Evolutionary and functional substitution of extrinsic musculature in Solifugae (Arachnida)

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Abstract
The locomotory system of Solifugae is distinct from that of other Arachnida in several ways. Only three pairs of legs are involved in locomotion, while the first pair function as sensory appendages. Morphologically, the proximal region of the locomotory system in Solifugae is characterized by fused coxae. Within the prosoma of Solifugae, an endosternite is missing; in other Arachnida, this endosternite serves as the proximal attachment site for a portion of the extrinsic musculature. How then do these skeletal modifications influence the muscular anatomy in the proximal region of the locomotory system? To answer this question, we studied the skeletomuscular anatomy of Galeodes granti at the interface between the prosoma and legs, reinvestigating the complex muscular anatomy of this body region for the first time in over 80 years and—for the first time—using detailed micro-computed tomography scans to analyze the skeletomuscular morphology. Specimens of three further species were checked for comparison. The analysis revealed differences in the number and composition of coxa-trochanter muscles in each of the four pairs of legs. These are compared in the light of serial homology. The comparison between the proximal locomotory system of Solifugae and that of other Arachnida unveils a series of analogies. Primarily, the coxa-trochanter joint is the most proximal joint to move the leg relative to the prosoma. Therefore, we argue that from a morpho-functional point of view, the coxa-trochanter muscles in Solifugae should be considered secondary extrinsic musculature. Thus, the legs gain a stable, articulated joint in the most proximal region of the leg to the prosoma, which might be advantageous for agile locomotion.

KEYWORDS
coxa, endosternite, intrinsic muscles, trochanter

1 | INTRODUCTION
Solifugae are well known as agile predators and also for their extensive exploratory activities (Cloudsley-Thompson, 1977; Punzo, 1998). The underlying morphology of the locomotory system is characterized by several modifications in comparison to other arachnids. Unlike the ground pattern of Arachnida, only three pairs of legs are used for locomotion in Solifugae. The first pair of legs is usually held in a raised position and functions as a sensory appendage (Cloudsley-Thompson, 1977; Punzo, 1998). The following three pairs of walking legs are distinctly longer and there is an additional subdivision of the femora in the posterior two pairs (following Shultz, 1989; termed...
trochanter in Manton, 1977). In contrast to other arachnids with hydraulic leg extension, such as Araneae (see Kropf, 2013), the extension in the patella-tibia and tibia-basitarsus joints is realized in Solifugae by elastic sclerites (Sensenig & Shultz, 2003). But the modifications of the locomotory system are not only restricted to the legs themselves. A central aspect in the locomotory apparatus is the movement of legs relative to the prosoma. In arachnids, this movement is generally realized in the joint between prosoma and coxa, which makes the coxa the most proximal mobile podomere. The associated musculature that moves the leg relative to the prosoma is called extrinsic musculature and is spanned between the prosoma and proximal podomeres. In contrast, the intrinsic musculature is completely located within the legs and serves to move each of the podomeres relative to each other. In Arachnida, the extrinsic musculature is generally composed of two muscle groups: (a) the tergo-coxal muscles, which are connected to the dorsal tergum (exoskeletal) and the coxae, and (b) the endosterno-coxal muscles, which are connected to the endosternite (endoskeletal) and the coxae (Shultz, 1991). In Solifugae, the coxae of the pedipalps and of the subsequent legs are fused and form two rigid plates on the ventral side of the prosoma (Bernard, 1896; Dunlop, Krüger, & Alberti, 2012; Kittary, 1848; Roewer, 1934; van der Hammen, 1986). However, our knowledge of the associated musculature is but fragmentary. This is due to the scarcity of investigations into the skeleton-muscular morphology of the most proximal region of the legs (coxa, trochanter) (Kittary, 1848; Roewer, 1934). Both of these previous studies differ, not only in the conception of muscles but also in their delimitation—thus the morphological descriptions and visualizations of this very complex muscular system can hardly be compared. It is also nigh on impossible to match muscles described by Roewer (1934) to those described by Kittary (1848) as the associated morphological descriptions differ substantially. It is, therefore, the aim of this study to conduct a detailed, 3D-morphological analysis of the proximal region of the locomotory system in Solifugae in general, and specifically in Galeodes granti Pocock, 1903, at the interface between prosoma and legs to highlight the modifications associated with impaired mobility of the coxae.

From an evolutionary point of view, we are faced with two questions: (a) what happened to the extrinsic musculature originally moving the coxa against the body and, subsequently, (b) whether, and if so how, the movement of the leg against the body is compensated for by muscles within the coxa running to the adjacent podomeres? This study provides further information in the context of our ongoing analysis of the locomotory systems of Arachnida from evolutionary and morpho-functional points of view (Grams, Wirkner, & Runge, 2018; Runge & Wirkner, 2019).

2 | MATERIAL AND METHODS

2.1 | Studied specimens

Detailed morphological descriptions and 3D reconstructions of the proximal locomotor system were generated for Galeodes granti Pocock, 1903 (Galeolidae). Live specimens (n = 4) of G. granti were purchased online (www.ThePetFactory.de). Species identification was rechecked using the species description (Pocock, 1903) and the identification keys of Harvey (2003) and Roewer (1934).

General aspects of the cuticle and musculature were investigated in non-contrasted specimens using micro-computed tomography scans of Gluviospilla discolor (Kraepelin, 1899) (Daesiidae) (NHMW 1486; n = 2) and Rhagodia obscurior (Penther, 1913) (Rhagodidae) (NHMW 1465; n = 2), which were provided by the Naturhistorisches Museum Wien, Austria (NHMW). An existing micro-computed tomography scan of Gluvia dorsalis (Latreille, 1817) (Daesiidae) showing details of the anterior prosoma was also inspected.

The solifugid taxonomy and systematic classification used here is based on Harvey (2003).

2.2 | Specimen preparation and micro-computed tomography (µCT)

Specimens of G. granti were treated with a lethal dose of ethyl acetate. The opisthosoma and the walking legs (distal to trochanter) were cut from the prosoma to aid the penetration of the fixative and contrasting solutions. The prosoma was fixed using Bouin's fluid (15 parts saturated aqueous picric acid, five parts 40% formaldehyde and one part acetic acid) for several days, then washed with distilled water and transferred into Lugol's solution (aqueous iodine potassium iodide solution) for at least 7 days to increase the contrast between tissues in subsequent µCT-scans (Metscher, 2009a, 2009b).

Before µCT-scanning, the prosoma contrasted in Lugol's solution was rinsed several times in distilled water over a period of at least 1 hr. The prepared prosoma was stored in a tube with a moist atmosphere (from distilled water) during µCT-scanning.

Virtual image stacks of all specimens were obtained by µCT-scans performed using an XRadia Versa 410 x-ray microscope (Carl Zeiss Microscopy GmbH, Jena, Germany) using the program Scout and Scan v.11.1 (Carl Zeiss Microscopy GmbH) (40–50 kV; 8 W; 1.601–2.001 projections; 12–25 s acquisition time; objective: x0.4; voxel size: 9.3–13.3 μm).

The specimens obtained from museum collections (G. discolor, R. obscurior) remained untreated. These specimens were stored in tubes with a moist atmosphere of 70% ethanol during µCT-scanning. G. discolor and R. obscurior were scanned with XRadia Versa 410 x-ray microscope (30–40 kV; 5–8 W; 2001 projections; 10–22 s acquisition time; objective: x0.4; voxel size: 5.1 μm).

The scans for G. dorsalis were performed using the Phoenix Nanotom (PhoenixX-ray, GE Sensing & Inspection Technologies) high-resolution µCT system in high-resolution mode.

2.3 | 3D reconstruction and image processing

All 3D reconstructions were created by uploading image stacks to the software Amira 2019 (FEI). Images of volume and surface renderings...
based on the segmented μCT-scans were made using the snapshot-tool in Amira 2019.

The figure plates were arranged using Corel Graphics Suite X3 (CorelCorp., Ottawa, Canada). Images were embedded into Corel Draw X3 files and edited in Corel PhotoPaint X3 using general imaging enhancement tools (contrast, brightness).

The electronic version (PDF) of this study contains interactive 3D content. The three-dimensional surface models resulting from the 3D reconstruction procedure described above were converted into .u3d-files using Adobe 3D Reviewer (version: 9.0.0.107). To activate the 3D content, click on the relevant images (Figure 2) and use the mouse buttons to navigate. The 3D content includes supplementary information on additional muscles, which are associated with the coxae of the legs, for example, (a) muscles attached to propeltidium and the coxae, (b) muscles attached to coxae and femora, and (c) longitudinal muscles attached to consecutive coxae.

2.4 | Terminology

The terminology and labeling scheme of the muscles essentially follows the scheme by Runge and Wirkner (2019) by using a prefix, a stem and a suffix to abbreviate muscle names. Deviations to this scheme belong to the prefix as the attachment sites of the intrinsic musculature, described in this study, are designated as proximal attachment sites (PrA) and distal attachment sites (DiA). Basically, the terminology of the muscles used is free of assumptions regarding homology and/or function (for a thorough discussion, see Richter & Wirkner, 2014). Thus, the numbering of the muscles represents their actual arrangement but carries no implications regarding serial or special homology.

Serial homology of the coxa-trochanter muscles is determined with regard to the position and the spatial relationships of their proximal and distal attachment sites, as well as the spatial relationship of the whole muscles. These points contribute to the morphological pattern, which is compared between the different coxae (following Szucsich & Wirkner, 2007). Serial homologous muscles are listed and matched in Figure 4 and color-coded throughout the illustrations.

The statements on functional interactions made in this study are deduced from the morphological results and reflect our morpho-functional approach in light of the numerous different ways of considering function in biology. With regard to intrinsic and extrinsic musculature, function is considered here as the general role of moving the podomeres relative to each other or relative to the prosoma.

Central terms:

coxa: The cuticular structures on the ventral side of the prosoma are regarded here to be formed by the fusion of the coxae (the most proximal podomeres in Arachnida). Internally, the anterior, posterior, and medial cuticular walls of the coxae are present. The anterior cuticular wall of these coxae is equipped with a horizontal coxal apodeme. In the anterior region of the prosoma, the coxae are separated by a small sternum. This terminology is in accordance with previous morphological studies (Dunlop et al., 2012; Manton, 1977)

coxal apodeme: A horizontal apodeme on the anterior coxal wall. The distal region of the coxal apodeme forms the anterior articulation in the coxal-trochanter joint. Coxal apodemes are present in a variety of other arachnid taxa (Couzijn, 1976; Dillon, 1952; Grams et al., 2018; Palmgren, 1981; Runge & Wirkner, 2019; Shultz, 1999). Synonyms: coxalseptum (Frank, 1957); costa coxalis (Clarke, 1986; Manton, 1977).

coxal septum: The medial cuticle that delimits the paired coxae.

coxal walls: The anterior and posterior cuticle that delimits the coxae in the longitudinal axis.

dorsal apodeme of coxae II: A strong apodeme connected to the cuticle of coxae II. Synonyms: apodemal arch (Firstman, 1973); endosternit (Roewer, 1934).

rim (of podomere): The proximal edging of a podomere (e.g., trochanter).

3 | RESULTS

The following morphological description focuses on the coxae of the four legs posterior to the pedipalps. It expands on cuticular and muscular aspects of the coxae. The morphological description of the musculature considers the muscles which are attached between the coxa and the adjacent podomere (traversing muscles are not included here). The main part of the description refers to the morphology of G. granti. In addition to this, the skeletonmuscular morphology of the locomotory system was checked in other species (Gluvia dorsalis, Gluviopsilla discolor and Rhagodis obscurior) to corroborate the generalization to Solifugae.

The terminology used to describe the muscles is independent of homology and function (for a thorough discussion, see Richter & Wirkner, 2014). Thus, the numbering of the muscles represents the arrangement, but does not imply homology (see Runge & Wirkner, 2019, for detailed explanation of the labeling scheme).

3.1 | Cuticular morphology of postpedipalpal coxae

The coxae of the pedipalps and the four pairs of legs cover the ventral region of the prosoma (Figure 1). The coxae are trough-like podomeres (not cylindrical like the other podomeres), which are open on their dorsal and distal sides (Figure 1a,c,d). The anterior coxal wall of all legs is equipped with a horizontal coxal apodeme. At the distal end, this coxal apodeme forms the anterior condyle in each of the coxa-trochanter joints.

The coxae of the pedipalps and the four pairs of legs are widely fused. The segmental paired coxae are fused along the midline. Medially, the coxal spaces are delimited by vertical cuticular septa (Figures 1c,d and 2 with 3D-model). It is only between coxae II, that this cuticular septum does not span the complete length and leaves a transverse connection in the posterior region (Figure 1c). Furthermore, the coxae are fused in longitudinal direction forming two distinct coxal plates (Figures 1b; 2 with 3D-model). The anterior plate is composed of the coxae of the pedipalps, legs I and II
The posterior plate is composed of coxae III and IV (Figures 1b,c; 2 with 3D-model). Along the midline in both plates, the medial septa are continuous and form rigid longitudinal apodemes, respectively (Figures 1b,c and 2 with 3D-model). The consecutive coxae of pedipalps and legs I, as well as legs III and IV, are delimited by single coxal walls, respectively (Figures 1b–d and 2 with 3D-model). Only coxae II are separated anteriorly to coxae I and posteriorly to coxae III by distinct coxal walls (Figure 1b). The coxae II and III are separated by a transverse furrow that contains a transverse joint with two articulations (Figures 1a,b and 2 with 3D-model). The coxae II form a large dorsal apodeme (dacxII), which is formed by two pairs of strong processes—one pair is based on the anterior walls and the second pair on the posterior walls of coxae II (Figures 1a,c,d and 2 with 3D-model). These four ascending processes converge in the center of the prosoma into a quadruped arch with strong lateral ridges (Figure 1c,d).

3.2 | Musculature between coxa and the trochanter

The following section provides morphological descriptions of the musculature connecting the coxae with the (first) trochanter of the four postpedipalpal legs. Coxal muscles that pass the first trochanter are not considered here.

The main part of the description refers to the morphology of *G. granti*. The muscular morphology has also been observed in the
There are five muscles connected to trochanter I, of which the most dorsal muscle (M:cx-tr_2) extends steeply into the prosoma.

**M:cxI-tr_1**: The muscle is located in the anteroventral region of coxa I and covers the whole side in the proximal region of the coxa. The muscle is situated ventral to M:cxI-tr_3. The proximal attachment site is located at a median process of the cuticular wall separating the pedipalpal coxa from coxa I. The muscle crosses coxa I anterodistally to its distal attachment site. The distal attachment site is located at the posterodorsal rim of the trochanter, posterior to DiA:cxI-tr_3 (Figures 2 and 3b).

**M:cxI-tr_3**: The muscle is located in the dorsal region of coxa I. The muscle is situated ventral to M:cxI-tr_2. The proximal attachment site is situated anterior to PrA:cxI-tr_2. The distal attachment site is located at the anterodorsal edge of coxa II at the first process of the dorsal apodeme of coxae II. The muscle crosses coxa I anterodistally to its distal attachment site. The distal attachment site is located at the anterodorsal rim of the trochanter, closely associated with DiA:cxI-tr_2 (Figures 2 and 3c).

**M:cxI-tr_4**: The muscle is located in the dorsal region of coxa I. The muscle is situated anterior to M:cxI-tr_3. The proximal attachment site is located at the posterior wall of coxa I. The distal attachment site is located at the anteroventral rim of the trochanter, posterior to DiA:cxI-tr_1 (Figures 2 and 3a).

**M:cxI-tr_5**: The muscle is located in the posteroventral region of coxa I. The muscle is situated dorsal to M:cxI-tr_1. The proximal attachment site is fanned out in the anteroproximal region of coxa I. It extends from the anterior coxal side, to the median cuticle and to the ventral region of the coxa. The distal attachment site is located at the anterdorsal rim of the trochanter, anterior to DiA:cxI-tr_6 (Figures 2 and 3a).

In sum there are seven muscles distally connected to trochanter II. Two of these muscles (M:cxII-tr_2 and M:cxII-tr_7) extend steeply into the prosoma.

**M:cxII-tr_1**: The muscle is located in the ventral region of coxa II. The muscle is situated anterior to M:cxII-tr_6 and ventral to the coxal apodeme. The proximal attachment site is fanned out from the anterior median septum, to the ventroproximal region of the coxa toward the posterior wall of coxa II. The distal attachment site is located at the anteroventral rim of the trochanter, anterior to DiA:cxII-tr_6 (Figures 2 and 3a).
**FIGURE 3** Dorsal view of the prosoma (left side) of *Galeodes granti* showing the sclerotized cuticle and coxa-trochanter muscles (M:cx-tr) of the legs I–IV in different layers. Tergal cuticle and chelicerae are removed. Muscles are successively added from (a)–(d); (a) shows the most ventral muscles to (d) shows the most dorsal muscles. Color coding of the muscles designates serial homologs. Dorsal apodeme of coxae II colored in brown. Anterior body region is left. M:cxI-tr coxa-trochanter muscles of coxa I; M:cxII-tr coxa-trochanter muscles of coxa II; M:cxIII-tr coxa-trochanter muscles of coxa III; M:cxIV-tr coxa-trochanter muscles of coxa IV

**M:cxII-tr_2**: The muscle is located far dorsally in coxa II and extends steeply into the prosoma. The muscle is situated lateral to M:cxII-tr_7. The proximal attachment site is located at the lateral side the dorsal apodeme of coxae II, posterior to PrA:cxI-tr_2. From there the muscle extends anterolaterally to its distal attachment site. The distal attachment site is located at the anterodorsal rim of the trochanter, anterior to DiA:cxII-tr_2 (Figures 2 and 3d).

**M:cxII-tr_3**: The muscle is located in the dorsal region of coxa II. The muscle is situated ventral to M:cxII-tr_3 and lateral to M:cxII-tr_7. The proximal attachment site is located at the posterior process of the dorsal apodeme of coxae II. The muscle crosses the coxa anterolaterally to its distal attachment site. The distal attachment site is located at the anterodorsal rim of the trochanter, posterior to DiA:cxII-tr_2 (Figures 2 and 3c).

**M:cxII-tr_4**: The muscle is located in the central region of coxa II. The muscle is situated ventral to M:cxII-tr_3 and lateral to M:cxII-tr_7. The proximal attachment site is located posteriorly on the anterior process of the dorsal apodeme of coxae II. From there the muscle extends...
posteroventrally to its distal attachment site. The distal attachment site
is located at the posterior rim of the trochanter, closely associated with
DiA:cxII-tr_5 and DiA:cxII-tr_6 (Figures 2 and 3b).

M:cxII-tr_5: The muscle is located in the central region of coxa II.
The muscle is situated posterodorsal to M:cxII-tr_1, anterior to M:cxII-tr_6,
and posteroventral to both M:cxII-tr_4 and M:cxII-tr_7. The proximal
attachment site is located at the median cuticular septum. The distal
attachment site is located at the posterior rim of the trochanter,
closely associated with DiA:cxII-tr_4 and DiA:cxII-tr_6. Further, the
distal attachment site is posterior to DiA:cxII-tr_7 (Figures 2 and 3b).

M:cxII-tr_6: The muscle is located in the posterior region of coxa II.
The muscle is situated posterodorsal to M:cxII-tr_1 and posterior to
M:cxII-tr_5. The proximal attachment site is located at the posterior
wall of coxa II. The distal attachment site is located at the posterior
rim of the trochanter, closely associated with DiA:cxII-tr_4 and DiA:
cxII-tr_5 (Figures 2 and 3a).

M:cxII-tr_7: The muscle is located in the central region of coxa II
and extends steeply into the prosoma. The muscle is situated medial
to M:cxII-tr_2 and passes M:cxII-tr_3 anteriorly, M:cxII-tr_4 ventrally,
and M:cxII-tr_5 anterodorsally. The proximal attachment site is
located at the ventral side of the dorsal apodeme of coxae II. The dis-
tal attachment site is located at the ventral rim of the trochanter, pos-
terior to DiA:cxII-tr_1 and anterior to DiA:cxII-tr_5 (Figures 2 and 3c).

3.5 | Coxa III

In coxa III, there are five muscles connected to the trochanter. They
are mostly orientated in the horizontal plane.

M:cxIII-tr_1: The muscle is located in the ventral region of coxa III.
The muscle is situated mostly ventral to the coxal apodeme and
ventral to the muscles M:cxIII-tr_3, 4, 5. The proximal attachment site
is fanned out from the median cuticular septum to the posteroventral
side of coxa III. The distal attachment site is located at the
anteroventral rim of the trochanter (Figures 2 and 3a).

M:cxIII-tr_2: The muscle is located in the anterodorsal region of
coxa III. The proximal attachment site is located at dorsal edge of the
anterior coxa in close relation to the articulation between coxa II and
coxa III. The distal attachment site is located at the anteroventral rim
of the trochanter (Figure 2 and 3d).

M:cxIII-tr_3: The muscle is located in the dorsal region of coxa III.
The muscle is situated anterior to M:cxIII-tr_4 and posterior to M:
cxIII-tr_5. The proximal attachment site is located at the median cutic-
ular septum. The distal attachment site is located at the posterior rim
of the trochanter, anterior to DiA:cxIII-tr_5 and in close association
with DiA:cxIII-tr_4 (Figures 2 and 3b).

M:cxIII-tr_4: The muscle is located in the posterior region of
coxa III. The muscle is situated dorsal to M:cxIII-tr_1 and posterior to
M:cxIII-tr_3. The proximal attachment site is located in the proximal
region at the posterior wall of coxa III. The distal attachment site
is located at the posterior rim of the trochanter, closely associated
with DiA:cxIII-tr_3 and lies posterior to DiA:cxIII-tr_5 (Figures 2
and 3a).

M:cxIII-tr_5: The muscle is located in the anterior region of coxa III. The muscle is situated dorsal to M:cxIII-tr_1 and anterior to M:
cxIII-tr_3. The proximal attachment site is located at the coxal
apodeme and dorsally at the anterior wall of coxa III. The distal attach-
ment site is located at the posteroventral rim of the trochanter, an-
terior to DiA:cxIII-tr_3 (Figures 2 and 3c).

3.6 | Coxa IV

Coxa IV contains four muscles that attach to the trochanter. They are
mostly orientated in the horizontal plane.

M:cxIV-tr_1: The muscle is located in the anterior and
anteroventral region of coxa IV, ventral to the coxal apodeme. The
muscle is situated anterior and anteroventral to M:cxIV-tr_4. The
proximal attachment site is fanned out from the anterior medium sep-
tum to the ventral side of the coxa. The distal attachment site is
located at the anterior rim of the trochanter (Figure 3a).

M:cxIV-tr_2: The muscle is located in the faranterodistal region
of the dorsal coxa IV. The proximal attachment site is located at the
anterodorsal side of the coxa, close to the distal margin. The distal
attachment site is located at the anterodorsal rim of the trochanter
(Figures 2 and 3d).

M:cxIV-tr_3: The muscle is located in the posterodorsal region
of coxa IV. The muscle is situated posterodorsal to M:cxIV-tr_4. The
proximal attachment site is located posterodorsally at the median
coxal septum. The distal attachment site is located at the post-
erodorsal rim of the trochanter, dorsal to DiA:cxIV-tr_4 (Figures 2
and 3b).

M:cxIV-tr_4: The muscle is located in the posterior region of coxa
IV. The muscle is situated anteroventral to M:cxIV-tr_3. The proximal
attachment site is located at the median cuticular septum. The distal
attachment site is located at the posteroventral rim of the trochanter,
ventral to DiA:cxIV-tr_3 (Figures 2 and 3c).

4 | DISCUSSION

Although quite a number of morphological studies from the latter
half of the twentieth century dealt with intrinsic leg musculature of
Solifugae (e.g., Manton, 1977; Shultz, 1989; van der van der
Hammen, 1984), the most proximal region of the legs received less
attention. Yet, this particular body region shows some notable
modifications in Solifugae, that is, immobile fused coxae and the
loss of the endosternite (Firstman, 1973). The consequences of
these modifications on the musculature in this body region are not
easy to comprehend since the hitherto existing descriptions of this
complex muscular system are contradictory (Kittary, 1848;
Roewer, 1934). Therefore, we present here detailed 3D-
morphological insights in the proximal leg musculature of G. granti
on the basis of μCT-scans, which are generalized here for Solifugae
due to the consideration of three further species (G. dorsalis,
G. discolor and R. obscurior).
The segmental comparison highlights a varying number and composition of coxa-trochanter muscles in the respective coxae. Serial homology of the coxa-trochanter muscles is determined with regard to the position and the spatial relationships of their proximal and distal attachment sites and also the spatial relationship of the whole muscles. These points contribute to the morphological pattern, which is compared between the different coxae (see Szucsich & Wirkner, 2007). Serial homologous muscles are listed and matched in Figure 4 and color-coded throughout the illustrations.

In the following, the skeletomuscular morphology of the coxal region is compared to other arachnid taxa to elucidate the modifications in Solifugae. Because of the fused coxae, the coxa-trochanter joint is the most proximal joint to permit leg movement relative to the body. This distal shift of leg movement has extensive effects on the morphology of the locomotory system in the transitional region between the prosoma and the legs but has rarely been discussed in Arachnida.

In contrast to other Arachnida, an endosternite is missing in Solifugae (Firstman, 1973). The dorsal apodeme of coxae II is, instead, in a comparable position (Figure 1c,d) (Firstman, 1973; Kittary, 1848; Millot, 1949; Pocock, 1902; Schinkewitsch, 1895). This apodeme is formed by dorsal processes composed of the dorsal edges of coxae II. This is indicated by the PrA:cxII-tr_2,3,4,7, which are located at the dorsal apodeme of coxae II. Compared to the other coxae, the corresponding proximal attachment sites (PrA) are located at the dorsal edges (Figures 2 with 3D-model; 3b–d; and 4).

The spatial correspondence between the dorsal apodeme of coxae II in Solifugae (also termed apodemal arch) and the endosternite in other arachnids has been observed by Firstman (1973): "This arch passes over the dorsal surface of the subesophageal ganglionic mass, where it serves as a functional analogue of the mesodermal endosternite." However, our results allow us to extrapolate more than the simple spatial analogies of the dorsal apodeme of coxae II and the endosternite. In coherence with the absent endosternite and the fixed coxae, Solifugae also lack the endosterno-coxal muscles. Therefore, the trochanter is the most proximal and moveable podomere that is moved by the coxa-trochanter muscles. Since they realize the movement of the legs relative to the prosoma, the coxa-trochanter muscles in Solifugae are considered here (from a functional point of view) as secondary extrinsic musculature. Thus, the dorsal apodeme of coxae II is the structure where secondary extrinsic muscles have their proximal attachment site, comparable to the endosternite of other arachnids (Palmgren, 1978; Runge & Wirkner, 2019; Shultz, 1993, 1999, 2007a). In Solifugae, however, this correspondence concerns only some of the secondary extrinsic muscles of coxae I and II. Particularly the proximal attachment sites PrA:cxI-
tr_2,3 and PrA:cxII-tr_2,3,4,7 are located at the dorsal apodeme of coxae II. Therefore, these muscles have a steeper position in the prosoma and an increased length compared to the remaining coxa-trochanter muscles in G. granti (Figures 2 and 5). Such a steep position can also be found in endosterno-coxal muscles in other Arachnida and depends, obviously, on the position of the endosternite (Figure 5).

Apart from the endosternite and the extrinsic muscles, further modifications concern the downsized sternum that does not interact with moveable podomeres in Solifugae. In arachnids, moveable coxae are frequently correlated with the presence of sternal plates; for instance, in Amblypyggi, Araneae, Palpigradi, and Uropygi (compare characters 3, 4, 21 in Shultz (1990)). In Solifugae, however, the fused coxae form two rigid ventral plates providing the counterparts for the most proximal mobile podomere, the trochanter and therefore correspond to the sternum in other Arachnida (Figure 5). Compared to other arachnid taxa, the correspondence in coxa morphology of Pseudoscorpiones and Solifugae is brought up where they meet along midline (Shultz, 2007b). Both taxa are frequently regarded as sistergroups (=Haplonemata/Apatellata) (Giribet, Edgecombe, Wheeler, & Bablitt, 2002; Shultz, 1990, 2007b; van der Hammen, 1989; Weygoldt & Paulus, 1979; Wheeler & Hayashi, 1998). Nevertheless, immobilized coxae are also present in Scorpionidae, Rininulei, some Acari and some Opilionidae (Laniatores) (Shultz, 1990, 2007a, 2007b). Considering the presence of mobile coxae in the other arachnid taxa and in Xiphosura, the immobilized condition is assumed to have evolved several times independently within Arachnida. However, the evolutionary changes on the skeletomuscular morphology of fixed coxae in arachnid taxa have not been studied in a comprehensive approach.

In conclusion, the whole proximal part of the locomotory system in Solifugae is the result of substantial evolutionary modifications with regard to the endosternite, endosterno-coxal muscles, and the sternum compared to other Arachnida. From a morphological and functional point of view, the integration of primary intrinsic structures into the prosoma (Figure 5) resulted in a boundary shift of the prosoma and the legs from the prosoma-coxa joints to the coxa-trochanter joints. Through these evolutionary transformations, the legs have gained a stable, articulated joint in the most proximal region of the leg, which might be advantageous for agile locomotion (Punzo, 1998). Comparable evolutionary tendencies are described within Araneae where a stable articulation evolved in the sternocoxal joint and has been primarily discussed in the light of hemolymph pressure generation (Runge & Wirkner, 2019). This highlights relevance for further functional and evolutionary studies of the most proximal leg region where the movement against the body is realized.

ACKNOWLEDGMENTS

The authors would like to thank Bastian-Jesper Klußmann-Fricke (Universität Rostock) for providing a μCT scan of G. dorsalis. For technical support, thanks are due to Stephan Scholz (Universität Rostock). Christoph Hörweg provided access to the collection of the Naturhistorisches Museum Wien, Austria (NHMW) and loaned collection material for μCT-scans. Helen Johnson improved the English text, which is gratefully acknowledged. The authors thank the two anonymous reviewers for their valuable comments, which helped to improve the manuscript. Jens Runge received a scholarship from the Landesgraduiertenförderung Mecklenburg-Vorpommern. Christian S. Wirkner received funding from the Deutsche Forschungsgemeinschaft (WI 3334/5-1). The μCT machines (DFG INST 264/38-1 FUGG, DFG INST 264/130-1 FUGG) were jointly sponsored by the Deutsche Forschungsgemeinschaft and the Land Mecklenburg-Vorpommern.

AUTHOR CONTRIBUTIONS

Jens Runge: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; resources; visualization; writing-original draft; writing-review and editing. Christian Wirkner: Conceptualization; data curation; formal analysis; funding acquisition; investigation; project administration; supervision; validation; visualization; writing-original draft; writing-review and editing.

CONFLICT OF INTEREST

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

The image stack of Galeodes granti is deposited in Morph-D-Base (https://www.morphbase.de/).

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