

RESEARCH ARTICLE

Extrinsic and intrinsic musculature of the raptorial forelegs in Mantodea (Insecta) in the light of functionality and sexual dimorphism

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Abstract

Prehensile raptorial forelegs are prey capturing and grasping devices, best known for praying mantises (Mantodea) within insects. They show strong morphological and behavioral adaptations toward a lifestyle as generalist arthropod predators. In the past, few species of Mantodea were investigated, concerning morphological variability of the raptorial forelegs. Especially the knowledge of foreleg anatomy in the light of functional and comparative morphology is scarce. Our comparative approach is based on the, for arthropods very common, “female-biased sexual size dimorphism” (SSD) that occurs in almost every Mantodea species. Within Mantodea, this SSD is likely leading to a shift of the exploited ecological niche between male and female individuals due to changes in, for example, the possible prey size; which might be reflected in the chosen ecomorphs. In this context, we analyzed the musculature of the raptorial forelegs of female and male specimens in five different species with varying SSD, using high-resolution microcomputed tomography and dissection. We were able to confirm the presence of 15 extrinsic and 15 intrinsic muscles—including one previously undescribed muscle present in all species. Thus, presenting a detailed description and illustrative three-dimensional anatomical visualization of the musculature in Mantodea. Interestingly, almost no observable differences were found, neither between species, nor between the sexes. Furthermore, we homologized all described muscles, due to their attachment points, to the comprehensive nomenclature established by Friedrich and Beutel (2008), discussed potential functionality of the muscles and possible homologies to the neuropteran *Mantispa styriaca* (Büsse et al., 2021) and the newly introduced leg nomenclature by Aibekova et al. (2022). By elucidating the anatomy, particularly in the context of functionality and SSD, our results complement previous knowledge of the raptorial forelegs, and facilitate a better understanding of the underlying biomechanical system of the predatory strike, and ultimately, a future comparison to other insect taxa.

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KEYWORDS

eco-morphology, functional morphology, praying mantis, prey capture, prothoracic legs, raptorial appendages, sexual size dimorphism (SSD)

1 | INTRODUCTION

Praying mantises (Mantodea) with more than 2500 known species are mostly generalist arthropod predators (Otte et al., 2022; Schwarz & Roy, 2019), and best known for their prominent prey capturing and grasping devices, the prehensile raptorial forelegs (Brannoch et al., 2017; Loxton & Nicholls, 1979; Prete, 1999; Wieland, 2013).

Mantodeans are behaviorally, neurologically, and morphologically adapted to their lifestyle as an ambush predator (Brannoch et al., 2017; Corrette, 1990; Iwasaki, 1990; Nityananda et al., 2018; Prete et al., 1999; Roy, 1999; Yamawaki et al., 2011).

The habitus of a mantis (e.g., *Hierodula majuscula* (TINDALE, 1923), Figure 1) features a strongly elongated prothorax, movably connected to the pterothorax, allowing high flexibility while aiming and

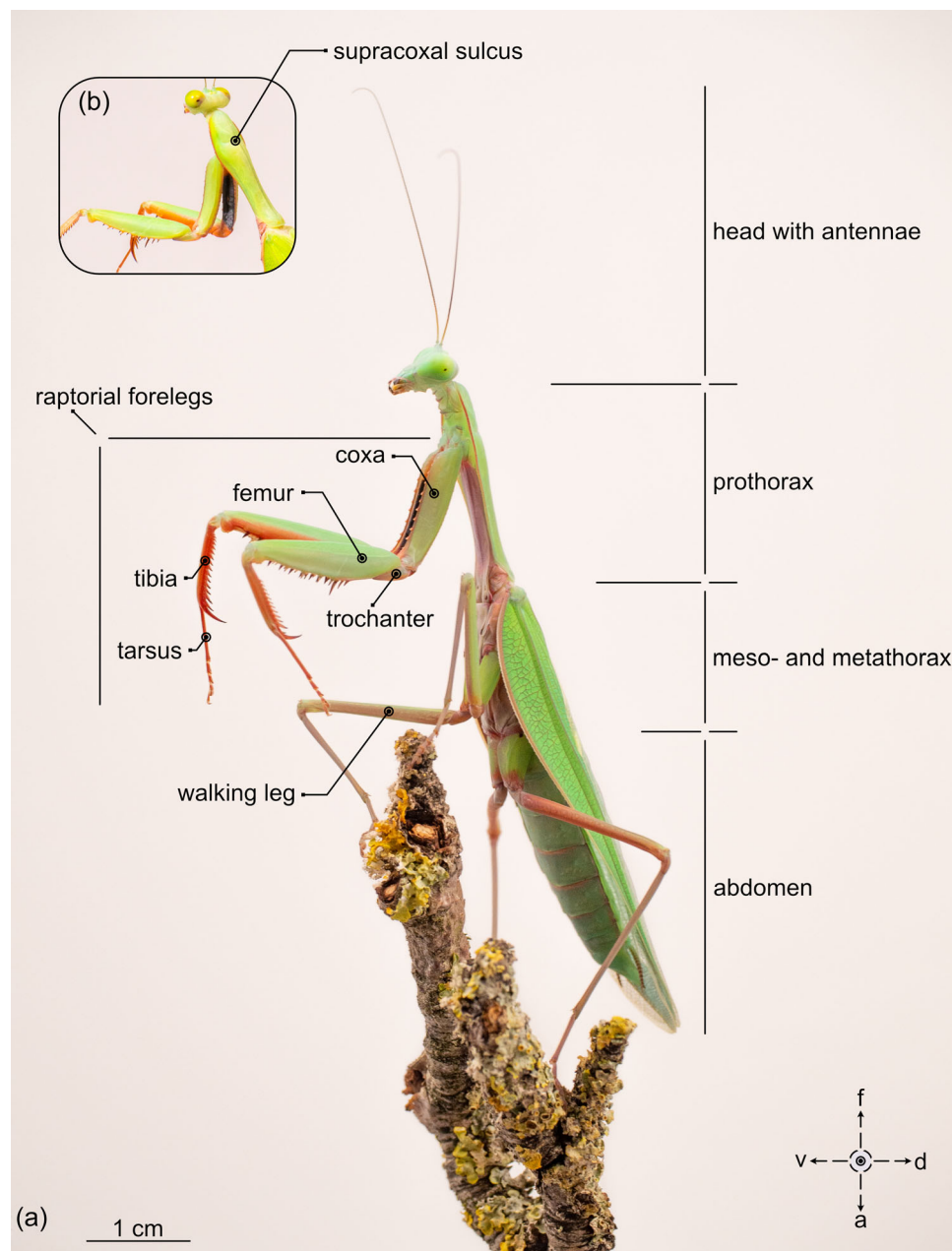


FIGURE 1 Adult, male *Hierodula majuscula*, lateral view (a) and latero-dorsal view (b). a, abdominal; d, dorsal; f, frontal; v, ventral.

striking for prey (Roy, 1999; Wieland, 2013). The pronotum is separated into the anterior prozone and the posterior metazone by the internal transversal ridge, visible as the prominent supracoxal sulcus from dorsal view (Figure 1b), that supports, together with the pleural ridge and furcasternum, the strong musculature of the forelegs (Brannoch et al., 2017; Frantsevich, 1998; Roy, 1999; Wieland, 2013). These prominent raptorial forelegs are characterized by a greatly elongated coxa and femur, with femur and tibia both equipped with a row of spines along the anterior and posterior ventral face, arranged opposed to each other, terminating in an arched apical tibial spur (Brannoch et al., 2017; Roy, 1999; Wieland, 2013). Additionally, an enlarged discoidal spine is located at the proximal end of the row of spines on the femur (Brannoch et al., 2017; Loxton & Nicholls, 1979).

This spination can differ due to interspecific as well as intersexual variations. Such a difference between female and male specimens, in general, can be driven by sex-specific selective pressure, as well as influenced by ecological factors (De Lisle, 2019; Li & Kokko, 2021; Shine, 1989; Slatkin, 1984) and is a widely spread phenomenon throughout Arthropoda (Mori et al., 2017). In insects, the magnitude of differences due to sexual dimorphism (SD) varies from slightly noticeable up to enormously diverse characteristics (Mori et al., 2017). Interestingly, a female-biased sexual size dimorphism (SSD) occurs more frequently, whereas a male-biased SSD is rather uncommon (Esperk et al., 2007; Mori et al., 2017). Furthermore, as the growth within one larval instar is proposed to be physiologically limited (Hutchinson et al., 1997), females commonly develop through an increased number of larval instars to achieve an even larger body size in comparison to males (Esperk et al., 2007; Sephton & Hynes, 1982; Mori et al., 2017); which positively correlates with fecundity (Esperk et al., 2007; Mori et al., 2017; Rutowski, 1997; Shine, 1989). Males on the other hand, develop more rapidly for benefits in regard to: intrasexual competition, female choice, or mating partner localization (Boisseau et al., 2022; Kawano, 2006; Mori et al., 2017; Rutowski, 1997; Shine, 1989). The mating success can further be increased, by deploying special mating tactics to, for example, avoid sexual cannibalism (Burke & Holwell, 2021). Here, males often show rather cautious and risk-minimizing strategies like: nuptial gifts or preference of currently feeding females in spiders (Fromhage & Schneider, 2005; Prokop & Maxwell, 2009) or avoiding detection by moving in a stealthy manner like the praying mantis species *Pseudomantis albofimbriata* (Stål, 1860) (Barry et al., 2008). In contrast, the highly cannibalistic springbok mantis *Miomantis caffra* (Saussure, 1871) (Figure 2i,j) shows a rather coercive premating tactic: males involve females in a physical battle, leading to a reduction in cannibalistic rate for a winning male and increasing the chances of mating success (Burke & Holwell, 2021).

Within Mantodea, the typical female-biased SSD occurs in almost every species (Edmunds & Brunner, 1999; Fairbairn, 2005; Roy, 1999; Svenson et al., 2016; Wieland, 2013) and is expressed through different external morphology (Figure 2) and/or behavioral traits (Svenson et al., 2016; Burk & Holwell, 2021). Although in most

species of mantises the expression of the SSD is slightly noticeable (e.g., *H. majuscula* Figure 2a,b), in a few species a considerable difference in size as well as behavior can be observed (e.g., *Hymenopus coronatus* (Olivier, 1792), Figure 2g,h; Roy, 1999; Svenson et al., 2016). For orchid mantises, Svenson et al. (2016) further suggested ecological niche exploitation as an additional reason for an extremely pronounced SSD. Here, juvenile animals use visual as well as chemical mimicry during the ontogenetic development to actively lure in prey, increasing hunting success (Mizuno et al., 2014; O'Hanlon et al., 2013, 2014). When reaching adulthood, males remain smaller, keeping an increased mobility and transitioning to an ambush predator lifestyle (Svenson et al., 2016). Female orchid mantises however, supported by their massively increased size, stick to a floral simulation strategy (Svenson et al., 2016), thereby expanding their access to a variety of larger pollinating insects as prey items (O'Hanlon et al., 2014). Thus, both sexes show a different prey size preference and hunting strategies, leading to the question if the prominent differences of external features and behavior are reflected in the internal anatomy.

Previously, only few studies focused on the internal morphology of the prothorax and the forelegs of adult Mantodea, including first approaches on functional descriptions of the muscular set-up: Maki (1938) examined *Hierodula patellifera*, Levereault (1938) *Stagmomantis carolina* (Johansson, 1763), Gray and Mill (1985) *Hierodula membranacea* Burmeister, 1838, and Frantsevich (1998) *Mantis religiosa* (Linnaeus, 1758). While Levereault (1938) and Gray and Mill (1985) studied both extrinsic and intrinsic musculature, Maki (1938) and Frantsevich (1998) focused solely on extrinsic musculature. The latter compared his results to *Ranatra* (Heteroptera) and *Mantispa* (Neuroptera) while Maki (1938) compared his results to a broad variety of other insect groups. All studies, except Maki (1938), used the nomenclature for extrinsic musculature introduced by Levereault (1938), but descriptions for the same muscles did not always match. Friedrich and Beutel (2008) attempted to homologize Levereaults (1938) results in context of their newly introduced thoracic muscle nomenclature, but reported uncertainties and did not provide the associated link to Levereaults (1938) descriptions. Overall, the existing information is partially incomplete and ambiguous between the different studies, leaving a substantial gap of knowledge about the present morphology as well as a function of the muscular set-up. More recently, studies focusing on the anatomy of the insect legs are: Büsse et al. (2021) on the prehensile raptorial forelegs in *Mantispa styriaca* (Poda, 1761), while Aibekova et al. (2022) focused on the worker ant *Formica rufa* (Linnaeus, 1761). Alongside descriptions of the present musculature, Aibekova et al. (2022) further proposed a first approach of an updated terminology for intrinsic musculature following the suggestions of Friedrich and Beutel (2008) for the thorax musculature in insects.

In this study, we focused on five phylogenetically distant species of Mantodea (Svenson & Whiting, 2009)—two with a weakly pronounced SSD (*H. majuscula*, Figure 2a,b, and *Phyllocrania paradoxa*, Burmeister, 1838, Figure 2c,d) and two with a prominent

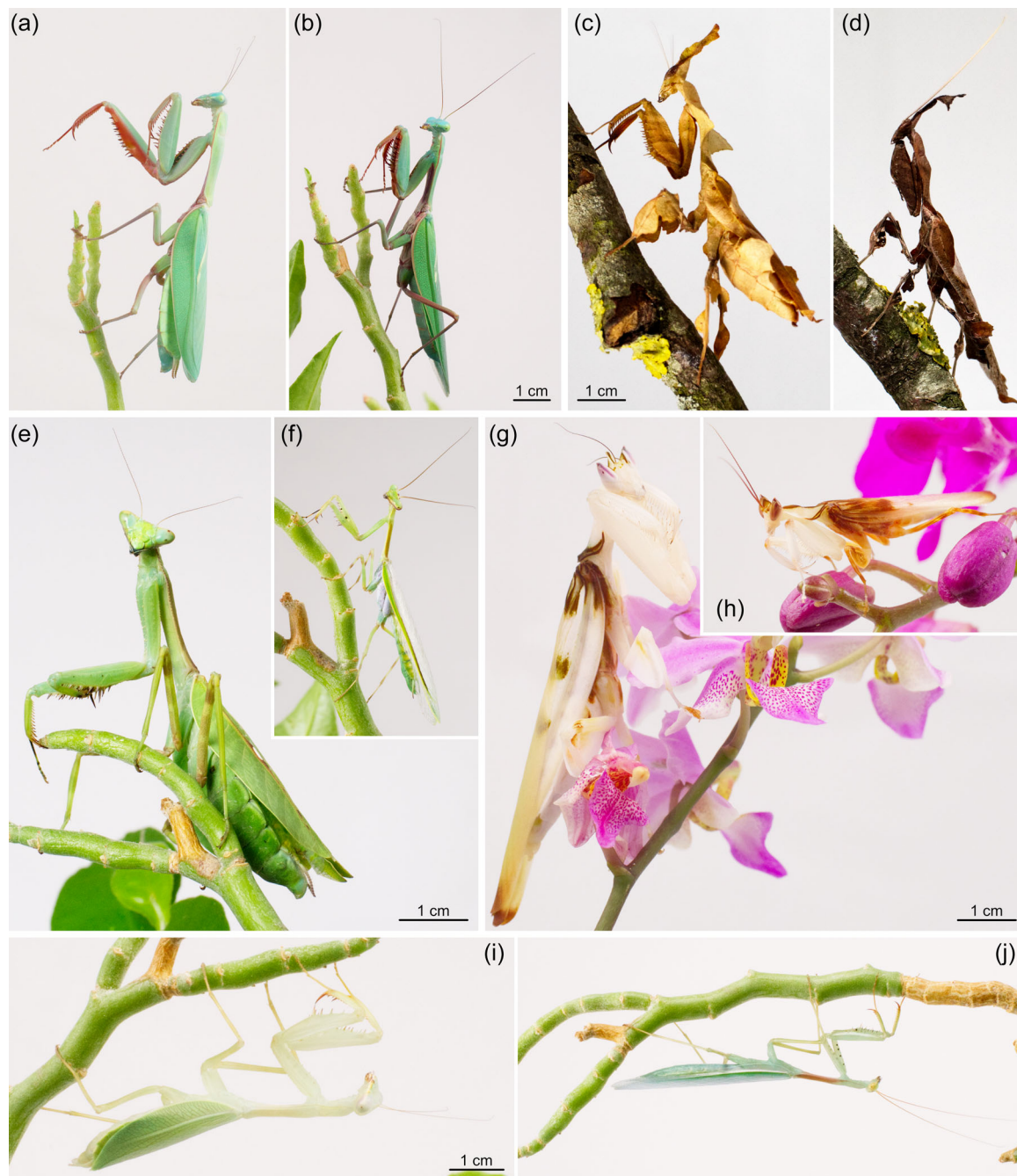


FIGURE 2 Adult, female (a) and male (b) *Hierodula majuscula*, adult female (c) and male (d) *Phyllocrania paradoxa*, adult female (e) and male (f) *Pseudoxyps perpulchra*, adult female (g) and male (h) *Hymenopus coronatus* and adult female (i) and male (j) *Miomantis caffra* in lateral view. Images of the same species have a shared scale bar.

SSD (*H. coronatus* Figure 2g,h, and *Pseudoxyps perpulchra*, WESTWOOD, 1889, Figure 2e,f). Furthermore, we included *M. caffra* (Figure 2i,j), as an example of a specialized premating behavior in praying mantises. Using microcomputed tomography in combination with dissection to compare number of muscles and attachment points, we aimed to reevaluate the muscle set-up in the prehensile raptorial forelegs from a functional perspective, while additionally identifying possible differences related to the commonly occurring

female-biased SSD within praying mantises. Presenting a complete description of all extrinsic and intrinsic muscles of the raptorial forelegs in praying mantises, we further elucidate interspecific as well as intersexual differences, including remarks regarding leg anatomy in species of Hymenoptera (Aibekova et al., 2022), Neuroptera (Büsse et al., 2021) and Blattodea (Carbonell, 1947); with a first attempt to adapt the newly introduced leg nomenclature by Aibekova et al. (2022).

2 | MATERIALS AND METHODS

Female and male specimens of the praying mantis species *H. majuscula*, *P. paradoxa*, *H. coronatus*, *P. perpulchra*, and *M. caffra* were obtained from private breeders or online shops in different larval stages, and raised in Kiel until adulthood.

Specimens (1 specimen of each sex, for each species respectively: 10 animals in total) for microcomputed tomography (μ CT) were euthanized with CO₂ before fixation in Bouin's solution (=Duboscq-Brasil, Romeis, 1989), rinsed and stored in 70% ethanol. Before the scan, the specimens were taken through an ascending ethanol series (70%, 80%, 90%, 95%, 99%) and subsequently dried, using a fully automatic critical point dryer (Leica EM CPD300, Leica). All scans were carried out using a Skyscan[®] 1172 micro-CT (Bruker micro-CT; CT-scanner settings: X-ray source: 40 kV, 250 μ A, 360° rotation, 0,2 rotation step, 10 frame averaging and 10 random movement; image pixel size: *H. majuscula* (female and male: 6,67 μ m), *H. coronatus* (female: 5,82 μ m; male: 3,95 μ m), *M. caffra* (female: 5,35 μ m; male: 5,09 μ m), *P. perpulchra* (female: 6,69 μ m; male: 4,89 μ m) and *P. paradoxa* (female: 4,35 μ m; male: 4,08 μ m), reconstructed in Nrecon[®] 1.0.7.4 (Bruker micro-CT), processed with Amira[®] 6.2 (Thermo Fisher Scientific) and subsequently visualized using the open-source 3D creation suite Blender 2.82a (Blender Foundation) and Affinity Designer (Serif). Additional specimens were freshly frozen at -70°C and dissected to confirm muscle attachment points, using a stereomicroscope, forceps and micro scissors.

In the following descriptions, the nonmoving end of each muscle will be called the point of origin (O) and its moving end will be called the point of insertion (I). Further important information is listed under characteristics (C). Extrinsic muscle names follow the nomenclature introduced by Friedrich and Beutel (2008), and intrinsic muscle names follow the nomenclature by Gray and Mill (1985). Cuticle structures are described, using the updated nomenclature introduced by Brannoch et al. (2017), supplemented by the work of Snodgrass (1935), Gray and Mill (1985), Beutel et al. (2013), and Wieland (2013) —all used abbreviations are shown in Table 1. Additionally, and to cover the most recent studies, terms for extrinsic musculature used by Gray and Mill (1985), and terms and numbering used by Frantsevich (1998) were synonymized with the nomenclature from Friedrich and Beutel (2008) and are listed in Table 2. Our results concerning intrinsic musculature were homologized to the results of the investigations in *M. styriaca* made by Büsse et al. (2021) and in *F. rufa* workers made by Aibekova et al. (2022), and are presented in Table 3.

3 | RESULTS

The general habitus as well as the sexual dimorphism can be seen in Figures 1 and 2. For an overview of sclerites and cuticular structures, see Figure 3. Generally, conditions present in the adult female *H. majuscula* are illustrated in three-dimensional visualizations and used as a reference. Only if characteristics (e.g., points of attachment etc.)

TABLE 1 Abbreviations used.

Term	Abbreviation
Accessory trochanteral flexor	latrf
Coxal trochanteral apodeme	lctra
Coxal trochanteral extensor	lctre
Distal tibial pretarsal flexor	ldtipf
Dorso-ventral muscle	dvm
Femoral pretarsal flexor	lfpf
Femoral reductor a	lfra
Femoral reductor b	lfrb
Femoral tibial flexor a (pennate)	lftifa
Femoral tibial flexor b (parallel)	lftib
Pleuro-coxal muscle	pcm
Posterior accessory trochanteral extensor	lpatre
Proximal tibial pretarsal flexor	lptipf
Sterno-coxal muscle	scm
Tarsal extensor	ltae
Tarsal flexor	ltaf
Tibial extensor	ltie
Tibial extensor apodeme	ltiea
Tergo-pleural muscle	tpm
Trochanteral extensor apodeme	ltrea
Trochanteral flexor	ltrf
Trochanteral tibial flexor	ltrtif

are differing for certain muscles in the other investigated species, it is additionally mentioned. In total, 15 extrinsic and 15 intrinsic muscles were found in adult female and male specimens of all investigated species. The extrinsic muscle Idvm20 could not be homologized with existing descriptions and was therefore given a new name according to the established nomenclature of Friedrich and Beutel (2008).

Extrinsic musculature of the raptorial forelegs (Figures 4 and 5).

Dorso-ventral musculature

Idvm13—M. pronoto-trochantinalis anterior

O: Prothoracic episternum.

I: On an apodeme of the anterior procoxal rim.

Idvm14—M. pronoto-trochantinalis

O: With three prominent strands: at median region of the prozone of the pronotum, anterior of the supracoxal infolding, at the median part of tergum, close to and posteriorly of the supracoxal infolding and at the median area of the metazone of the pronotum.

I: Trochantin, posterior of Idvm13.

Idvm15—M. pronoto-trochantinocoxalis

O: Lateral part of the prozone of the pronotum.

I: On an apodeme of the anterior procoxal rim.

TABLE 2 Homologized prothoracic, extrinsic muscle nomenclature from Gray and Mill (1985) with Friedrich and Beutel (2008).

Name according to Friedrich and Beutel (2008)	Abbreviation	Name following Gray and Mill (1985)	Name following Frantsevich (1998)
<i>Dorso-ventral musculature</i>			
M. pronoto-trochantinalis anterior	ldvm13	Pleural coxal promotor	7, 8
M. pronoto-trochantinalis posterior	ldvm14	Anterior tergal coxal adductor; intermediate tergal coxal adductor; posterior tergal coxal adductor	2, 3, 5
M. pronoto-trochantinocoxalis	ldvm15	Tergal coxal promotor	1
M. pronoto-coxalis anterior	ldvm16	Tergal posterior coxal rotator; posterior coxal remotor	19
M. pronoto-coxalis posterior	ldvm17	Lateral coxal remotor	18
M. pronoto-coxalis lateralis	ldvm18	Posterior medial coxal abductor	11, 13
M. pronoto-trochanteralis	ldvm19	Anterior tergal trochanteral extensor; intermediate tergal trochanteral extensor; posterior tergal trochanteral extensor	25, 26, 27
M. pronoto-coxalis medialis (following established nomenclature)	ldvm18	-	-
<i>Pleuro-coxal musculature</i>			
M. propleuro-coxalis superior	lpcm4	Intermediate coxal abductor; posterior lateral coxal abductor	12
M. propleuro-coxalis posterior	lpcm6	-	-
M. propleuro-trochanteralis	lpcm8	Pleural trochanteral extensor	23
<i>Sterno-coxal musculature</i>			
M. profurca-coxalis anterior	lscm1	Sternal coxal adductor	22
M. profurca-coxalis lateralis	lscm4	Anterior coxal rotator	6
<i>Tergo-pleural musculature</i>			
M. pronoto-apodemalis anterior	ltpm4	Anterior coxal abductor	10
M. pronoto-apodemalis posterior	ltpm5	Pleural coxal abductor	10

ldvm16—M. pronoto-coxalis anterior

O: Postero-lateral part of the metazone of the pronotum.

I: In a tendon, connected to the postero-lateral procoxal rim.

C: Most posterior foreleg muscle, inserts posterior of ldvm17.

ldvm17—M. pronoto-coxalis posterior

O: Lateral part in the middle region of the metazone of the pronotum.

I: In a tendon, connected to the postero-lateral procoxal rim.

C: Inserts anterior of ldvm16.

ldvm18—M. pronoto-coxalis lateralis

O: Postero-median region of the metazone of the pronotum.

I: Anterolateral procoxal rim, antero-median of the lpcm4.

ldvm19—M. pronoto-trochanteralis

O: With three strands: lateral of the anterior area of the metazone of the pronotum, at the median part of the metazone of the pronotum, and at the metazone of the pronotum, lateral and very close to the ldvm14.

I: Trochanteral extensor apodeme.

C: Together with the lpcm8 at the trochanteral extensor apodeme.

ldvm20—M. pronoto-coxalis medialis

O: Postero-median region of the metazone of the pronotum, anterior to ldvm18 and posterior to ldvm16.

I: Anterolateral procoxal rim and same attachment point as lscm4.

C: Newly described muscle for Mantodea, without known homolog in other insects (see Friedrich & Beutel, 2008).

Pleuro-coxal musculature

lpcm4—M. pleuro-coxalis superior

O: Lateral region of the metazone of the pronotum, just posterior of the ltpm4.

I: Lateral procoxal rim, posterior of the lscm4.

lpcm6—M. propleuro-coxalis posterior

O: Dorsal area of prothoracic lateral infolding.

I: Latero-medial procoxal rim.

lpcm8—M. propleuro-trochanteralis

O: On the ventral area of the prothoracic lateral infolding.

I: Trochanteral extensor apodeme.

C: Together with the ldvm19 at the trochanteral extensor apodeme.

Sterno-coxal musculature

TABLE 3 Results of intrinsic musculature from *Hierodula majuscula* linked to the results in *Formica rufa* workers made by Aibekova et al. (2022) and in *Mantispa styriaca* (PODA, 1761) made by Büsse et al. (2021).

Name following Gray and Mill (1985)	Abbreviation	Name following Büsse et al. (2021)	Name following Aibekova (2022)
Pleural trochanteral extensor	M. propleuro-trochanteralis (lpcm8)	lpcm8	lpcm8
<i>Coxa</i>			
Accessory trochanteral flexor	latrf	-	M. procoxa-trochanteralis posterior (lctm2)
Coxal trochanteral extensor	lctre	M. pleura-trochanteralis (M20)	M. procoxa-trochanteralis medialis (lctm3)
Posterior accessory trochanteral extensor	lpatre	M. coxa-trochanteralis medialis (M21)	
Trochanteral flexor	ltrf	M. Coxa-trochanteralis lateralis (M22)	M. procoxa-trochanteralis anterior (lctm1)
<i>Trochanter</i>			
Femoral reductor a	lfra	M. reductor femoris (M23)	M. trochantero-femoralis (ltfm1)
Femoral reductor a	lfrb		
Trochanteral tibial flexor	ltrtif	-	-
<i>Femur</i>			
Tibial extensor	ltie	M. levator tibiae (M25)	M. femuro-tibialis dorsalis (lftm1)
Femoral pretarsal flexor	lfpf	-	M. femuro-pretarsalis (lfpm1)
Femoral tibial flexor (pennate)	lftifa	M. depressor tibiae a (M24a)	M. femuro-tibialis ventralis (lftm2)
Femoral tibial flexor (parallel)	lftifb	M. depressor tibiae b (M24b)	
<i>Tibia</i>			
-	-	M. depressor tibiae (24c)	-
Distal tibial pretarsal flexor	ldtipf	-	M. tibio-basitarsalis anterior (ltbm2)
Proximal tibial pretarsal flexor	lptipf	-	M. tibio-pretarsalis (ltipm1)
Tarsal extensor	ltae	-	M. tibio-basitarsalis ventralis (ltbm1)
Tarsal flexor	ltaf	M. depressor pretarsi (M26)	M. tibio-basitarsalis posterior (ltbm3)

lscm1—M. profurca-coxalis anterior

O: Most anterior part of the profurcal stem.

I: Antero-medial part of ventral procoxal rim.

lscm4—M. profurca-coxalis lateralis

O: Tip of the furca sternite.

I: Anterolateral procoxal rim and same attachment point as ldvm20.

Tergo-pleural musculature

ltpm4—M. pronoto-apodemalis anterior

O: Lateral region of the metazone of the pronotum, just posterior to the supracoxal infolding.

I: Anterolateral procoxal rim, at the base of a large apodeme of the procoxal rim.

ltpm5—M. pronoto-apodemalis posterior

O: Anterior region of prozone of the pronotum, posteromedial of the ltpm4.

I: At the distal region of the large lateral apodeme of the procoxal rim, posterior of the ltpm4.

Intrinsic musculature of the raptorial forelegs (Figures 6 and 7).

Coxa

latrf—Accessory trochanteral flexor

O: Vento-posterior area of the distal part of the coxa, posteromedial of the posterior accessory trochanteral extensor.

I: Trochanteral flexor apodeme.

lctre—Coxal trochanteral extensor

O: Ventral to postero-ventral area over nearly the whole coxa.

I: Distal part of the extensor apodeme.

C: Runs together with lpcm8 and ldvm19.

lpatre—Posterior accessory trochanteral extensor

O: Vento-posterior area of the distal part of the coxa.

I: Trochanteral extensor apodeme, posterior of the coxal trochanteral extensor.

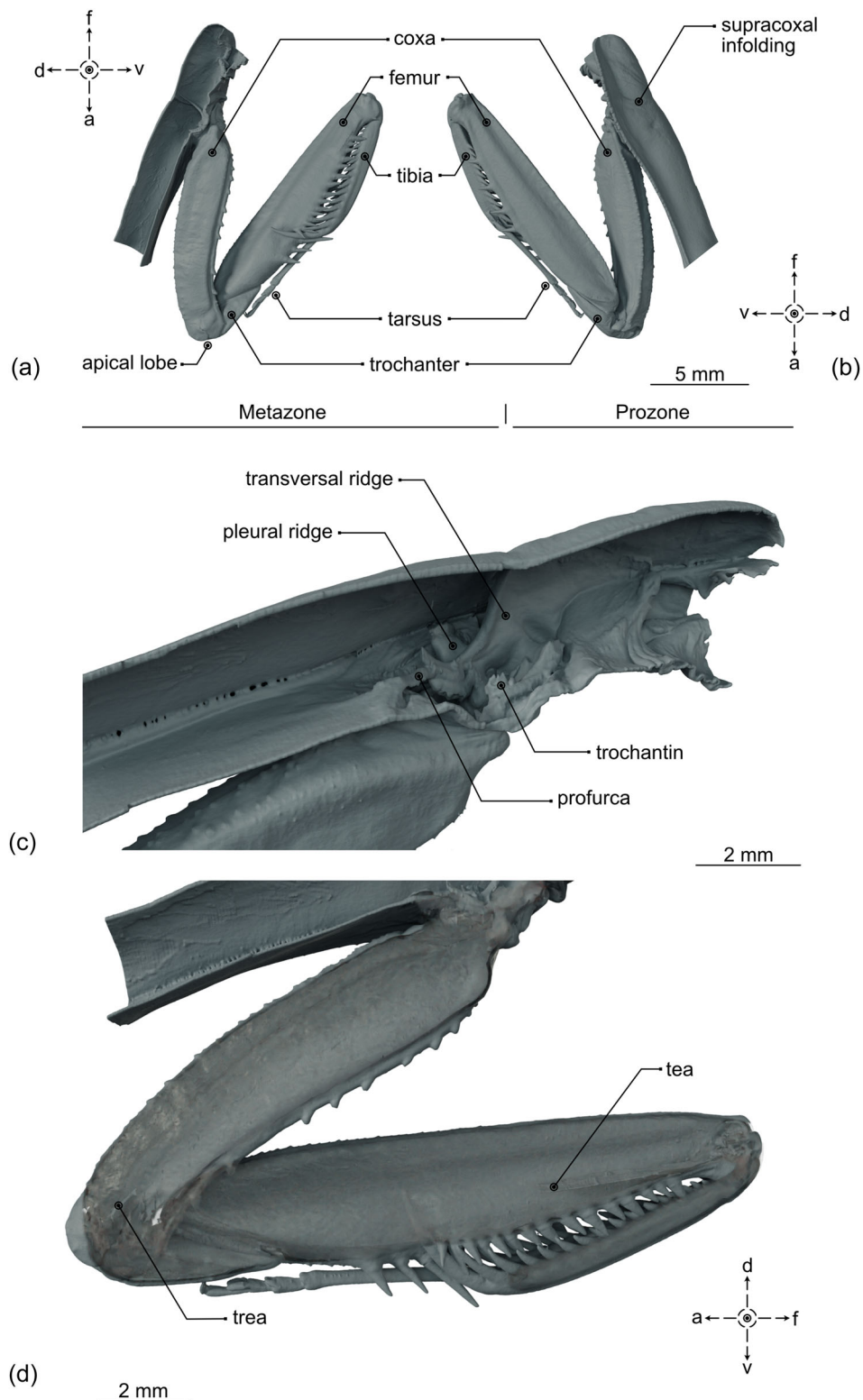


FIGURE 3 Three-dimensional visualization of the sclerites and cuticle structures of an adult, female *Hierodula majuscula*'s prothorax and raptorial forelegs in medial (a) and lateral view (b) as well as internal structures in medial view (c, d). a, abdominal; d, dorsal; f, frontal; tea, tibial extensor apodeme; trea, trochanteral extensor apodeme; v, ventral.

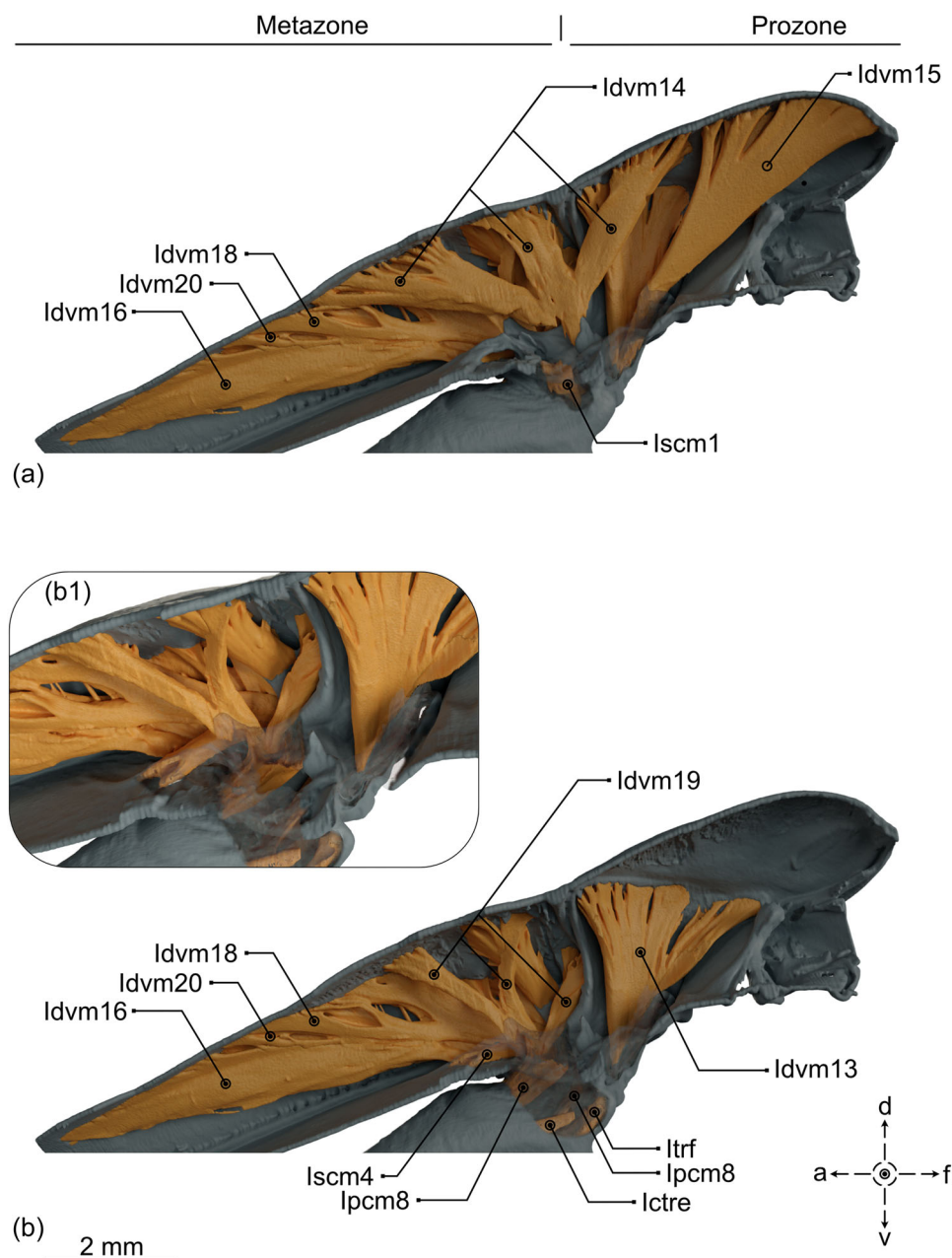


FIGURE 4 Three-dimensional visualization of the extrinsic musculature of an adult female *Hierodula majuscula* from μ CT data, medial view. In certain areas, the cuticle is displayed transparent, to get a better view of the musculature. Muscles are subsequently removed in every layer, to enable an understanding of the spatial location. (a) first layer; (a1) first layer viewed from steeper angle; (b) second layer; (b1) second layer viewed from a steeper angle. a, abdominal; d, dorsal; ctre, coxal trochanteral extensor; dvm, dorso-ventral muscle; f, frontal; pcm, pleuro-coxal muscle; scm, sterno-coxal muscle; v, ventral.

Itrf—Trochanteral flexor

O: Antero-dorsal, via dorsal till postero-dorsal area over nearly the whole length of the coxa.

l: Long flexor apodeme of the trochanter.

Trochanter

Ifra—Femoral reductor a

O: Anterio-ventral area of the trochanter.

I: Posterior basal rim of femur, anterior of the femoral reductor b.

lfrb—Femoral reductor b

O: Ventral area of the trochanter.

I: Posterior basal rim of femur, posterior of the femoral reductor a.

Itrtif–Trochanteral tibial flexor

O: Anterior area of the distal part of the trochanter.

l: Tibial flexor apodeme.

Femur

Iliotibial band—Tibial extensor

O: Dorso-posterior area of the proximal femur.

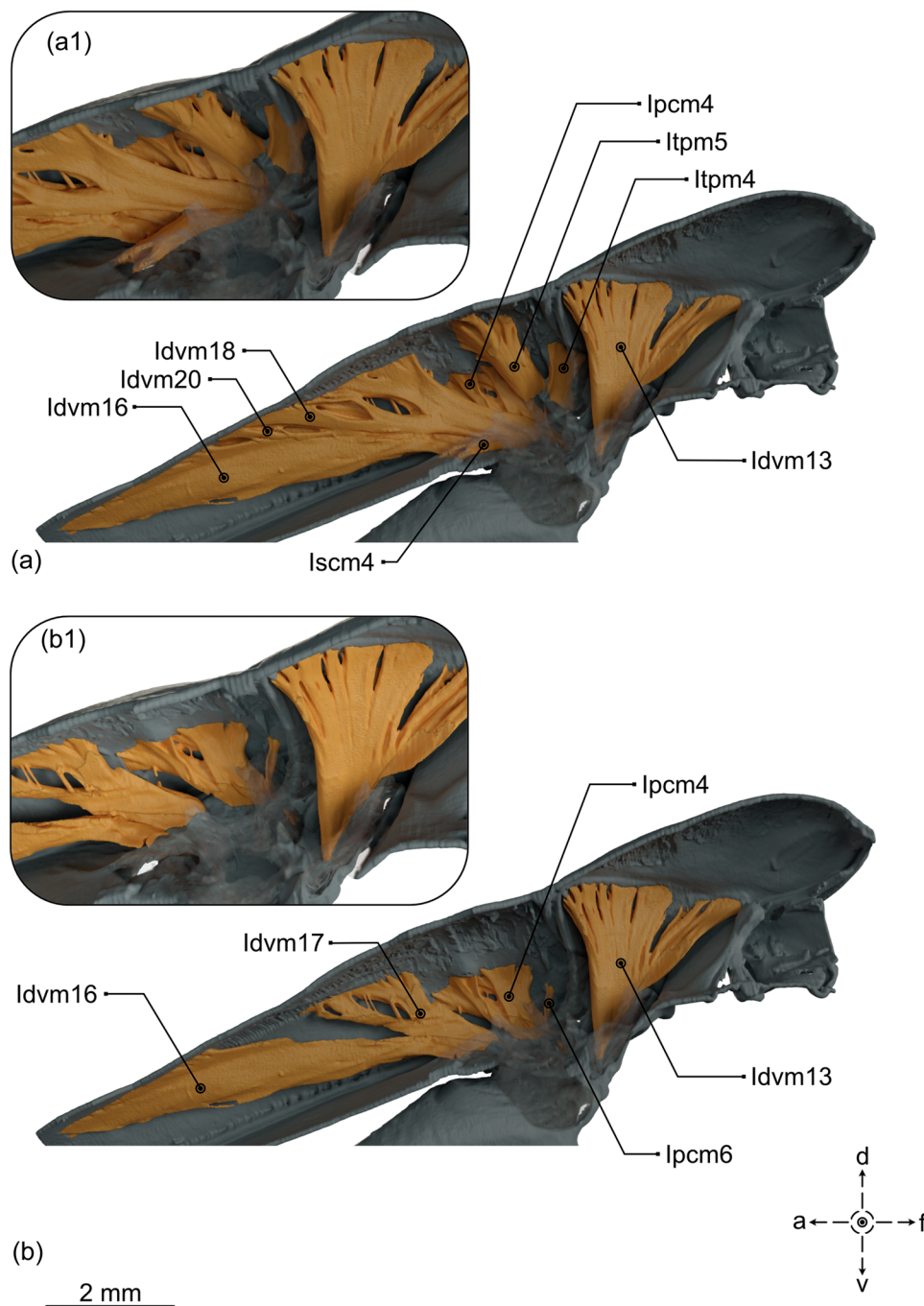


FIGURE 5 Three-dimensional visualization of the extrinsic musculature of an adult female *Hierodula majuscula* from μ CT data, medial view. In certain areas, the cuticle is displayed transparent, to get a better view of the musculature. Muscles are subsequently removed in every layer, to enable an understanding of the spatial location. (a) third layer; (a1) third layer viewed from steeper angle (b) fourth layer; (b1) fourth layer viewed from a steeper angle. a, abdominal; d, dorsal; dvm, dorso-ventral muscle; f, frontal; pcm, pleuro-coxal muscle; tpm, tergo-pleural muscle; scm, sterno-coxal muscle; v, ventral.

I: Extensor apodeme of tibia.

Ifpf—Femoral pretarsal flexor

O: Postero-lateral proximal end of femur.

I: Proximal end of tibial flexor apodeme.

Iftifa—Femoral tibial flexor (pennate)

O: Anterior area of the proximal part of the femur.

I: Tibial flexor apodeme.

Iftifb—Femoral tibial flexor (parallel)

O: Anterior via ventral until posterior area of the proximal part of the femur.

I: Distal, ventral surface of the tibial flexor apodeme.

Tibia

Idtipf—Distal tibial pretarsal flexor

O: Distal third of the anterior tibial region.

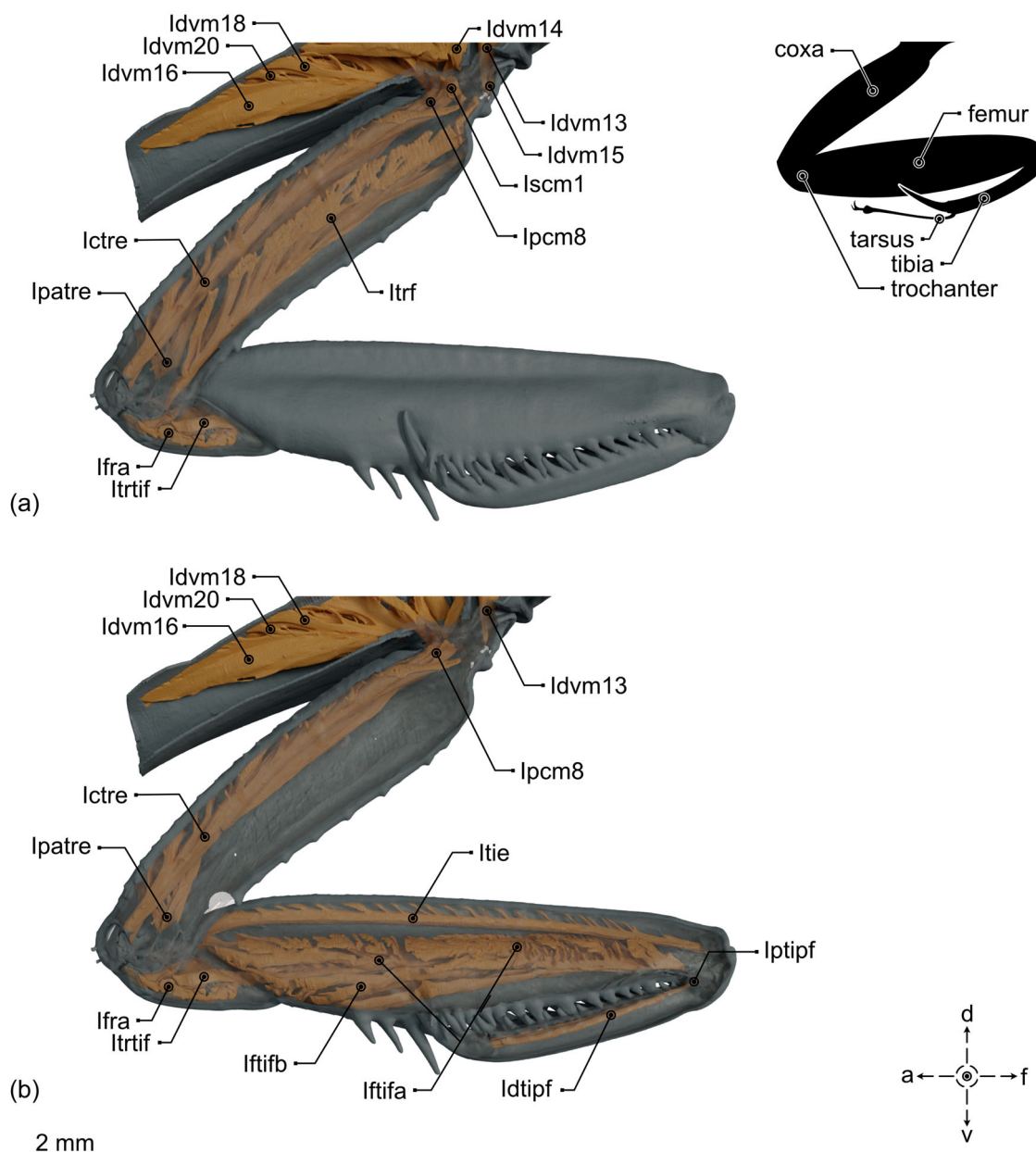


FIGURE 6 Three-dimensional visualization of the intrinsic musculature of an adult female *Hierodula majuscula* from μ CT data, medial view. In certain areas, the cuticle is displayed transparent, to get a better view of the musculature. Muscles are subsequently removed in every layer, to enable an understanding of the spatial location. (a) first layer; (b) second layer. a, abdominal; atrf, accessory trochanteral flexor; ctre, coxal trochanteral extensor; d, dorsal; dtipf, distal tibial pretarsal flexor; dvm, dorso-ventral muscle; f, frontal; fra, femoral reductor a; ftifa, femoral tibial flexor a; ftifb, femoral tibial flexor b; patre, posterior accessory trochanteral extensor; pcm, pleuro-coxal muscle; ptipf, proximal tibial pretarsal flexor; tae, tarsal extensor; tie, tibial extensor; v, ventral.

I: Apodeme of the unguitractor plate (Gray & Mill, 1985).

Iptipf—Proximal tibial pretarsal flexor

O: Most proximal, dorsal area of the tibia.

I: Apodeme of the unguitractor plate (Gray & Mill, 1985).

Itae—Tarsal extensor

O: Proximal, dorsal region of tibia.

I: Dorsal, basal tarsal rim.

Itaf—Tarsal flexor

O: Ventral, distal region of the tibia.

I: Ventral, basal tarsal rim.

4 | DISCUSSION

4.1 | General results and comments on previous work

In total, we propose a reduced number, in comparison to existing descriptions, of 15 extrinsic and 15 intrinsic muscles for the raptorial forelegs of mantodeans (Figures 4–7) in all investigated species. Although, the muscle set-up of praying mantises was already investigated, resulting descriptions are unclear between authors and

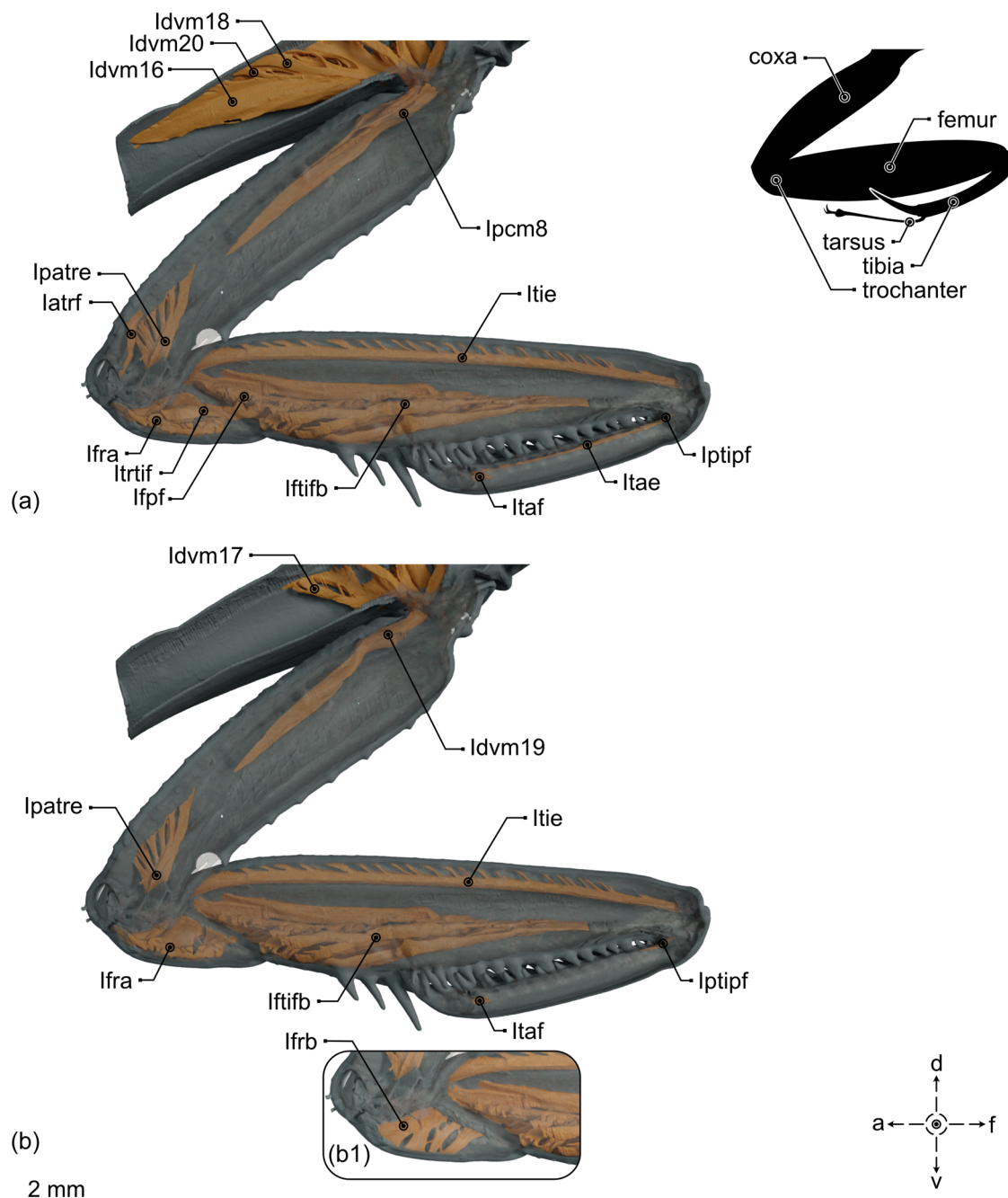


FIGURE 7 Three-dimensional visualization of the intrinsic musculature of an adult female *Hierodula majuscula* from μ CT data, medial view. In certain areas, the cuticle is displayed transparent, to get a better view of the musculature. Muscles are subsequently removed in every layer, to enable a better understanding of the spatial arrangement. (a) third layer; (b) fourth layer; (b1) Ifra removed to get a better view on Ifrb. a, abdominal; d, dorsal; dvm, dorso-ventral muscle; f, frontal; fra, femoral reductor a; frb, femoral reductor b; ftifb, femoral tibial flexor b; patre, posterior accessory trochanteral extensor; pcm, pleuro-coxal muscle; tpm, tergo-pleural muscle; scm, sterno-coxal muscle; tae, tarsal extensor; taf, tarsal flexor; tie, tibial extensor; trf, trochanteral flexor; v, ventral.

difficult to compare. The nomenclature for intrinsic musculature provided by Levereault (1938), which was further adopted by Gray and Mill (1985), was suitable, but descriptions of the extrinsic musculature were ambiguous. To allow for a simplified future interspecies comparison of musculature in mantodeans, the previously described extrinsic muscles and names from earlier publications were homologized, due to their attachment points, to the

homologous muscles described in this study, using the nomenclature of Friedrich and Beutel (2008), as shown in Table 2. In a similar manner, we homologized the intrinsic musculature described by Aibekova et al. (2022) for workers of *F. rufa* as a representative insect with legs for walking, and Büsse et al. (2021) for *M. styriaca* as an example of a prehensile raptorial foreleg of another group of insects, to the muscles found and described in the present study (Table 3).

We were able to homologize most of the previously described musculature with our results, though several muscles that were previously described as individual muscles had to be condensed into a single muscle throughout our analysis. For example, *M. pronoto-trochantalis posterior* (ldvm14), as described by Friedrich and Beutel (2008), consists of three muscle strands with three different points of origin (in consensus with Levereault, 1938) that merge at some point, ending at the same point of insertion. Gray and Mill (1985) described the same muscle, due to its spatial separated points of origin, as three individual muscles (Anterior tergal coxal adductor; Intermediate tergal coxal adductor; Posterior tergal coxal adductor; Table 2). Interestingly, the extrinsic muscle ldvm20 could not be homologized with the descriptions of Friedrich and Beutel (2008), and was therefore given a new name following the established nomenclature. The muscle likely serves as a posterior coxal rotator.

Previously, Gray and Mill (1985) have described 18 extrinsic and 16 intrinsic muscles, for the raptorial forelegs of *H. membranacea*. Here, we were not able to confirm the sternal posterior coxal rotator (lspcr) and the anterior accessory trochanteral extensor (laate). Originating at the profurca, the muscle lspcr is described as a long and flat muscle, inserting on the coxa, next to the tergal posterior rotator (here homologized as part of the muscle ldvm16), enabling rotational as well as abduction movement. In contrast to *H. membranacea* (cf. Figure 5 in Gray & Mill, 1985), the profurca of the species investigated here appears to be fused (or at least being in close contact) to the pleural ridge as well as to the transversal ridge (Figure 1b). It is imaginable, that the origin of the muscle lspcr is shifted, due to the differences of the involved cuticle structures, and is here interpreted as part of the muscle ltpm4. Nevertheless, it is still possible that this represents an interspecific difference and the muscle is not present in the species investigated here. The muscle laate was described as a small muscle, situated in the distal part of the coxa, anterior of the coxal trochanteral extensor (lctre). It inserts at the base of the trochanteral extensor apodeme, playing a role in the extension of the trochanter, and the connected femur, while simultaneously adjusting its movement in anterior direction (Levereault, 1938; Gray & Mill, 1985). Furthermore, it has probably an antagonistic function to the accessory trochanteral flexor (latrf; Gray & Mill, 1985). As the muscle was described for two different species of Mantodea (Gray & Mill, 1985; Levereault, 1938), its absence in the species investigated here, is probably due to an interspecific difference. Its function is either redundant, or compensated by the adjacent musculature (e.g., by the posterior accessory trochanteral extensor; Figure 7). Here, Gray and Mill (1985) further suggested the probability that the accessory muscles are either functionless due their size, or likely redundant, due to the fact that the trochanter-femur joint in dictyopterans has only one degree of freedom. Frantsevich (1998) described 19 different extrinsic muscles for the raptorial forelegs of *M. religiosa*. In the same manner as previously described, we were able to homologize most of them with our results, with some cases of merging musculature throughout the homologization process. Unfortunately, we were not able to confirm

muscle number 14 (sternal posterior rotator). As this muscle is homologous to the muscle lspcr described by Gray and Mill (1983), the same statements previously made for the muscle lspcr apply.

4.2 | Comments on possible muscle functionality

In terms of their main function for movements and in agreement with the literature, the musculature of the raptorial forelegs in mantodeans can be divided in several groups (Gray & Mill, 1985). For extrinsic muscles, five groups can be classified. The promotor muscles ldvm13 and ldvm15 lift the legs in dorsal direction in front of the animal. Its antagonists, the remotor muscles ldvm16 and ldvm17, move the legs in ventral direction in front of the animal. For lateral movement, the abductor muscles ldvm18, lpcm4, lpcm6, ltpm4, and ltpm5 move the legs in dorsal direction lateral of the animal. Its antagonists, the adductor muscles ldvm14 and lscm1 move the legs in ventral direction lateral of the animal. Additionally, an inwards rotation of the coxa, and therefore the entire leg, is achieved by muscle lscm4. For intrinsic muscles, three groups can be classified. The extensor muscles lctre, lpatre, ltie and ltae extend the individual parts, and therefore the whole leg. Its antagonists, the flexor muscles ldvm19, lpcm8, ltrf, latrf, ltrtif, lftifb, lftifa, lptipf, ldtpif, and ltaf are flexing the individual parts, and therefore the whole leg. Similar to the extrinsic musculature, a rotation of the femur is achieved by muscles lfra and lfrb.

4.3 | Comparison to *M. styriaca*

Although, the most striking features and key characteristic for Mantodea are the prominent raptorial forelegs, a homologous system can be found in other groups as well, like in the neuropteran Mantispidae (Büsse et al., 2021; Ferris, 1940; Prete et al., 1999; Ullrich, 1965). As shown in the morphological investigation of *M. styriaca* by Büsse et al. (2021), apart from the similar external appearance of the raptorial forelegs, additional analogies can be found concerning their anatomy. Especially noticeable is the difference in posture: while almost all mantodeans keep their raptorial forelegs in front of the prothorax, Mantispidae are holding them in a steady and secure resting position held up laterally, close to the prothorax (Lequet 2018). Additionally, while Mantispidae typically only use their mid- and hindlegs for walking (Faluke, 2010; 0:50-1:05), praying mantises use their forelegs extensively to move around (walking, climbing, etc.; Rossoni & Niven, 2020). In the video footage, it is especially noticeable, that even though the forelegs are sometimes placed on the ground, they are very quickly pulled back in their resting position (Faluke, 2010; 0:50-1:05). Moreover, the raptorial forelegs of Mantispidae show a differing external morphology, with the tarsus forming a seemingly immobile elongation of the sickle shaped tibia, making most tarsal muscles redundant (Büsse et al., 2021; Ferris, 1940; Ullrich, 1965). The immobile tarsus is probably further compensating for the missing tibial spur that can be

found in praying mantises, and is described to form a lever-ratchet system together with the discoidal spine (Loxton & Nicholls, 1979). Furthermore, in contrast to the exclusively muscle driven movement of the mantodeans predatory strike (Gray & Mill, 1983), *M. styriaca* most likely relies on a latch-mediated spring actuation system (LaMSA; "catapult-system"), activated by the muscle M24c that is only known from *M. styriaca* (respectively, likely in all Mantispidae), as the main driving force of the predatory strike (cf. Figure 6 in Büsse et al., 2021).

Overall, the differing requirements to the forelegs in the two groups is also reflected in the inner morphology, especially in the number of muscles. Here, praying mantises show almost twice as many muscles, especially regarding extrinsic muscles, that are certainly needed to fulfill the complex additional tasks of a walking leg (Rossoni & Niven, 2020). More specifically, in contrast to the 15 extrinsic muscles in mantodeans, only 6 muscles are present in Mantispidae, showing minor differences to the corresponding muscles in praying mantises. *M. styriaca* has an additional pleuro-coxal muscle (lpcm5), that, together with muscle lpcm6 and ldvm15, serve as promotor of the raptorial foreleg. The additional muscle and the in comparison to Mantodea enlarged muscle lpcm6, likely work as promotor muscles of the forelegs, giving support for the previously mentioned resting position lateral of the prothorax (Lequet 2018). Mantispidae further show a different set of sterno-coxal muscles (lscm1 and lscm3) in comparison to Mantodea (lscm1 and lscm4). While muscle lscm1 functions as an adductor muscle in both groups, lscm4 creates an inwards rotation of the coxa in Mantodea, and lscm3 is likely to only function as an abductor muscle in Mantispidae. For intrinsic musculature, *M. styriaca* shows a similar set-up, but again, with a reduced number of muscles in contrast to Mantodea. Mantispidae are lacking the latrf in the coxa, the ltrtf in the trochanter, the lfpf in the femur and both the ldtipf and lptipf as well as the ltae in the tibia. It is not surprising to find almost no muscles in the tibia, as the tarsus is seldomly used and rather immobilized. For the coxa, trochanter and femur, the differing muscle set-up is most likely related to the different functional morphological requirements for the differing kinematics of the predatory strike (muscle-driven movement vs. LaMSA-system). As described by Büsse et al. (2021), *M. styriaca* is fully opening the femur-tibia joint at the beginning of the strike, representing the loading process of the LaMSA-system (Granier, 2019; 1:25-1:28). Here, a different and reduced set of muscles is likely to be sufficient in Mantispidae to execute the movement. The increased number of muscles in Mantodea is probably needed to facilitate the walking motions and to enable more precise adjustments during the predatory strike (Oufiero, 2021; Oufiero et al., 2016; Prete & Cleal, 1996; Prete et al., 1990).

4.4 | Comparison to Blattodea

The cockroaches (Insecta: Blattodea), as member of the Dictyoptera and a sister group to Mantodea, are probably the best example for a comparison of the strongly modified raptorial forelegs to an

unmodified walking leg. Unfortunately, the morphology of the legs of cockroaches is understudied, and only few authors investigated the musculature of the legs in Blattodea (Alsop, 1978; Carbonell, 1947; Maki, 1938). Maki (1938) studied the thoracic musculature only, reporting a total of 32 muscles for the prothoracic musculature of *Periplaneta australasiae* (FABRICIUS, 1775), with little comments concerning functionality. Carbonell (1947) studied the prothorax of *Periplaneta americana* (LINNAEUS, 1758), including coxa and trochanter, reporting a total of 55 muscles in the prothorax and the two associated leg articles. Lastly, Alsop (1978) focused on the intrinsic musculature of the legs of *P. americana*, stating 368 muscles, that are inserting on postcoxal segments of the leg. It is unclear, if this number is accounting for all six legs combined, or for three legs of one half of the body, and no complete list of all described muscles is given. Alsop (1978) also stated differences between the prothoracic legs in comparison to the meso- and metathoracic legs, with the latter showing an increased number of muscles and a partial difference in flexor muscle composition. The reason for the extreme increased number of muscles, is simultaneously the main issue with this study: the author rejects Snodgrass' (1935) interpretation of how to characterize a single muscle. As Snodgrass (1935) stated, musculature of the insect body with its specific function can be represented by one single or several individual muscles, and should be considered rather as functional groups of fibers than individual fiber bundles. Overall, to allow for a meaningful comparison between the leg musculature of Blattodea and Mantodes, a comprehensive morphological study is needed, that further puts previous results into context with modern nomenclature (e.g., Friedrich and Beutel, 2008). Here, it would be particularly interesting to include species from the genus *Metallyticus*, given its phylogenetic placement (Svenson & Whiting, 2009) as well as its blattodean-like appearance.

4.5 | Comparison to *F. rufa*

Muscle homologizations among insect taxa and a joint nomenclature like the comprehensive thoracic nomenclature introduced by Friedrich and Beutel (2008), tremendously help to study the evolution of body parts and facilitate working with complex anatomies in general. Even though, a typical walking leg and the strongly modified raptorial forelegs show many peculiarities and differences, we tried to cooperate the newly established leg nomenclature (Aibekova et al., 2022); stating homologies between muscles and translating this new nomenclature onto the mantodean species investigated here. Looking at the musculature set-up presented by Aibekova et al. (2022), many similarities between ants and mantises can be observed, but also distinct differences can be found. In the coxa, the single muscle lctm3 found in ants, is represented by the two muscles lctre and lpatre in Mantodea. As attachment and insertion points match between the muscles, we believe that lctm3 consists of two functionally different muscles, that is, one anterior and one posterior muscle. The coxa in praying mantises is strongly elongated facilitating to determine the true

nature of these muscle strands. Furthermore, one additional muscle (Itrtif) is found in Mantodea that is missing in ants. As praying mantises heavily rely on precision of the predatory strike, the additional muscle presumably helps adjusting the correct orientation of the catching movement. Likewise, in the femur, the muscle Iftm2 in ants is represented by two muscles (Iftifa and Iftifb) in Mantodea. As both muscles in praying mantises have structurally differently oriented fibers (one is pennate, while the other one consists of parallel fibers as described by Gray & Mill, 1985), we again suggest that this additional separation in two functionally different groups of muscle fibers facilitates a more precise movement of the segments of the raptorial foreleg during the prey capture process. Furthermore, some additional muscles may support other movements of the forelegs (e.g., for cleaning the eyes and antennae).

4.6 | Comments on SSD

All species investigated in the here presented study are found in a similar habitat, the shrub stratum, with *H. coronatus* favoring the proximity to flowers as hunting ground (Mizuno et al., 2014). They all typically hunt as ambush predators relying on camouflaging mechanisms or aggressive mimicry (Edmunds & Brunner, 1999; Hurd, 1999; Mizuno et al., 2014) and, even though they favor winged and flying prey, all species are amongst the generalist predators (Hassel, 1978). Although all individuals are winged in the adult stage, typically, the smaller and slenderer male uses the increased mobility to follow the pheromones sent out by the female, facilitating the mate-locating process (Kawano, 2006; Mori et al., 2017; Rutowski, 1997; Shine, 1989). In *H. majuscula* and *P. paradoxa*, the SSD is only slightly noticeable and both sexes can be assumed to have similar hunting preferences and exploiting the same ecological niche. In contrast, due to the extreme female-biased SSD in *H. coronatus* and *P. perpulchra* and the differences in size of possible prey items associated, it is imaginable that the two sexes also exploit slightly different ecological niches for their foraging. Svenson et al. (2016) demonstrated in *H. coronatus*, that the female-biased SSD can also be (at least partly) driven by the increased hunting success associated with the female gigantism. As proposed by Svenson et al. (2016), male specimens of *H. coronatus* retain the ancestral strategy as ambush predators, while the considerably larger females focus on aggressive mimicry (Wickler, 1968). This means that female orchid mantises use visual as well as chemical mimicry to draw in potential prey items (Mizuno et al., 2014). Minimizing intersexual resource competition by the exploitation of different foraging niches is most likely advantageous for the fitness of both sexes. Although it is unknown whether a similar mechanism exists in *P. perpulchra*, the female-biased SSD seems to be sufficient to assume different foraging niches for the sexes. As mentioned, a behavioral dimorphism can be found in *Miomantis caffra*, with a male-biased coercive pre-mating tactic to reduce the cannibalistic rate, while increasing the male's chance of a mating success (Burke & Holwell, 2021). Interestingly, even though the female-biased SSD is noticeably present in almost all species of

Mantodea, favoring a larger sized female positively correlating with fecundity (Esperk et al., 2007; Mori et al., 2017; Rutowski, 1997; Shine, 1989), no observable differences were found in the herein studied species—neither between species, nor between sexes. Both sexes of all species use the identical musculature set-up for to control the prothoracic legs.

5 | CONCLUSIONS

Using literature data and μ CT analysis, we summarized and extended the existing knowledge of the extrinsic and intrinsic musculature of the prehensile raptorial forelegs of mantodeans, in light of a potential functionality and the described SSD. We reported 15 extrinsic, including one previously undescribed muscle, and 15 intrinsic muscles, and present detailed descriptions as well as three-dimensional visualizations of the raptorial foreleg musculature. To ease future handling of these data, we homologized the names of all described extrinsic muscles according to their attachment points to the homologous thoracic muscles described in the nomenclature of Friedrich and Beutel (2008), as well as discussed possible homologies and functional aspects to the previously studied *M. styriaca* (Büsse et al., 2021), and to the newly introduced leg nomenclature for *F. rufa* by Aibekova et al. (2022). For a future comparative study, it would be especially insightful, to comprehensively investigate the musculature of cockroaches (Insecta: Blattodea) particularly in the context of modern nomenclature, and species of *Metallyticus*, because of its phylogenetic placement (Svenson & Whiting, 2009) and blattodean-like appearance. Interestingly, our results show no considerable differences neither between species nor between males and females.

AUTHOR CONTRIBUTIONS

Sebastian Büsse: Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; supervision; validation; writing—review and editing. **Fabian Bäuml:** Conceptualization; formal analysis; investigation; methodology; project administration; resources; validation; writing—original draft; writing—review and editing. **Stanislav N. Gorb:** Conceptualization; data curation; funding acquisition; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data supporting our findings are presented in the paper and the Supporting Information, respectively. The CT raw data can be made available upon reasonable request.

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