

Small but powerful: the oribatid mite *Archezogozetes longisetosus* Aoki (Acari, Oribatida) produces disproportionately high forces

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Summary

We investigated the holding and pulling forces generated by claws of the microarthropod *Archezogozetes longisetosus* (Chelicerata, Acari, Oribatida) on three substrates with different roughness ($R_a=0.05\ \mu\text{m}$, $1\ \mu\text{m}$, $30\ \mu\text{m}$). Holding forces were measured perpendicular to the substrate using a strain gage force transducer; pulling forces were measured parallel to the substrate using an analytical scale. We found a significant positive correlation of surface roughness and the forces generated. Mites produced holding forces on horizontal rough surfaces ($R_a=30\ \mu\text{m}$) of up to 1180 times their weight; on vertical rough surfaces ($R_a=30\ \mu\text{m}$) they can pull with 530 times their weight,

effectively involving only two pairs of legs. The relative forces are five times higher than theoretically expected for organisms of this size ($<1\ \text{mm}$, $100\ \mu\text{g}$) and higher than any relative forces reported for insect claws. Muscles involved in claw action produced stresses up to $1170\ \text{kN m}^{-2}$, a value that is only excelled by decapod crustacean claw closer muscles. Ours is the first study of performance by chelicerate apoteles and claws and also the first to measure forces generated by any microarthropod.

Key words: Acari, Oribatida, force measurement, performance, claw.

Introduction

Apoteles are the terminal elements of postcheliceral limbs in members of the Chelicerata, where a three-clawed appearance probably represents the plesiomorphic state (Dunlop, 2002). The morphology of claws can be understood in the context of adaptation to interact with diverse rough surfaces (Nachtigall, 1974). Specialized adhesive attachment devices for smooth surfaces, such as pulvilli and tarsal hairs, occur in chelicerates and insects, and in the latter they have been studied experimentally in a variety of taxa (Beutel and Gorb, 2001). However, the claw action and its relation to surface structure have been little investigated. While the performance and functional morphology of insect tarsi have been studied to some extent (Stork, 1980; Lees and Hardie, 1988; Federle et al., 2000; Dai et al., 2002; Betz, 2002), we are unaware of any studies investigating the performance of chelicerate claws. The only available study investigated a general correlation of the size of adhesive devices and body mass in a variety of arthropods, including the spider species *Cupiennius salei* and *Aphonopelma seemanni*, but without measuring performance or taking claws into account (Arzt et al., 2003).

Tremendous degrees of apotele modifications appear in different lineages of chelicerates and have been used together with general leg morphology for large-scale phylogenetic analyses (Shultz, 1989; Shultz, 2007; Dunlop, 2002). Both the simplest and the most complex apoteles appear in the Acari (Evans, 1992; Alberti and Coons, 1999; Dunlop, 2002). Acari

are grouped into two large taxa, the Anactinotrichida (=Parasitiformes+Opilioacarida) and the Actinotrichida (=Acariformes). While the monophyly of Acariformes, Parasitiformes and Opilioacarida is generally accepted, monophyly of Acari as a whole has been questioned several times, not least due to the variations in apotele morphology (Alberti, 2005). Regressive apoteles comprise two claws, a single claw or no claws at all and are present in various taxa of Actinotrichida; however, the Anactinotrichida usually retain their two lateral claws, while the middle claw is modified into a cushion-like pulvillus (Evans, 1992). Movements of the claws are effected through the action of depressor and levator muscles, which connect by tendons to the ventral and dorsal edges of the basilar piece, respectively (Figs 1, 2). The claws are formed of modified setae and contain birefringent actinopilin in the Actinotrichida (Grandjean, 1941; Grandjean, 1943).

The high range of apotele morphology presumably corresponds to adaptation into different niches. Evaluation of the performance of specific apotele morphologies can provide information on differential adaptive values from an ecomorphological point of view (e.g. Bock, 1988; Betz, 2002). However, due to the small size of most of the Acari ($<1\ \text{mm}$ length), measuring of forces of the claws ($\sim 50\ \mu\text{m}$ length) is particularly difficult.

The size-grain hypothesis (Kaspari and Weiser, 1999) states that the environmental rugosity significantly increases with decreasing body size of walking organisms. Hence,

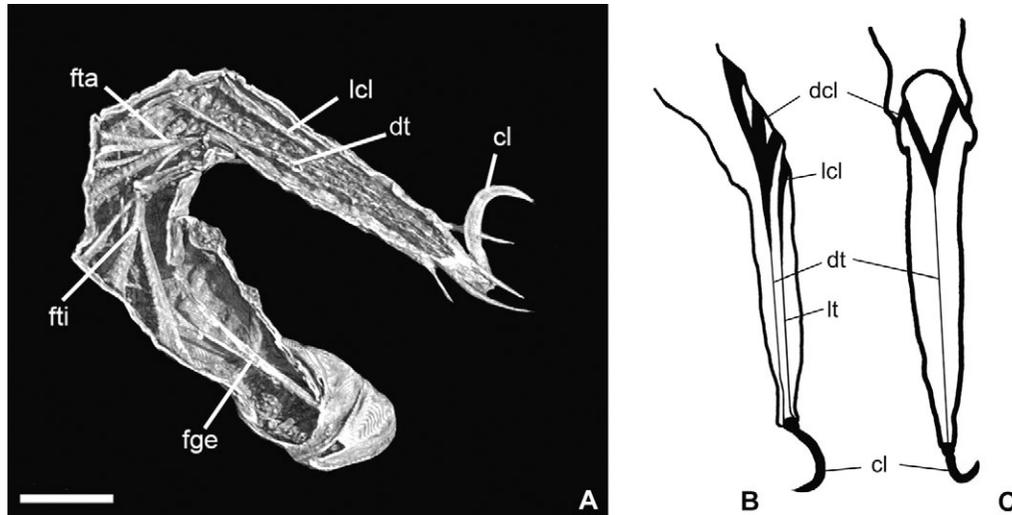


Fig. 1. (A) General morphology and muscular configuration of the first left walking leg of *Archegozetes longisetosus*: 3D image obtained by X-ray microtomography. Setae on legs were removed during image processing. (B,C) Schematic organization of the claw muscles in sagittal (B) and horizontal (C) view. Note that only the apotele acts through both a levator and a depressor muscle; all other visible muscles are flexors. The claw levator muscle is divided into two subcomponents (not shown), each consisting of one bundle. The claw depressor muscle originates in the tibia and consists of two subcomponents, each with three bundles, which join at a single tendon in the tarsus. cl, claw; dcl, depressor of claw; dt, depressor tendon; fta, flexor of tarsus; fti, flexor of tibia; fge, flexor of genu; lcl, levator of claw; lt, levator tendon. Scale bar, 50 μm .

microarthropods experience their environment as a three-dimensional habitat of interstices and gaps. In this context, small organisms are thought to walk 'through' rather than 'over' a landscape. The wide range of ecological niches inhabited by Acari (predatory, parasitic, herbivorous, fungivorous, saprophytic) suggests that the landscape microstructure is highly variable for the different ecological groups. Thus requirements of the locomotory system to perambulate these landscapes should reflect this variability. We expect the highest

forces of the locomotory appendages in soil-living mites, due to the necessity of movement within a heterogeneous and unpredictable environment.

In the present study we provide the first force measurements for such microarthropods. We used two approaches to measure different forces of a single-clawed oribatid mite, *Archegozetes longisetosus* Aoki: the holding forces perpendicular to the substrate and the pulling forces parallel to the substrate on three test surfaces with different roughness. Our results provide the

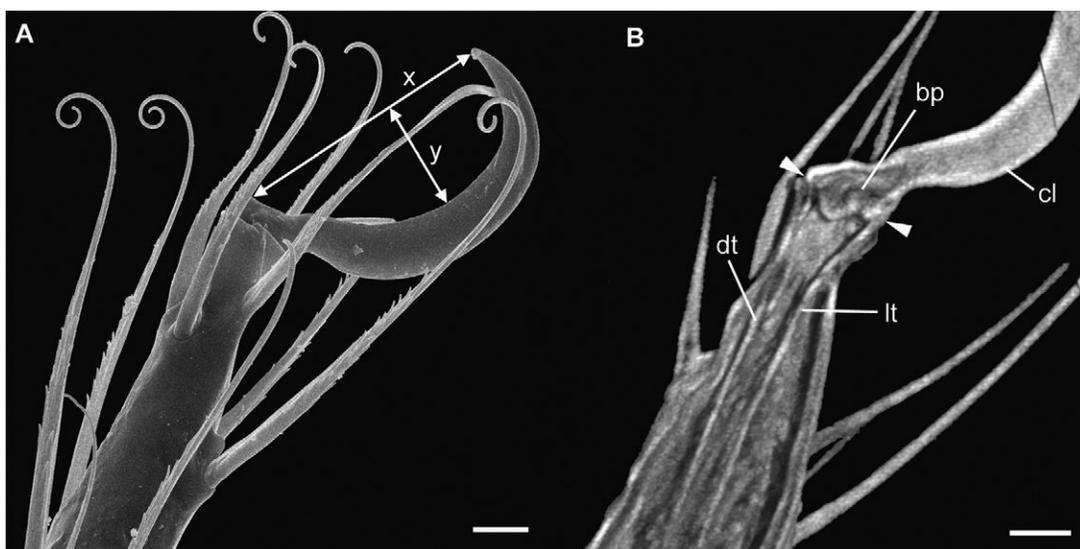


Fig. 2. Distal tarsus and apotele of the first left walking leg of *Archegozetes longisetosus* showing the single claw. (A) SEM micrograph. (B) 3D image (sagittal virtual section) obtained by X-ray microtomography. Arrowheads indicate the insertion sites of the levator and depressor tendons on the apotele. bp, basilar piece; cl, claw; dt, depressor tendon; lt, levator tendon; x, diameter of claw opening; y, height of claw opening. Scale bars, 10 μm .

opportunity for future comparative studies of the performance and adaptive values of different apotele morphologies within the Acari and other microarthropods.

Materials and methods

Animals used in this study

Archegozetes longisetosus Aoki (Oribatida, Trhypochthoniidae) is a soil saprophagous, parthenogenetic oribatid mite, established as a model system for chelicerate evolution [for an overview, see Heathoff et al. (Heathoff et al., 2007)]. This species usually inhabits isolated litter pockets of the soil (Haq, 1982), so that we expect high forces of the locomotory system due to digging activity. With exception of the claw, the primitive chelicerate condition of missing extensor muscles in the legs is retained, as in all Acari (Shultz, 1989) (Fig. 1); the four pairs of walking legs each have a single claw that is entirely fused with the basilar piece (Fig. 2) and linked by condylophores with the sclerotized tarsal cuticle.

The average individual mass of adult specimens, taken from our laboratory strain *A. longisetosus* ran (Heathoff et al., 2007), was approximately 100 μg , determined by weighing five samples of 30–50 adults. Adult specimens chosen from our laboratory culture were actively moving, had fed, and contained no eggs. The latter two parameters could be easily checked due to the translucent cuticle of adults.

Surfaces used in this study

Three different surfaces with defined texture roughness (R_a) were chosen for force measurements, available as lapping and polishing films with applied Al_2O_3 particles of defined sizes (Ultratec Manufacturing Inc., USA). Roughnesses of 0.05 μm , 1 μm and 30 μm were chosen to span a wide range of claw–surface interaction strength (Fig. 3).

Imaging

For SEM imaging, adult specimens were dissected to remove the legs, which were then dehydrated in an ethanol series, critically point dried in CO_2 , and sputter-coated with a 20 nm thick layer of gold–palladium. Claws were examined in a Cambridge Stereoscan 250 MK2 scanning electron microscope at 20 keV. Test surfaces were also sputter-coated and examined by SEM. Morphological parameters of the claws (Fig. 2) were measured using the software tpsDig 1.40 (F. James Rohlf 2004, <http://life.bio.sunysb.edu/morph/soft-dataacq.html>).

We used X-ray microtomography for the non-invasive analyses of leg and muscle morphology. This technique is a valuable tool for studying the internal anatomy of small organisms with sub- μm resolution (Betz et al., 2007). Fresh adult specimens were placed in glutaraldehyde for 60 h, dehydrated in an ethanol series and critically point dried in CO_2 . Scans of whole animals were taken at the European Synchrotron Radiation Facility (ESRF, Grenoble, France) at beamline ID19 (experiment SC2127) with a detector–sample distance of 20 mm and a pixel resolution of 0.7 μm (Fig. 1A) and 0.3 μm (Fig. 2B) at 20.5 keV. Image analyses of the voxel data and measurements of muscle diameters were performed using the software VGStudio Max 1.2.1. (Volume Graphics, Heidelberg, Germany).

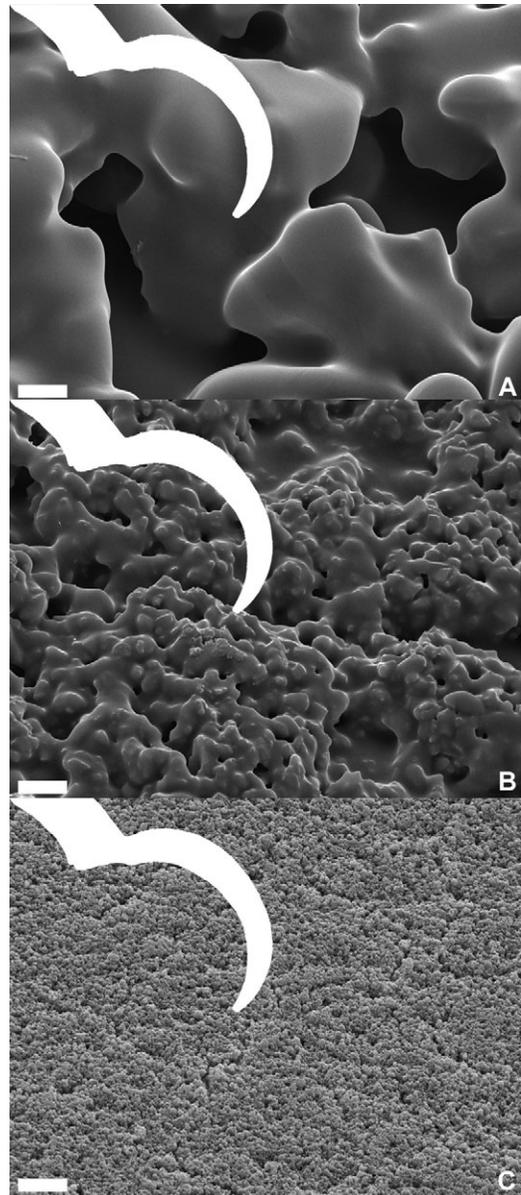


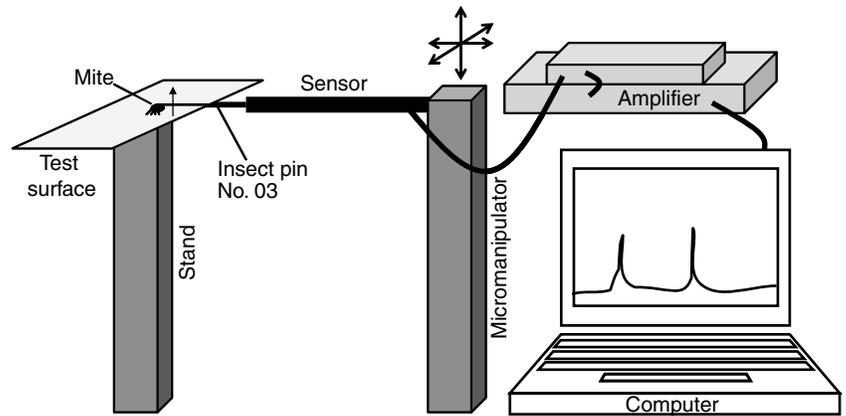
Fig. 3. SEM-micrographs of surface textures. (A) $R_a=30 \mu\text{m}$ particle size, (B) $R_a=1 \mu\text{m}$ particle size, (C) $R_a=0.05 \mu\text{m}$ particle size. The silhouette of the *Archegozetes longisetosus* claw (setae removed) illustrates the claw size relative to surface texture. Scale bars, 10 μm .

Force measurements on living mites

Two kinds of forces were measured on each of the three surfaces: (i) holding forces and (ii) pulling forces.

(i) Holding forces (also termed attachment forces) (Federle et al., 2000) were calculated as the capability of the mite to remain attached to the surface when lifted up vertically (Fig. 4). Data were acquired as mass (m) and transformed into force (F) using the formula $F=mg$ (where $g=981 \text{ m s}^{-2}$). The MP100 WSW data acquisition system (BIOPAC Systems Inc., USA) with a strain gage force transducer (FORT25, WPI Inc., USA) was used to calculate the holding forces. The signal was amplified by a transducer amplifier (BIOPAC Systems Inc.) and calibrated by a 2 g mass. Mites were super-glued with the notogaster (dorsal

Fig. 4. System for measuring holding forces of *Archezogetes longisetosus*. The test surfaces were fixed horizontally on a stand. The mite was glued to an insect pin and mounted to the strain gage force transducer (FORT25, WPI Inc., USA), which was connected to a micromanipulator. Forces generated by the mites were transferred to the sensor, amplified by the MP100 system (BIOPAC Systems Inc., USA) and recorded with a personal computer and the software AcqKnowledge 3.8.2 (BIOPAC Systems Inc., USA).



shield) on an insect pin (No. 03) and the pin was mounted to the force sensor on a micromanipulator. The mite was then carefully touched to the horizontal test surface using the micromanipulator and allowed to attach with all walking legs (checked with a stereo microscope). The force sensor was then moved upwards until the mite detached with all legs from the surface, and the masses were measured. This procedure was repeated 30 times with all specimens and five specimens were tested on each surface. The difference between the maximum amplitude of the force sensor and the zero-line (mite hanging free, not attached to surface, Fig. 6) was calculated using the software AcqKnowledge 3.8.2 (BIOPAC Systems Inc., USA); maximum forces were used for subsequent analyses.

(ii) Pulling forces (also termed friction forces) (Dai et al., 2002) were measured as the capability to move upwards on vertical surfaces. Data were acquired as mass using an analytical scale (GR-202-EC, A&D Instruments Ltd, UK, Figs 5, 8) and transformed into forces using the formula $F=mg$. Mites were glued with the notogaster on the tip of an insect pin (No. 00); the pin was thoroughly mounted with the pin head in a ~2 g piece of modelling clay, so that it could not slip. The piece of modelling clay was then placed on the scale and the scale was set to zero. The test surfaces were mounted vertically on a micromanipulator and moved towards the mite until all walking legs were attached to the surface (checked with a stereo microscope). The scale was connected to a computer and the mass was continuously recorded for 2 min with the software RsKey 1.34 (A&D Instruments Ltd, UK). A negative mass was recorded whenever the mites tried to walk upwards, thereby pulling the modelling clay away from the scale (Fig. 8). On each surface, seven specimens were tested; the maximum forces from each replicate were used for subsequent analyses.

Statistical analyses

Morphological parameters (x,y ; Fig. 2) of claws and forces on different surfaces were analysed using one-way ANOVA in SPSS (SPSS Inc., USA); homogeneous groups were identified with a Tukey *post-hoc* test ($P<0.05$). Values are means \pm standard deviation (s.d.).

Results

Morphology

All claws had the same values for the measured parameters x and y : $49.7\pm 3.49\ \mu\text{m}$ (mean \pm s.d.; $N=12$) and $20.9\pm 1.93\ \mu\text{m}$ ($N=12$), respectively, without significant differences among the different legs ($N=3$). The claw levator muscle is divided into two subcomponents, each consisting of one bundle. It originates near the joint of tibia and tarsus, and the components join at the levator tendon in the tarsus (Fig. 1). The claw depressor muscle originates in the tibia and consists of two subcomponents, each with three bundles, which join at a tendon in the tarsus. The diameter of each claw depressor muscle bundles was $6\pm 0.3\ \mu\text{m}$ ($N=6$) leading to a bundle cross-sectional area of $2.83\times 10^{-11}\ \text{m}^2$ and a functional cross-sectional area (adding all six bundles) of $1.7\times 10^{-10}\ \text{m}^2$.

Holding forces

Holding forces were calculated in relation to different substrate roughness; see Fig. 6 for a typical example of a measurement. Maximum holding forces significantly increased

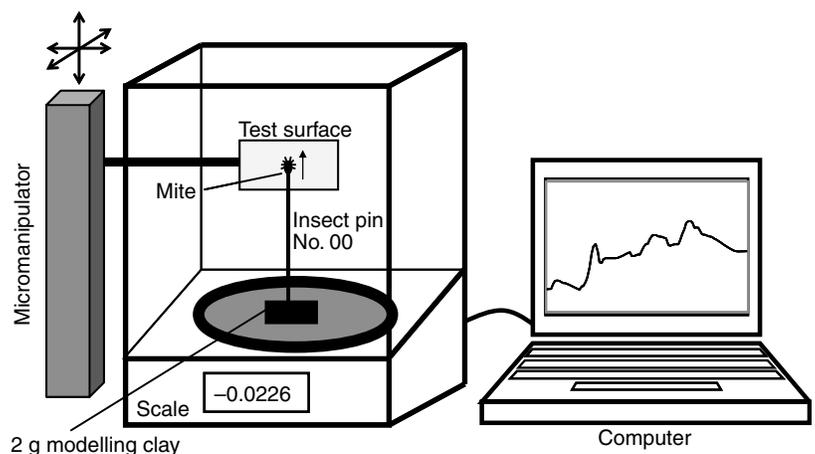


Fig. 5. System for measuring pulling forces of *Archezogetes longisetosus*, using an analytical scale (A&D Instruments Ltd., UK). Mites were glued by the notogaster to an insect pin, which was mounted to a piece of modelling clay. Mites were attached to the vertical test surfaces and the scale was set to zero. Changes in masses were recorded with a personal computer and the software RsKey 1.34 (A&D Instruments Ltd., UK). Negative changes corresponded to pulling forces.

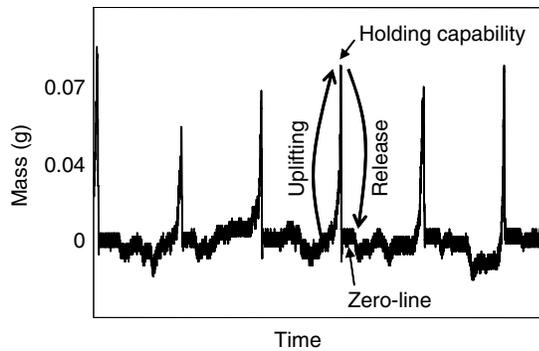


Fig. 6. Example of continuously recorded forces and repeated measures of the holding capability of *Archezogetes longisetosus*.

with the particle diameter of the surfaces for all three values of R_a ($F_{(2,14)}=57.2$, $P<0.001$; Table 1; Fig. 7). On surfaces with $R_a=0.05 \mu\text{m}$, mites produced forces of 0.0715 mN. Surfaces with $R_a=1 \mu\text{m}$ provided the mites with enough irregularities to cling to cavities with forces eight times higher compared to the $0.05 \mu\text{m}$ substrate (0.5888 mN). On the roughest surface ($R_a=30 \mu\text{m}$), observed holding forces were exceptionally high, reaching 1.1592 mN. This was 1.8 times higher when compared to $R_a=1 \mu\text{m}$ and corresponds to 1180 times the body weight.

Pulling forces

Pulling forces were also calculated in relation to substrate roughness. A typical example of a measurement is given in Fig. 8. Maximum pulling forces were different among the surfaces ($F_{(2,20)}=16.8$, $P<0.001$; Table 1; Fig. 9), although differences between $R_a=1 \mu\text{m}$ and $R_a=30 \mu\text{m}$ were not significant. The substrate with $R_a=0.05 \mu\text{m}$ led to pulling forces up to 0.196 mN. On surfaces with $R_a=1 \mu\text{m}$, pulling forces were 1.5 times higher than on the $0.05 \mu\text{m}$ substrate (0.3237 mN). Observed forces on the roughest surface were 2.8 times higher when compared to $R_a=0.05 \mu\text{m}$ and the pulling capability reached up to 530 times the body weight.

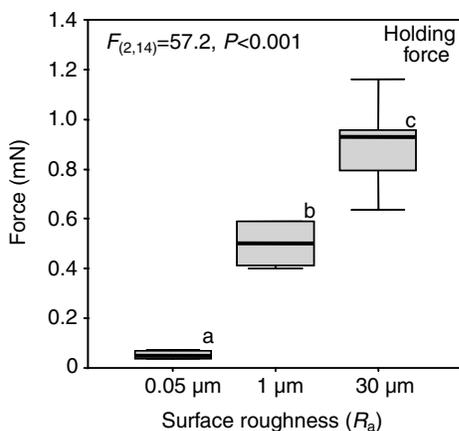


Fig. 7. Box-plot of maximum holding forces on different substrates. Substrate roughness (R_a) significantly affects the holding forces. Holding forces increase with increasing R_a (a, b, c: homogeneous groups, Tukey test).

Table 1. Holding and pulling forces of *Archezogetes longisetosus* on substrates of different roughness

Force (mN)	Roughness (R_a)		
	0.05 μm	1 μm	30 μm
Holding			
Average	0.0534 \pm 0.017	0.4997 \pm 0.092	0.8959 \pm 0.195
Maximum	0.0715	0.5888	1.1592
Pulling			
Average	0.1275 \pm 0.033	0.2690 \pm 0.048	0.3546 \pm 0.114
Maximum	0.1962	0.3237	0.5199

Averages are arithmetic means \pm s.d.

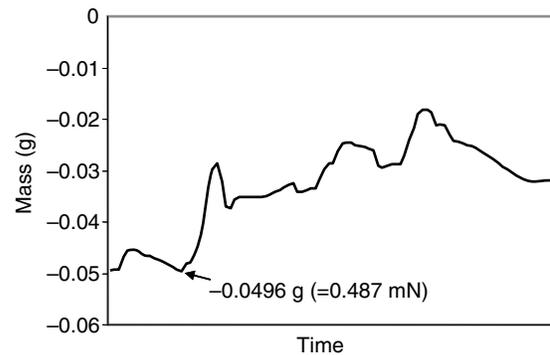


Fig. 8. Example of continuously recorded measures of the pulling forces exerted by *Archezogetes longisetosus*. The maximum attained force is indicated.

Discussion

Morphology of the apotele and the test surfaces

The spheroid particles were not homogeneously distributed on the test surfaces (Fig. 3), which led to a higher-order-organization. Therefore, it is currently not possible to calculate a precise interaction model of claws and surfaces. It is also not

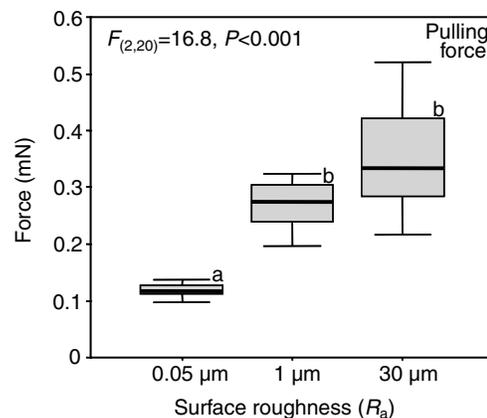


Fig. 9. Box-plot of maximum pulling forces exerted by *Archezogetes longisetosus* on different substrates. Substrate roughness (R_a) significantly affects the pulling forces. The pulling forces of the claw increase with increasing R_a (a, b: homogeneous groups, Tukey test).

possible at present to develop a suitable model for the precise claw movement since the claws are too small to observe the maximum angles of deflection *in vivo*. These would be interesting topics for future research.

Our results clearly suggest, however, that the interaction strength of claws and the substrate significantly increases with substrate roughness. This is a result of the correlation of claw size and surface particle diameter, together with overall heterogeneity of the surface. A similar correlation of surface roughness and claw forces has been shown for larger arthropods, including the beetle *Pachnoda marginata* (Dai et al., 2002), beetles of the genus *Stenus* (Betz, 2002) and the true bug *Pyrrhocoris apterus* (Tölke, 2005).

Holding and pulling forces

To compare holding and pulling forces, it is important to take the positioning and orientation of the legs on the surfaces into account. The holding forces were measured at a right angle to the longitudinal axis of the mite. Thus all legs should make the same contribution to the holding forces irrespective of the horizontal angle between body and leg, as long as all claws are the same size. Forces measured along the longitudinal axis, however, relate only to the first two pairs of walking legs. In oribatid mites, as generally in Actinotrichida, these are directed anteriorly, while the third and fourth pairs are directed posteriorly (Evans, 1992). Pulling forces are thereby generated only by half of the legs and should therefore be only about half the magnitude of the holding forces. For rough surfaces ($R_a=1\ \mu\text{m}$, $R_a=30\ \mu\text{m}$) this is a suitable approximation; average holding forces divided by pulling forces were 1.86 and 2.43 for $R_a=1\ \mu\text{m}$ and $R_a=30\ \mu\text{m}$, respectively. However, on the smooth surface ($R_a=0.05\ \mu\text{m}$) this relation is completely different and even inverted (0.42).

The reason for this is apparent from Fig. 3. The particles and the surface heterogeneity on the smooth surface (Fig. 3C) are too small for the claw to fit very far into cavities, thereby losing much of their ability to resist detachment at a right angle to the surface. However, the production of forces along the longitudinal axis is still possible to some extent (approx. twice as high as the holding forces), because here, only the very tip of the claw has to interact with the surface. Correspondingly, mite behaviour is different on the three surfaces. On surfaces of $R_a=1\ \mu\text{m}$ and $R_a=30\ \mu\text{m}$, mites almost immediately find a good position with their legs; they keep the legs in one position and start pulling. On the smooth surface, the mite undergoes behaviour more like 'ice-skating', where the forces are produced while the claws scratch over the surface to find a position to hook into.

Force/weight ratio and muscle stress

Generally, large animals exert higher forces than small ones. However, these forces are expected to be proportional to the volume rather than the body mass because the weight is proportional to the cube of the body length (Alexander, 1985; Federle et al., 2000). Thus force/weight should be proportional to body mass^{-1/3} (Alexander, 1985); accordingly, force should be proportional to body weight^{2/3} as long as animals have comparable shapes and densities (Federle et al., 2000). However, animals of equal mass may exert different maximum

forces. Therefore, an upper and lower threshold for the force/weight ratio of $0.5 \times \text{body mass}^{-1/3}$ and $20 \times \text{body mass}^{-1/3}$, respectively, can be given to describe a range of maximum force/weight ratios (Alexander, 1985). Using this assumption and the given body mass of $100\ \mu\text{g}$ for *A. longisetosus*, we expect a force/weight ratio of 215 (or a value within the force/weight range between 108 and 4309). The maximum exerted force of 1.1592 mN leads to a force/weight ratio of 1182. This value is more than five times higher than expected, but within the theoretical range of maximum possible forces.

Forces, however, depend not only on the weight and size of an organism but also on the properties of muscles involved in force production. Some muscles can produce higher stresses (force/cross-sectional area) than others and this can also be compared among different groups of muscles and animals (Taylor, 2000). While vertebrate and insect flight muscles yield stresses of $100\text{--}300\ \text{kN m}^{-2}$, the closer muscle of decapod crustacean claws can generate stresses up to $1350\ \text{kN m}^{-2}$ (Taylor, 2000).

The functional cross-sectional area of the whole claw depressor muscle of *A. longisetosus* was calculated by adding the cross-sectional areas of all six bundles. Since the generated holding forces are the result of the action of all eight legs, this value was multiplied by eight and led to a functional cross-sectional area of $1.3568 \times 10^{-9}\ \text{m}^2$. Together with the maximum holding force of 1.1592 mN, this results in a muscle stress of $1171\ \text{kN m}^{-2}$, four times higher than the highest values reported for insect flight muscles and vertebrate muscles, but within the exceptionally high range of decapod claw closing muscles.

Comparisons with insect forces

It is difficult to compare forces generated by the claws of insects directly with those generated by mites because of the different mechanisms responsible for movements of the claws. The insect unguitactor apparatus is connected to the tendon of the claw flexor muscle on one side and to the claw on the other side (Heinzeller et al., 1989). Gorb (Gorb, 1996) hypothesized that this structure enables an interlocking mechanism that allows a claw engaged with the surface to be held in a bent position with a reduced muscular energy investment. Oribatid mites, in contrast, have no unguitactor apparatus and the claw is actively moved in both directions by direct muscular action (Evans, 1992) (Fig. 1, Fig. 2B). Other differences are the number of claws on each leg and the number of legs. While insects have six legs to generate attachment forces, most mites have eight; and while most insect species have two claws on each leg, *A. longisetosus* has only one. Furthermore, as already described, the contribution of each leg to the measured pulling forces depends on the positioning of the leg on the surface (Dai et al., 2002), information that unfortunately is not available for most of the studies.

Betz (Betz, 2002) reported that the beetle *Stenus cicindeloides* generates maximum pulling forces with claws on rough surfaces (filter paper) with a force/weight ratio of 73 after the tenent setae had been neutralized by covering them with a thin layer of superglue. Claw forces of the beetle *Pachnoda marginata* were investigated by Dai et al. (Dai et al., 2002); on rough surfaces, the force/weight ratio was 38. Tölke (Tölke, 2005) found that the true bug *Pyrrhocoris apterus* could pull with an equivalent of 36

times its weight, after pulvilli were removed. On rough filter paper, Lees and Hardie (Lees and Hardie, 1988) reported the aphid *Megoura viciae* having a claw pulling force/weight ratio of 17, after the pulvilli were inactivated.

If the pulling forces generated by claws of insects are thus compared with our results, we can conclude that *A. longisetosus* has the highest pulling force/weight ratio, seven times higher than the highest so far reported in insects (Betz, 2002). Federle et al. (Federle et al., 2000) reported holding force/weight ratios of 145 for the ant *Crematogaster*, which is eight times less than the holding force/weight ratio reported here. Unfortunately, they used intact tarsi, hence no holding forces are available for arthropod claws only for comparison with our results.

However, as described above, the comparison of force/weight ratios can lead to questionable results due to errors occurring by linear scaling of parameters that are not linearly proportional. Therefore, we also compared the force/weight^{2/3} ratio. Insects have an arithmetic mean for force/weight^{2/3} of 3.12±3.01 (mean ± s.d., range: 0.055–8.15). The lowest value was observed in the aphid, *M. viciae* (Lees and Hardie, 1988), the highest in the beetle, *P. marginata* (Dai et al., 2002). Most insects studied [*S. cicindeloides* (Betz, 2002); *P. apterus* (Tölke, 2005); *Crematogaster* (Federle et al., 2000)], however, have a force/weight^{2/3} ratio between 2.1 and 2.95, indicating that the factor of proportionality lies within this range. With 2.36, the median is possibly a good approximation to the factor of proportionality. Taking this into account, we argue that force/weight^{2/3} ratios much less than 2 describe disproportional weakness and ratios much higher than 3 describe disproportional strength. The aphid *M. viciae* produces much lower forces than theoretically expected for an insect; accordingly *P. marginata* produces disproportionate high forces. The force/weight^{2/3} ratio of *A. longisetosus* reported here is 11.74, five times higher than theoretically expected.

To conclude, we have shown that the soil-dwelling microarthropod *A. longisetosus* produces exceptionally high relative claw forces. The high force/weight ratios are not scaling artefacts; on the contrary, *A. longisetosus* produces disproportionately high forces with its claws. As hypothesized, these high forces are presumably important to move and burrow effectively in soil. The simple organization of its apotele (single claw, direct muscular movement with flexor and depressor), the high muscle stresses, and the high relative forces make *A. longisetosus* a valuable model system for further investigations of the functioning of arthropod claws.

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