

RESEARCH ARTICLE

Functional morphology and bite performance of raptorial chelicerae of camel spiders (Solifugae)

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SUMMARY

Solifugae are an understudied group of relatively large arachnids with well over 1000 species distributed on almost all major continents. These highly active predators utilize their large chelicerae for feeding, defense, burrowing and mating. We investigated the differences in cheliceral morphology and performance of two ecologically divergent species from North Africa; the cursorial *Galeodes* sp. and the burrowing *Rhagodes melanus*. Morphological data show differences in aspect ratio between the two species. Bite force measurements show *Rhagodes* ($N=11$) to be a much stronger biter than *Galeodes* ($N=8$), in terms of both absolute maximum force (*Rhagodes* 5.63N, *Galeodes* 2.12N) and force relative to cheliceral size. Synchrotron microtomographs of one specimen for each species reveal large differences in physiological cross-sectional area (PCSA) and estimated muscle stress, resulting in a much higher muscle stress in *Rhagodes*. This species also showed a longer muscle fiber length. Muscle volume and PCSA were found to differ between the two chelicerae in the two scanned specimens. Whereas *Rhagodes* reflects this morphological asymmetry in having a higher bite force in the right chelicera, *Galeodes* shows no such bias.

Key words: Solifugae, *Rhagodes*, *Galeodes*, bite force, functional morphology.

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INTRODUCTION

Bite force is an important ecological performance parameter relevant to feeding, intraspecific competition and defense against predators. In comparative analyses in particular, differences in bite force between closely related species might indicate specialization of the jaw apparatus for an ecologically relevant task. Thus, bite force has been measured or estimated in many groups of vertebrates, such as mammals (e.g. Christiansen, 2007; Aguirre et al., 2002; Wroe et al., 2005; Christiansen and Wroe, 2007; Herrel et al., 2008), squamates (e.g. Herrel and O'Reilly, 2006; Kaliontzopoulou et al., 2012), turtles (e.g. Herrel et al., 2002; Vervust et al., 2011), birds (e.g. van der Meij and Bout, 2004; Herrel et al., 2005) and fish (e.g. Huber et al., 2005; Huber et al., 2006; Huber et al., 2008). These groups cover a range of sizes from small birds and lizards to some of the larger vertebrates. Because of their small size, however, many invertebrates are less suitable for direct force measurement using parallel plate bite force meters. Therefore, only pinch forces of crustaceans and scorpions have been studied experimentally in more detail (e.g. Taylor, 2000; Claussen et al., 2008; Van der Meijden et al., 2010; Van der Meijden et al., 2012) or estimated by biomechanical modeling in oribatid mites (Heethoff and Norton, 2009).

The chelicerae, the eponymous two- or three-segmented oral appendages of Chelicerata, are used in the handling of food around the oral cavity. Only camel spiders (Solifugae), some groups of mites (Acari) and harvestmen (Opiliones) use their venom-less chelicerae for prey prehension and subjugation. In most other chelicerates, prey

is first seized and immobilized with specialized appendages. Prey is apprehended using raptorial pedipalps (Amblypygi, Pseudoscorpiones, Scorpiones and Uropygi) or immobilized using venom injected by the chelicerae (Araneae), the pedipalps (Pseudoscorpiones) or the telson (Scorpiones). Solifugae simply immobilize their prey by rapidly crushing it, and swiftly reduce it with alternating chewing motions of the large mobile chelicerae.

Solifugae consist of well over 1000 described species (Harvey, 2002) and occur worldwide on all major landmasses with the exception of Australia, Madagascar and Antarctica. They mostly inhabit desert or Mediterranean climate zones, and are important predators in such arid environments. Solifuges are active hunters, generally active at dusk and at night, although several diurnal species are known (Brookhart and Cushing, 2008). In contrast to the desert-specialized scorpions, Solifugae have a high metabolism (Lighton et al., 2001) and rapid growth rate. Like derived spiders, solifuges have a tracheal system. To fuel their high metabolism they actively pursue and catch any small animal they can subdue with their large raptorial chelicerae. Hence, solifuges are generalists, preying on arthropods like beetles, cockroaches, flies, locusts, myriapods and scorpions, but also on vertebrates like frogs, lizards and mice (Cloudsley-Thompson, 1961; Moritz, 1993; Punzo, 1998; Hrušková-Martišová et al., 2007; Duval and Whitford, 2009). The prey is captured with the chelicerae, often assisted by the pedipalps, which carry a specialized adhesive organ and cage the prey (Klann et al., 2008; Willemart et al., 2011). The chelicerae of Solifugae are also employed in mating (Heymons, 1902; Cloudsley-Thompson, 1967;

Hrušková-Martišová et al., 2010) – the male uses them to position the female's body and insert the spermatophore (Punzo, 1998). They are additionally used for burrowing (Hingston, 1925; Muma, 1966; Cloudsley-Thompson, 1977) and for moving objects such as pebbles from the burrow (Wharton, 1987). A solifuge can build up to 40 burrows in its lifetime (Muma, 1966). The chelicerae therefore feature prominently in the life history of Solifugae. Although asymmetric chelicerae do exist in arachnids (Taylor, 2009), Solifugae chelicerae are symmetrical in shape. However, asymmetry has been described for the flagellum organ that male solifugae carry on the chelicerae (Delle Cave, 1979).

The chelicera in solifuges consists of two segments. The basal segment is bulbous at the base but tapers out anterodorsally in an immovable fingerlike extension termed the digitus fixus. This finger has several teeth on its ventral side, the most proximal of which lie in two rows. Opposite to the immovable finger is the second segment of the chelicera called the movable finger or digitus mobilis. Its tip lies medially to the digitus fixus in the closed chelicera. The dentition of the digitus mobilis is arranged in a single row; among several smaller teeth, the relative sizes of which vary between species, there is one big main tooth (Fig. 1). The two cheliceral segments are articulated by a membrane and two articulation points defining a rotation axis. Although the musculature of the solifuge chelicerae has been described previously (Roewer, 1932; Millot and Vachon, 1949) and meets the general organization of two-segmented chelate–denate chelicerae as described, for example, for oribatid mites (Heethoff and Norton, 2009), little is known about their performance. Bite force has been studied in the superficially similar pedipalpal chelae of scorpions (Van der Meijden et al., 2010), the pincers of crabs (e.g. Taylor, 2000; Taylor, 2001; McLain et al., 2010), and indirectly in the chelicerae of mites (Heethoff and Norton, 2009). To our knowledge, cheliceral bite force has thus far never been measured directly.

In this study, we compared the cheliceral morphology and performance of two species of solifuges (Fig. 2) from two families: *Galeodes* sp. (Family: Galeodidae, Sundevall 1833) and *Rhagodes melanus* Olivier 1807 (Family: Rhagodidae, Pocock 1897). Both selected species occur in desert habitats in North Africa, and we have observed *Rhagodes* and *Galeodes* occurring syntopically in Morocco. The most basal solifuge family is the Rhagodidae (Roewer, 1932). Members of this family are burrowing species with relatively short legs. Males are smaller in overall body size than females, but have much larger chelicerae. This may suggest a reproductive function, possibly in male–male antagonism or mating. The members of the Galeodidae, and *Galeodes* in particular, are highly active surface hunters with longer legs. Males in *Galeodes* generally do not have enlarged chelicerae. Specific life history information of the Solifugae is sparse, and further data that may shed light on the different demands these two species make on their chelicerae is currently unavailable.

MATERIALS AND METHODS

Force measurements

Live animals were procured from Egypt through the pet trade (*Rhagodes*) or collected in the field in Morocco (*Galeodes*). Live *Rhagodes* were kept in plastic boxes with soil and tissue paper for nesting material, and were fed twice a week with living crickets (*Acheta* sp.) or cockroaches (*Blattella* sp.). Bite forces of *Galeodes* were first measured within hours of collection. In the subsequent 3 days, specimens were kept in plastic containers and fed once with assorted grasshoppers during the trial period. Solifugae are notoriously difficult to maintain in captivity, and quickly diminish in health

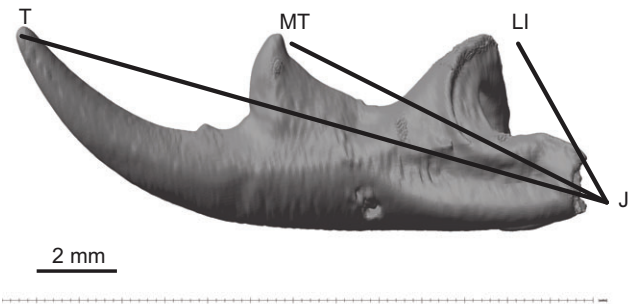


Fig. 1. Rendering of movable finger of *Rhagodes*. Measurements were taken on the movable finger to calculate mechanical advantage. T, tip; MT, main tooth; LI, muscle insertion for levator muscle; J, joint.

(Wharton, 1987). The *Rhagodes* females were kept in a healthy state for several months after bite forces were measured. *Rhagodes* males only survived for days after force measurements, and were therefore excluded from analyses. The *Galeodes* did not show apparent reduction of their health during the trial period. *In vivo* bite forces were measured either using a Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland) mounted on a purpose-built holder (see Herrel et al., 1999) or using a similar setup with a Sauter FH20 external force sensor (Sauter, Balingen, Germany). Both instruments were calibrated using small weights, and similarity under dynamic loading was previously tested by measuring bite forces of a single species of scorpion on both instruments. All specimens bit readily when handled. Five trials were performed, separated by at most 1 day. For each trial, the bite force of each of the chelicerae was first measured in arbitrary order, followed by a measurement with both chelicerae biting on the plates. Only the maximum values for the left, right and both chelae were kept for further analyses. Specimens were killed and preserved in 96% ethanol. Body mass was measured during the bite force trials (*Rhagodes*) or after preservation (*Galeodes*). The reduction in body mass for the ethanol-preserved specimens was corrected using a correction factor derived from the ratio of live body mass to preserved body mass in *Rhagodes* (factor 1.14).

Several morphological measurements were taken on the preserved specimens using digital calipers (see Table 1). In order to measure the in-lever of the lever system formed by the movable finger, the latter was removed from the basal segment by section of the connective membranes, followed by slowly overstretching the joint until the movable finger was free from the basal segment.

Both bite force data of solifuges and linear measurements were \log_{10} transformed before statistical analysis in order to achieve linear relationships between variables scaling in proportion to length, area and volume, as well as homoscedasticity of the data. Maximum bite forces were correlated with linear dimensions of the chelicerae, and compared between species. Statistical tests on the solifuge data were carried out in R version 2.14.0 (R Development Core Team, 2011), except OLS linear regressions, which were performed in Microsoft Excel 2007.

3D morphological analyses

Synchrotron X-ray microtomography (SR- μ CT) was conducted with both species. While *Galeodes* was scanned at the ANKA Light Source at the Topo-Tomo beamline in Karlsruhe, *Rhagodes* was scanned at beamline ID19 at the ESRF in Grenoble.

The female specimen of *R. melanus* was fixed in 3.7% formaldehyde solution and placed in a small polypropylene tube



Fig. 2. Dorsal view of *Galeodes* (left) and *Rhagodes* (right). Clearly, the burrowing *Rhagodes* has relatively larger chelicerae and shorter legs than the cursorial *Galeodes*. These images are not to scale.

for X-ray phase contrast synchrotron microtomography (Betz et al., 2007; Boistel et al., 2011). Images were taken with an effective pixel resolution of 14.8 µm at 967 mm sample–detector distance. The beam energy was set at 25 keV. We acquired 900 radiographic images (CCD 2048×2048 pixels, with binning at 1024×1024 pixels) using a FReLoN CCD Camera (Labiche et al., 2007). Exposure time was 0.15 s.

The female specimen of *Galeodes* sp. was prepared as follows; it was fixed in FAE (three parts formaldehyde, one part acetic acid and six parts ethanol 70%), dehydrated in an ethanol series (2× in 70% for 1 h, 1× in 70% overnight, 3× in 80% for 2 h, 3× in 90% for 2 h, 1× in 95% overnight, 2× in 95% for 2 h, 2× in 99% for 2 h, 1× in 99% overnight), critical-point dried (CPD 020, Balzers Union, Vaduz, Liechtenstein) and glued onto a piece of polystyrene, which was glued on a stub. The sample was mounted on a Huber goniometer head. At a sample–detector distance of about 15 cm, 1500 projections were taken (with an acquisition time of 1 s each) with a Photron CCD-camera (1024×1024 pixels) and 20 µm pixel size at 20 keV beam energy.

The program Amira (version 5, Mercury Computer Systems Inc., Chelmsford, MA, USA) was used to generate 3D surface models of the cuticular elements, ligaments and muscles. In order to estimate average muscle fiber length of the left levator muscle, 20–24 muscle

Table 1. Bite force and linear measurements from specimens used in bite force trials

	<i>Rhagodes melanus</i>	<i>Galeodes</i> sp.
Maximum force, left chelicera (N)	5.37±1.17	2.12±1.08
Maximum force, right chelicera (N)	5.63±0.84	2.06±1.13
Maximum force, both chelicerae (N)	10.27±2.16	3.82±0.23
Total body length (mm)	47.17±6.61	36.13±4.77
Chelicera length (mm)	14.16±1.08	13.16±1.76
Chelicera aspect ratio (length/height)	1.95±0.061	2.41±0.12
Mechanical advantage	0.26±0.022	0.24±0.019
Mechanical advantage main tooth	0.44±0.048	0.47±0.052

Data are means ± s.e.m. for *N*=11 *R. melanus* and *N*=8 *Galeodes* sp.

fibers, selected to include each of the subunits of the muscle, were modeled and measured. The physiological cross-section of the muscle was determined by two different methods: by calculating the contact surface between the tendon and the muscle in Amira, and by dividing the muscle volume by the estimated average fiber length.

Comparative analysis

We compared the solifuge bite force data with other arthropod values, including more than 80 direct bite force measurements from six crab (Taylor, 2000) and 11 scorpion species (Van der Meijden et al., 2010) (this study). As inspired by Alexander (Alexander, 1985) and suggested by Heethoff and Norton (Heethoff and Norton, 2009), we calculated a bite force quotient, $BFQ = \text{force}/\text{bodymass}^{0.66}$, and compared the logBFQ among the different arthropod groups using ANOVA in SPSS20.

RESULTS

Descriptive morphology

Two muscles insert on the movable finger of the chelicerae, and allow the opening and closing of the chelicerae: the depressor digiti mobilis and the levator digiti mobilis.

Depressor digiti mobilis

In both species, the pennate depressor digiti mobilis feathers from its tendon to several origins, at the inner surface of the basal ring and the inner ventral surface of the basal segment. From there, it runs anteroventrally to its point of insertion – the ventral part of the base of the movable finger, where it attaches *via* its tendon (Fig. 3).

Levator digiti mobilis

The multipennate levator digiti mobilis fills the larger part of the basal segment. It originates from the basal segment's inner surface and inserts, *via* its tendon, onto the dorsal part of the base of the movable finger (Fig. 4B, Fig. 5B). It has several longitudinal spaces running through it, the largest of which (in the ventral region) accommodates the depressor muscle. The wide longitudinal grooves in the dorsal and lateral regions (see caudal view in Fig. 3D, Fig. 4D) accommodate the tracheae and the nerves, and allow hemolymph circulation. The relatively large size of these intramuscular spaces (compared with a similar scan of the chelicerae a scorpion, *Heterometrus laoticus*; data not shown) may be related to the high level of cheliceral muscle activity typical of solifugae, allowing increased circulation of hemolymph and large tracheae. The tendon is divided into five subunits (Fig. 4D, Fig. 5D). Muscle fibers attach at each side of these subunits, resulting in a 10-fold pennation of the levator muscle. The pennation angle is 90 deg in the anterior part of the muscle and decreases along the muscle in the posterior direction down to 10 deg. Because of the complex subdivided shape of the tendon and the widely ranging angles the muscle fibers make with the different subunits of the tendon, we were unable to calculate a single representative average pennation angle for the muscle.

Rhagodes muscle data

Depressor digiti mobilis

The volume of the depressor digiti mobilis muscle was measured separately for the left and right chelicera: 5.7 and 5.4 mm³, respectively.

Levator digiti mobilis

The volume of the levator digiti mobilis muscle was likewise measured separately for the left and right chelicera: 38.5 and

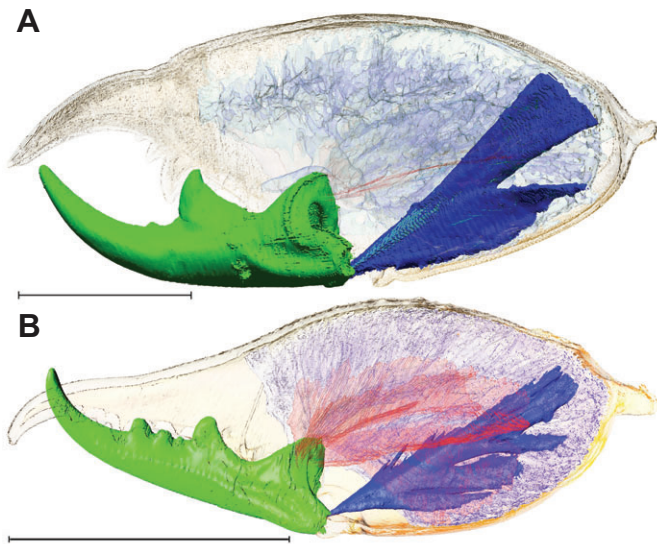


Fig. 3. Renderings of *Rhagodes* (A) and *Galeodes* (B) showing the position of the depressor digiti mobilis (dark blue) relative to the movable finger (green), tendon (transparent red) and levator muscle (transparent blue). Scale bars are 5 mm.

46.0 mm³, respectively. The physiological cross-section area (PCSA) of the muscle determined from the tendon–muscle surface was 28.1 mm² (left) and 30.4 mm² (right). The mean (\pm s.d.) muscle fiber length was estimated to be 1.98 \pm 0.42 mm. Dividing the muscle volume by the estimated muscle fiber length gives a PCSA of 19.5 mm² (left) and 23.2 mm² (right). Dividing the maximum bite force by the PCSA gives the muscle stress. As the actual bite force of the scanned specimen was not recorded, its bite force was estimated based on its chela length, using a linear regression of maximum bite force on chela length of all *Rhagodes* specimens. This yielded a predicted bite force of 6.8 N (left) and 7.2 N (right), resulting in estimated muscle stresses of 936 kPa (left) and 905 kPa (right) based on the tendon–muscle interface PCSA (Table 2).

Galeodes muscle data

Depressor digiti mobilis

As for *Rhagodes*, the volume of the left and right muscles was measured separately: 2.53 and 1.81 mm³, respectively

Levator digiti mobilis

The volume of the left muscle was measured to be 24.9 mm³ and that of the right muscle was 17.5 mm³. A mean fiber length of 1.4 mm was determined by measuring 20 arbitrarily chosen fibers. The PCSA of the muscle determined from the tendon–muscle surface was 24.8 mm² (left), and 21.0 mm² (right). The mean (\pm s.d.) muscle fiber length was estimated to be 1.4 \pm 0.43 mm. Dividing the muscle volume by the estimated muscle fiber length gives a PCSA of 17.8 mm² (left) and 12.5 mm² (right). Dividing the maximum bite force by the PCSA gives the muscle stress. As the actual bite force of the scanned specimen was not recorded, its bite force was estimated based on its chela length, using a linear regression of maximum bite force on chela length of all *Galeodes* specimens. This yielded a predicted bite force of 1.03 N (left) and 1.03 N (right), resulting in estimated muscle stresses of 173 kPa (left) and 203 kPa (right) based on the tendon–muscle interface PCSA (Table 2).

Bite force measurements

A Mann–Whitney test showed the mean of the maximum bite forces to differ significantly between the two species ($P<0.001$). Multiple regression using the general linear model, with chelicera length, width and height as explanatory variables gave R^2 values of 0.75 (*Rhagodes*) and 0.91 (*Galeodes*). Across species, the explanatory variable ‘chelicera height’ showed the highest correlation with maximum bite force (Pearson correlation coefficient, $PCC=0.96$, $P<0.001$, linear regression $R^2=0.92$). Other variables also showed high correlations: chelicera width ($PCC=0.86$, $P<0.001$, $R^2=0.73$), chelicera length ($PCC=0.77$, $P<0.001$, $R^2=0.59$), and the product of length, width and height ($PCC=0.90$, $P<0.001$, $R^2=0.88$; see Fig. 6). Maximum bite forces were corrected for chelicera size using the residuals of the regression on chelicera height. A Mann–Whitney test based on the size-corrected data showed a significant difference in the mean bite force between *Galeodes* and *Rhagodes* ($P<0.001$).

Neither species showed a preference for biting with a single chelicera *versus* biting with both at the same time. A linear regression of the maximum force from single chelicera bites against bites with both chelicerae, for both species, showed that the force from the latter was nearly double that of the single-sided bites (slope 1.87).

A Mann–Whitney test ($P=0.17$) and Student’s *t*-test ($P=0.39$) were not able to show a difference between the bite force of the two chelicerae in *Galeodes* when all specimens were pooled. The

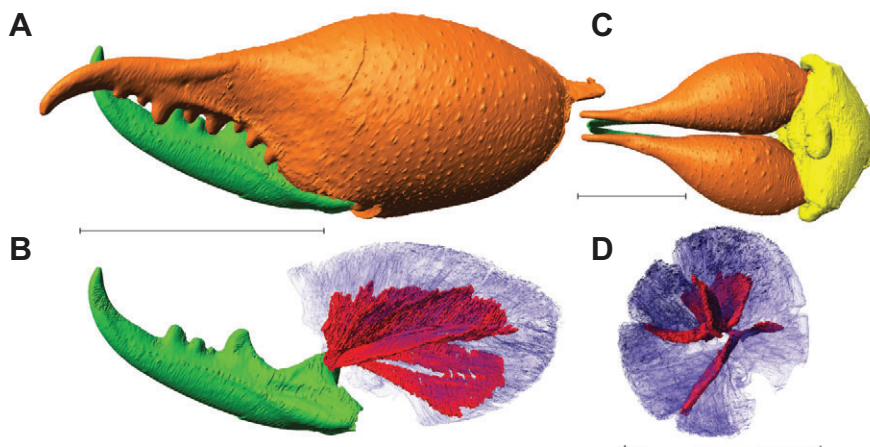


Fig. 4. Renderings of *Galeodes* chelicerae. (A) Lateral view of left chelicera. (B) Movable finger (green), tendon (red) and levator muscle (transparent blue). (C) Dorsal overview image of chelicerae and propeltidium (yellow). (D) Caudal view of levator muscle and tendon, showing the five lobes of the tendon, as well as the large longitudinal spaces (dorsal) and the space occupied by the depressor muscle (ventral). All scale bars are 5 mm.

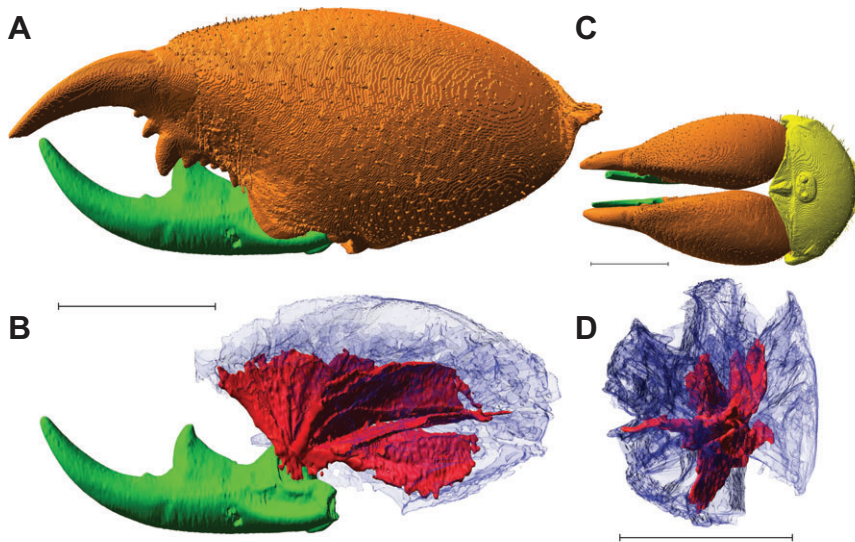


Fig. 5. Renderings of *Rhagodes* chelicerae. (A) Lateral view of left chelicera. (B) Movable finger (green), tendon (red) and levator muscle (transparent blue). (C) Dorsal overview image of chelicerae and propeltidium (yellow). (D) Caudal view of levator muscle and tendon, showing the five lobes of the tendon, as well as the large longitudinal spaces (dorsal) and the space occupied by the depressor muscle (ventral). All scale bars are 5 mm.

pooled data for all specimens of *Rhagodes*, however, showed a significantly higher bite force in the right chelicera (Mann–Whitney and *t*-test, $P < 0.001$). We also tested for asymmetry in bite force per individual. This did not yield any significant (> 0.05) results. In these tests per individual, the lowest *P*-value for any *Galeodes* was 0.19, whereas seven of the 11 *Rhagodes* specimens had near-significant *P*-values as low as 0.06. The lack of significance of these results is probably due to the limited number of bite trials per specimen. The results from the pooled data show that *Rhagodes* bites harder with one of its chelicerae, whereas *Galeodes* shows no such bias. We also tested the linear measurements (length, width, height) of the

chelicerae, but no significant asymmetry in external morphology could be detected for either species.

We found the mechanical advantage (in-lever/out-lever) of the movable finger of *Rhagodes* to be higher than that of *Galeodes* (one-sided Wilcoxon signed rank test $P < 0.001$). Also, the mechanical advantage due to the position of the major tooth differed significantly between the species ($P = 0.025$). In this case, however, *Galeodes* had a higher mechanical advantage. The reconstructed fibers of *Rhagodes* ($N = 24$) and *Galeodes* ($N = 20$) differed significantly in length (two-sided Wilcoxon signed rank test $P < 0.001$), with *Rhagodes* having longer muscle fibers.

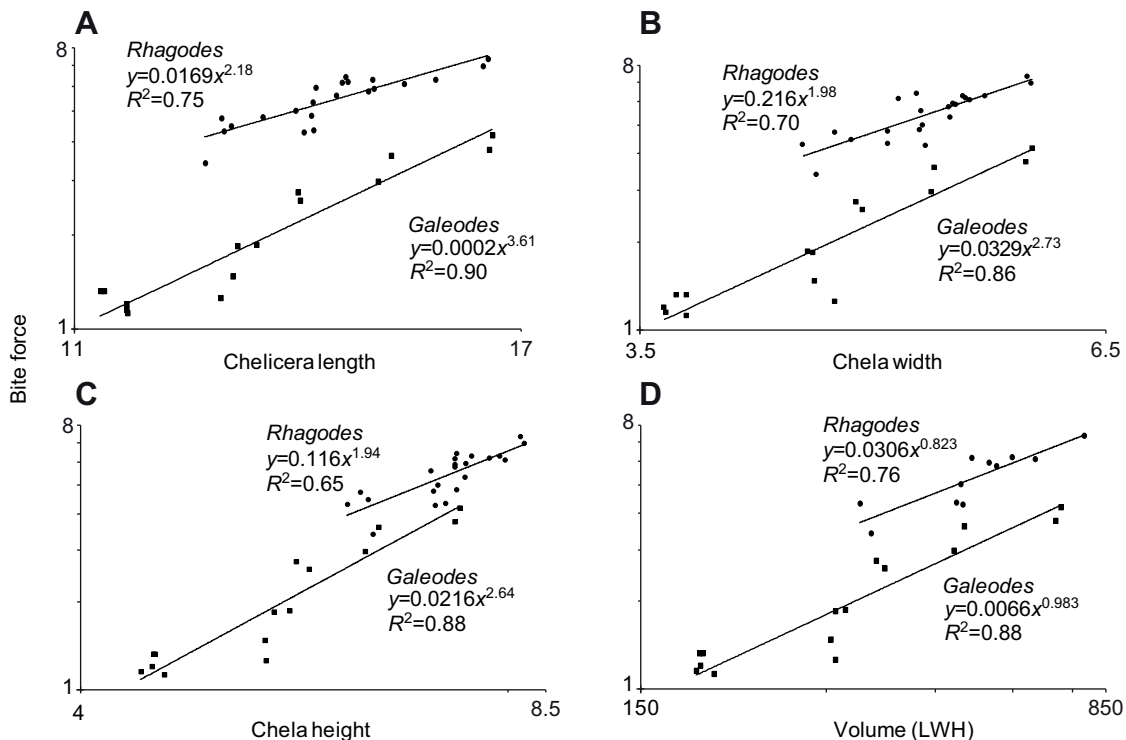


Fig. 6. Maximum bite force plotted against chelicera length (A), width (B), height (C) and the product of length \times width \times height (LWH, D) on log–log axes. Although overlap exists between the two species in chela measurements, *Rhagodes* (circles) has higher bite forces than *Galeodes* (squares) for similar chela dimensions.

Table 2. Measurements from scanned specimens for left and right chelicera

	Absolute values				Units	Corrected for chela length			
	<i>Rhagodes melanus</i>		<i>Galeodes</i> sp.			<i>Rhagodes melanus</i>		<i>Galeodes</i> sp.	
	L	R	L	R		L	R	L	R
Chelicera length	15.7	16.1	10.7	10.7	mm				
Depressor digitus mobilis volume	5.67	5.36	2.54	1.81	mm ³	1.45E-03	1.29E-03	2.09E-03	1.50E-03
Levator digitus mobilis volume	38.5	46.0	24.9	17.5	mm ³	9.88E-03	1.11E-02	2.05E-02	1.45E-02
Tendon levator volume	4.03	3.19	1.38	1.34	mm ³	1.03E-03	7.67E-04	1.14E-03	1.11E-03
Fiber length depressor, mean ± s.d.	3.06±0.74		3.9		mm				
Fiber length levator, mean ± s.d.	1.98±0.42		1.4±0.43		mm				
Tendon–muscle interface PCSA	28.1	30.4	24.8	21.0	mm ²	1.13E-01	1.18E-01	2.18E-01	1.86E-01
Volume/fiber length PCSA	19.5	23.2	17.8	12.5	mm ²	7.87E-02	8.99E-02	1.56E-01	1.10E-01
Estimated bite force	6.83	7.15	1.03	1.03	N	2.76E-02	2.77E-02	9.07E-03	9.05E-03
Levator muscle force at insertion	26.3	27.5	4.29	4.28	N				
Levator muscle stress	936	905	173	203	kPa				

Volume and surface data were corrected for chela length by dividing by the cube and square of chelicera length, respectively, as having only two scanned specimens precludes linear regression and calculation of residuals.

Levator muscle force at the insertion was calculated by dividing estimated bite force by the mechanical advantage (Table 1).

PCSA, physiological cross-sectional area; L, left; R, right.

Comparative analyses

Galeodes had a logBFQ of 2.25 and for *Rhagodes* this was 2.38; these values were significantly different ($F_{1,21}=6.03$, $P=0.023$). The overall logBFQ of arthropods ranged from 0.98 to 2.96 with a mean of 2.24. While scorpions and solifuges had nearly identical logBFQs (2.19 versus 2.27, $F_{1,98}=0.782$, $P=0.379$), crabs showed significantly higher values than chelicerates (2.78 versus 2.21, $F_{1,104}=11.12$, $P=0.001$). Although only based on a theoretical estimation of bite force (see Heethoff and Norton, 2009), an oribatid mite had a logBFQ of 1.6, which fits well in the range observed here.

DISCUSSION

We found anatomical differences between the chelicerae of the two species of camel spiders, leading to significant differences in bite performance. Both in terms of absolute force and relative to its chelicerae size and body mass, *Rhagodes* produces higher bite forces than *Galeodes*. Neither species seemed to prefer biting with a single chelicera at a time versus with both chelicerae simultaneously. There was a remarkable difference in the asymmetry of maximum bite force between the two species. Whereas *Galeodes* did not show any difference in the maximum bite force produced with either chelicera, *Rhagodes* specimens clearly produced higher bite forces with the right chelicera. This relationship could not be verified at the individual level, presumably because of the limited number of observations per specimen. The asymmetry in bite performance was reflected by the larger volume of the right levator muscle in *Rhagodes*, as well as a larger PCSA based on the muscle–tendon interface (the fact that the PCSA calculated from muscle volume and fiber length is larger in the right muscle is simply a reflection of the larger muscle volume, as only the mean fiber length of the left muscle was measured and used in this calculation). Also *Galeodes* showed asymmetry in the volume of the levator muscles and the PCSA (Table 2) but, as stated above, no asymmetry was found in the maximum bite force of this species. It is conceivable that *Galeodes* have an individual asymmetry of chelicera strength. However, such a pattern was not detectable in our limited dataset, as even in *Rhagodes* we were not able to discern asymmetry at the individual level. Future studies therefore need to include more trials per individual. The observed asymmetry in muscle size did not correspond to an asymmetry in external chelicera dimensions. Apart from asymmetric flagellae in a single individual (Delle Cave, 1979),

no asymmetry has been recorded in the external morphology of solifugae chelicerae. Whether the observed asymmetry in muscles and performance has an adaptive significance, like the asymmetric pincers of brachyuran crabs (with one robust ‘crusher’ and a more slender ‘cutter’ chela) (Hughes, 2000), remains unclear. Unlike fiddler crabs, in which chela size may not be an honest signal of pinch force (Lailvaux et al., 2009), the observed intra-individual independence of external chelicera size and bite force is unlikely to be attributable to sexual selection on competing males, as all *Rhagodes* included in this study were female. As digging behavior in compacted soil usually involves both chelicerae (Hingston, 1925), the observed asymmetry of maximum bite force cannot be explained by the difference in burrowing habits. For some functional purposes, however, e.g. cracking a tough exoskeleton of a prey item, it may be beneficial to have a single stronger chelicera than two less-strong chelicerae. Further ecological and behavioral studies of *Rhagodes* will be required to uncover the functional benefit of the asymmetric performance of the chelicerae.

Although the internal anatomy of the two species is roughly similar, there were some large differences in relative size of the muscles. When muscle volume is corrected for chelicera length (by dividing by the cube of chelicera length; Table 2), giving the relative size of the muscle, the values for the depressor digiti mobilis do not differ very much between the two species. The relative size of the levator muscles, however, shows a considerable difference: 0.0099 (left) and 0.0111 (right) in *Rhagodes* versus 0.0205 (left) and 0.0145 (right) in *Galeodes*. Similar differences are found in the relative size of the PCSA, thus reflecting the differences in bite force. Muscle stress (force at muscle insertion/PCSA) differs greatly between the two species, being much greater in *Rhagodes*. The value of 173–203 kPa for *Galeodes* is comparable to muscle stresses observed in other invertebrates, e.g. the cockroach *Blaberus discoidalis* (260–470 kPa) (Ahn and Full, 2002) or the spider *Cupiennius salei* (253 kPa) (Siebert et al., 2010). The estimated muscle stress in *Rhagodes* is very high at 905–936 kPa, but within the range known for mites (1170 kPa) (Heethoff and Koerner, 2007) or crabs (740–1350 kPa) (Taylor, 2000). Given that in crabs these high muscle stresses are attributed to longer sarcomere lengths (Taylor, 2000), it is likely that a similar adaptation has taken place in *Rhagodes*. The complex shape of the tendon and large range of observed muscle fiber angles did not allow us to estimate a single

value for the pennation angle of the levator muscle. We thus were not able to correct the estimates for the PCSA for the angle the muscle fiber makes with the line of action of the tendon. This leads to an overestimate of the PCSA. The actual value of the muscle stress may therefore be even higher than reported here.

Both species showed two remarkable longitudinal grooves along the dorsal and lateral surface of the levator muscle. These grooves provide space for tracheal air and, possibly, hemolymph circulation. As *Galeodes* use their chelicerae nearly continuously for several minutes during the reduction of prey, with a mean frequency of 1.6 Hz (F.L., unpublished data), repetitive muscle action may aid in forcing tracheal air, hemolymph, or both, through the chelicerae. The existence of such a mechanism would enable these animals to sustain a high level of muscle activity, and merits further study.

In the external morphology of the chelicerae, *Rhagodes* shows the lower aspect ratio of the two species. Low aspect ratio has been correlated to higher bite force in chelae of scorpions (Van der Meijden, 2010) and decapods (Lee, 1993) (but see Sneddon et al., 2000). Low aspect ratio morphologies have been shown to reduce deformation and stress in the chelae of scorpions (Van der Meijden, 2012), and may therefore represent an adaptation to reduce the risk of structural failure under high force loads. Also, the mechanical advantage of the lever system of the movable finger differed between the two studied species. Although *Galeodes* has a lower mechanical (force) advantage if force is transmitted at the tip of the movable finger, it has a higher mechanical advantage than *Rhagodes* if the force is transmitted at the main tooth. This may enable *Galeodes* to crush hard prey (such as beetles) despite having relatively weaker chelicerae. Having large and heavy chelicerae will probably be a greater burden on the highly cursorial *Galeodes* than on the burrowing *Rhagodes*. Placing the main tooth closer to the joint, while increasing the mechanical advantage, would reduce the maximum gape at the main tooth, and thus the size of the hard prey items to be crushed there. Wharton (Wharton, 1987) observed that, in sandy soil, chelicerae are only rarely used in digging, which would release the chelicerae from their function in loosening compacted soil in sandy habitats. Whereas in captivity we observed *Rhagodes* constructing extensive tunnels in compacted soil, *Galeodes* was found in the field in relatively shallow burrows under stones. It is therefore possible that *Galeodes* uses its chelicerae much less for digging, particularly in compacted soil, than *Rhagodes*. Unfortunately, conclusions cannot be drawn from these scant observations, and further ecological observations of these two ecomorphotypes of solifuges may shed more light on the adaptive significance of their difference in chelicerae morphology and performance.

We calculated a BFQ that should be independent of body mass. Using this BFQ, we found that crabs are thus far the strongest arthropod biters (Taylor, 2000), followed by solifuges and scorpions. Scorpions are characterized by species with strong pincers and species with weak pincers (Van der Meijden et al., 2010; Van der Meijden et al., 2012) and their BFQ covers a wide range of almost three orders of magnitude ($\log_{10} \text{BFQ} = 0.98\text{--}2.89$), suggesting very different needs in terms of pincer bite performance. Hence, this group seems to be highly suitable for further investigation of bite forces in an ecological context.

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