (e.g., *Locusta*: Albrecht 1953; *Schistocerca*: Misra 1947), toad grasshoppers (Pamphagidae) (*Lamarckiana*: Thomas 1952), and gaudy grasshoppers (Pyrgomorphidae) (*Atractomorpha*: Maki 1938; *Zonocerus*: Ewer 1954). However, none of these muscles are developed in the pterothorax of the tridactylid *Xya* (this study), the proscopiid *Cephalocoema* (de Zollessi 1968), and the grasshopper *Lentula* (Ewer 1958). The presence or absence of these muscles might be related to the occurrence of wings, since the aforementioned representatives are either completely wingless (*Cephalocoema* or *Lentula*) or at least brachypterous (*Xya*). This view was shared by Zechner et al. (1999) based on a study on *Xya pfaendleri* Harz. In populations of this usually brachypterous tridactylid species, fully winged specimens are regularly documented. In contrast to the brachypterous morphs, the fully winged specimens are reported to be good flyers and to have well-developed flight musculature (Zechner et al. 1999).

In Ensifera, the occurrence of the muscles dvm1 and spm1 in the pterothorax is quite different from that of the Caelifera. In the former, both muscles are exclusively developed in the mesothorax. Additionally, these indirect flight muscles are not present in all representatives of the Ensifera. The muscle IIdvm1 (M. mesonoto-sternalis) is present in Gryllidae (e.g., Voss 1905c,d, Carpentier 1923, Maki 1938), some members of the Tettigoniidae (*Tettigonia*: this study; *Conocephalus*: Maki 1938), and the prophalangopsid *Cyphoderris* (this study). To the contrary, the muscle IIsp1 (M. mesopleura-sternalis) is solely found in *Cyphoderris* (this study) and documented for some representatives of the Gryllidae (*Gryllus*: Carpentier 1923; *Acheta*: Voss 1905c; *Tarbinskiellus*: Maki 1938). Surprisingly, IIsp1 is not found in the specimen of *Gryllus* examined in the present study. The occurrence of IIsp1 might be related to the sex of the studied specimen as it is probably only present in males. Among our examined specimens, only *Cyphoderris* (Prophalangopsidae) is represented by a male. No author of past studies provided



Muscle present in groundpattern of
 ●—● Orthoptera or ●—● Ensifera.
 Groundpattern uncertain, muscle present
 in some ●- - - ● Ensifera.

Fig. 12. Tergopleural musculature in the pterothorax of winged Orthoptera. 1/2/3ax (first/second/third axillary sclerite), ba (basalare), pla (pleural arm), sa (subalare).

information on the sex of the examined species (e.g., Voss 1905a, Carpentier 1921b, 1923, Maki 1938). It is a striking observation that IIspm1 as well as IIdvm1 are solely developed in ensiferan taxa that communicate by tegminal stridulation. However, both muscles are not directly involved in the process of sound production since the horizontal movement is caused by the action of certain tergo-pleural muscles (Voss 1905b, Pfau and Koch 1994). Nonetheless, it is plausible that the presence of both muscles in the mesothorax of stridulating ensiferans enables a more effective and coordinated tegminal movement. Additionally, at least the basalare muscle IIspm1 is reported to be involved in a warm-up phase before stridulation, thus regulating the body temperature (Heller 1986). To answer the question of a sex-related occurrence of these indirect flight muscles in Ensifera, more studies investigating and comparing both sexes of a widespread selection of ensiferan species that communicate by tegminal stridulation should be conducted.

Conclusions and Outlook

The present study is an essential contribution to gain a deeper knowledge on the consistency and variability of thoracic characters among Orthoptera. Yet, due the limited taxon sampling, it must still be considered as a first step providing the basis for more extensive future studies. Characters potentially useful in upcoming phylogenetic analyses mainly concern the anatomy of the internally exposed sternal apophyses, like the triramous structure of the metafurca, or peculiar muscles hitherto only found in a subgroup of Ensifera, like the *M. cervico-occipitalis dorsalis* (Idlm4) in Tettigoniidae. When examined,

in particular the shape of the apophyses is easy to be recognized and could effortlessly be coded for numerous ensiferan representatives. μ CT is an innovative noninvasive morphological technique providing a convenient possibility for the investigation of insects (Friedrich et al. 2013). Without causing any mechanical damage, this technique even enables to investigate dried or alcohol-preserved material, allowing access to the examination of specimens, even valuable type material, stored in worldwide museum collections.

The phylogenetic reconstruction of an evolutionary lineage based on characters of a single anatomical system can be impeded by functional constraints, parallel losses caused by a potential trend of simplification, and also by diverse specializations occurring in the outgroup taxa chosen (Friedrich and Beutel 2010). In subsequent studies, morphological characters of the thoracic skeleton of representatives of Polyneoptera should be combined with available data on the morphology of other body parts, such as the head (Wipfler et al. 2011, Friedemann et al. 2012) and tarsal attachment structures (Beutel and Gorb 2006, 2008). Nonetheless, simply adding more morphological data to a data set can only partly compensate for misinterpretations of character transformations caused by a high degree of homoplasy, character loss, and/or reversals (Wiens 2004). Simulation studies have confirmed the benefits of an increased taxon sampling for phylogenetic accuracy in morphological studies, in particular outlining the importance of sampling multiple species when inferring relationships among higher taxa (Wiens 1998). With regard to the presented survey, more research on the morphology of yet neglected ensiferan taxa like Stenopelmatidae or Gryllacrididae, for which only a single representative is included in the current study, is needed to arrive at a comprehensive understanding of character variability within the respective lineage.

Supplementary Data

Supplementary data is available at *Insect Systematics and Diversity* online.

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