

1 Slit sense organ distribution on the legs of two species of orb-weaving spider (Araneae:
2 Araneidae)

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4 **Keywords:**

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6 Orb-weaver, mechanosensor, slit sense organ, proprioception, vibrations

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8 **Author list:**

9
10 Thomas E. Miller

11 Graham K. Taylor

12 Beth Mortimer – Corresponding author: beth.mortimer@zoo.ox.ac.uk

13
14 Department of Zoology

15 Zoology Research and Administration Building

16 11a Mansfield Road

17 Oxford

18 OX1 3SZ

21 Abstract

22

23 Biotic and abiotic mechanical stimuli are ubiquitous in the environment, and are a widely used source
24 of sensory information in arthropods. Spiders sense mechanical stimuli using hundreds of slit sense
25 organs (small isolated slits, large isolated slits, groups of slits and lyriform organs) distributed across
26 their bodies and appendages. These slit sense organs are embedded in the exoskeleton and detect
27 cuticular strain. Therefore, the spatial pattern of these sensors can give clues into how mechanical
28 stimuli from different sources might be processed and filtered as they are transmitted through the
29 body. Here, we map the distribution of slit sense organs on the legs in two species of orb-weaving
30 spider, *Araneus diadematus* and *Trichonephila edulis*, in which slit sense organ distribution has not
31 previously been investigated. We image the spiders' legs using scanning electron microscopy, and
32 trace the position and orientation of slits on these images to describe the distribution and external
33 morphology of the slit sense organs. We show that both species have a similar distribution of slit sense
34 organs, with small isolated slits occurring in consistent lines parallel to the long axis of the legs, whilst
35 large isolated slits, groups of slits and lyriform organs appear in fixed positions near the leg joints. Our
36 findings support what has been described in the literature for several other species of spider, which
37 indicates that slit organ arrangement is conserved across spiders in different evolutionary lineages
38 and with disparate hunting strategies. The dispersed distribution of small isolated slits along the whole
39 length of the leg may be used to detect large-scale strain of the leg segment as a result of muscle
40 activity or internal changes in haemolymph pressure.

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59 1. Introduction

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61 Arthropods possess a wide range of internal and external sensory structures that enable them to

62 detect biotic and abiotic sources of information in their environment. Mechanosensation in

63 arthropods often involves detecting cuticular strains caused by internally or externally applied forces.

64 The resulting strains range in type from transient slow strains to high frequency vibrational waves.

65 The latter are key for spiders, which are an excellent model system for studying vibration sensing

66 (Barth, 2002; Mortimer, 2019). Spiders sense vibrations through materials such as silk, the surface of

67 water, plant stems, soil and rocks, and in many species this is the dominant sensory modality (Hebets,

68 2008). They use material-bound vibrations as an information source for prey and predator detection

69 (Klärner and Barth, 1982; Masters, 1984; Landolfa and Barth, 1996; Mortimer et al., 2018) and

70 courtship (Schüch and Barth, 1985, 1990; Elias et al., 2003; Elias et al., 2005). Mechanical stimuli are

71 also used for proprioception (Seyfarth, 1978; Seyfarth et al., 1985).

72

73 The sensory structures that are involved in mechanosensing in spiders include mechanosensory setae

74 (hairs attached to the cuticle) and slit sense organs (Pringle, 1955). Slit sense organs, the focus of this

75 study, are embedded sensors that consist of a slit in the cuticle surrounded by a smooth raised border

76 (Figure 1). Each slit is innervated by two dendrites – one ending at the outer slit membrane and a

77 second close to the inner membrane (Molina et al., 2009). An action potential is generated as a result

78 of cuticle strain, typically compression perpendicular to the long axis of the slit, which bends the

79 membrane (Barth, 1972a, b). The mechanical sensitivity of the slits is high, with compression of only

80 2.5 nm sufficient to generate an action potential in *Cupiennius salei* (Barth and Geethabali, 1982).

81 Cuticle strain can be induced both by externally generated vibrations that are transmitted from an

82 environmental substrate into the body of the spider, or can be internally generated by muscle

83 contraction and changes in haemolymph pressure (Seyfarth et al., 1985; Blickhan and Barth, 1985).

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103 Slit sense organs are widely distributed on the walking legs, pedipalps, chelicerae, prosoma,
 104 opisthosoma and spinnerets, indicating that cuticle strain is an important source of information across
 105 the whole body of the spider. Slits can be arranged singly, in loose groups, or as discrete arrays of two
 106 or more slits known as lyriform organs. Lyriform organs are up to two orders of magnitude more
 107 sensitive than the single slits (Speck and Barth, 1982) and are thought to be particularly important for
 108 the detection of externally generated vibrations. The HS10 lyriform organ, defined by its location at
 109 the distal end of the metatarsus, is thought to be particularly involved in vibration sensing, because it
 110 detects dorsal-ventral movement of the tarsus via a pad at the joint which acts as a high-pass filter
 111 (McConney et al., 2007; Schaber et al., 2012; Morley et al., 2016). It has been identified in most species
 112 of spider previously described in the literature (see 6. Discussion). Isolated slits are extremely
 113 numerous in some species (around 1500 in *Cupiennius salei*) and are found on all body segments
 114 (Barth and Libera, 1970; Barth, 2002). Lyriform organs, on the other hand, tend to be located in fixed
 115 positions close to the joints of the walking legs, chelicerae and spinnerets (Patil et al., 2006; Barth,
 116 2019; Seo et al., 2020). Cuticular strain is predicted to be higher in these areas, leading to maximal slit
 117 strain and hence detectability of motion (Blickhan and Barth, 1985). Strain is influenced by the mass
 118 distribution, body and leg geometry, and cuticle stiffness of the spider (Miller and Mortimer, 2020).
 119 These different aspects of morphology vary between and within species, and could therefore be
 120 expected to result in interspecific differences in slit sense organ distribution across the legs and body
 121 of the spider.

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123 Most research has focused on the structure and morphology of individual slit sense organs in model
 124 species such as *Cupiennius salei* (Barth, 2019), but as the whole body of the spider is used as a
 125 transmission platform for vibrational information, and as different frequencies of vibration are
 126 represented more strongly at different points on the body (Mhatre et al., 2019), their overall
 127 distribution along this transmission pathway is likely to be key for vibration sensing as well as sensing
 128 other mechanical stimuli (Miller and Mortimer, 2020). It is therefore surprising that relatively few

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147 spider species have had the distribution of their slit sense organs mapped – these species are
 148 *Cupiennius salei* (Barth and Libera, 1970), *Argiope bruennichi* (Ganske and Uhl, 2018), *Larinioides*
 149 *sclopetarius* (Vogel, 1923), *Trichonephila clavata* (Seo et al., 2020) and *Comaroma simonii* (Kropf,
 150 1998). In these select species, most of the single slits are arranged along lines parallel to the long axis
 151 of the leg, with the exception of the dwarf species *Comaroma simonii*, which has a reduced number
 152 of rather sporadically distributed slits (Kropf, 1998). Aside from these studies, most other research has
 153 focused solely on the lyriform organs rather than including the single slits (Seo et al., 2020). However,
 154 single slits may still be important in sensing externally generated vibrations, as spiders are still able to
 155 orient towards a vibration source (albeit with reduced accuracy) after ablation of the lyriform organs
 156 (Seyfarth, 1978; Seyfarth et al., 1982). The wealth of other slit sense organs found across the spider is
 157 therefore a comparatively overlooked, and potentially important, source of mechanosensory
 158 information for the animal.

160 The types of mechanosensory inputs relevant for different spider taxa likely depend on their hunting
 161 strategy and mode of life. Orb-weavers, for instance, utilise silk webs to snare their prey rather than
 162 hunting on leaves like *C. salei*, and hence differ in the substrate materials through which vibrations
 163 are transmitted. Because of this, orb-weavers and sit-and-wait hunters experience different cues from
 164 prey (e.g. flying insects struggling on a web versus footsteps on leaves and branches) and internally
 165 generated cuticular strains (e.g. because of differences in posture and activity levels). But is this
 166 reflected in the distribution of their slit sense organs, or are arrangements conserved despite these
 167 ecological and behavioural differences? It is difficult to probe these questions currently, owing to the
 168 low number of species examined to date, so mapping the distribution of slit sense organs in species
 169 other than the well-studied *Cupiennius salei* is of value in enabling further comparative study.

171 In this paper, we examine the number, distribution, external structure, and intraspecific variation of
 172 single slits, groups of slits, and lyriform organs on the walking legs of the females of two species of

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orb-weaving spider, *Araneus diadematus* and *Trichonephila edulis*. Both species are in the family Araneidae (comprising orb-weaving spiders) but are placed in two different subfamilies (Scharff et al., 2020), with Nephilinae being a more basal clade. Therefore, comparison between *A. diadematus* and *T. edulis* is of value as it allows comparison across these two lineages within Araneidae.

As well as their divergent evolutionary history, *A. diadematus* and *T. edulis* differ in their web structure and body morphology. Both *Araneus* and *Trichonephila* produce a planar web with an oval capture spiral to snare flying insects, and sense vibrations from struggling prey by resting their walking legs on the radial threads. However, members of Nephilinae, including *Trichonephila*, retain the non-sticky spiral scaffold in their completed webs, in contrast to *A. diadematus* (Hormiga et al., 1995). In addition, *T. edulis* webs differ from *A. diadematus* in containing stabilimenta, often being constructed at oblique angles and frequently connected to webs built by smaller individuals. In terms of body morphology, *Trichonephila* is larger than *Araneus* and has a significantly different body plan, with much longer and proportionally thinner legs (Figure 2). These factors combined indicate that the type of mechanical stimuli experienced by *A. diadematus* and *T. edulis* on their webs may well differ, despite sharing the same basic hunting strategy.

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We produce comprehensive slit organ distribution maps and describe the external morphology of the individual slit organs in both species. Females were chosen for the comparison as in both species they exclusively construct orb webs, whereas males tend to wander or, in the case of *Trichonephila*, occupy the orb webs of females in order to steal prey (Liebsch et al., 2020).

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2. Methods

1. Studied species

248 *Araneus diadematus* were collected from the wild in Oxfordshire, UK in 2020, kept in Perspex frames
249 measuring 30cm x 30cm x 5cm and separated by greased Perspex sheets to prevent webs being
250 attached to the sides. The spiders were fed with live *Drosophila melanogaster* and *Calliphora*
251 *vomitioria* and sprayed with water twice per week. *Trichonephila edulis* were taken from a captive
252 population that is maintained in a temperature-controlled room (20°C±5°C) with an accompanying fly
253 population. The spiders were sprayed with water twice per week and allowed to feed ad libitum on
254 *Drosophila melanogaster* and *Calliphora vomitoria*.

255

256 2.2 Specimen preparation

257

258 Adult female specimens of both species were anaesthetised using ethyl acetate vapours. Specimens
259 were then preserved in 70% ethanol solution before being transferred to a 95% ethanol solution to
260 further dehydrate them.

261

262 The right-hand side legs were removed from the specimens and air dried before being shaved of all
263 setae and trichobothria using a mounted pin and scalpels under a stereomicroscope, in order to
264 prevent these structures from obscuring the slit sense organs beneath them. The legs were divided
265 into 3 or 4 sections in *Araneus* and 4 or 7 sections in *Trichonephila* using scalpels. Where possible the
266 legs were divided at the natural split between segments – if this was not possible, a single incision was
267 made in the middle of the segment. It is possible, although unlikely, that these incisions may have led
268 to the loss of a very low number of small isolated slits which happened to coincide with the incision
269 pathway. The sections were then mounted along their long axis by gluing the ends of the leg sections
270 onto a pin using cyanoacrylate. The specimens were sputter coated with gold-palladium for 150
271 seconds at 18 mA using an Emitech SC7620 sputter coater. The pins were mounted on a rotating
272 specimen holder using conductive tape, such that the long axis of the leg segment was oriented
273 perpendicularly to the imaging beam. Each leg segment was imaged using a scanning electron

274 microscope (SEM; Neoscope JCM-5000) at 0, 90, 180 and 270° angles of rotation around the long axis
275 of the leg, in order to image the dorsal, medial, ventral and lateral sides of the leg segment. This
276 enabled us to image the entire surface of each leg specimen, which would have been impossible using
277 a conventional stub-mounted setup.

278

279 2.3 Image mapping

280

281 The SEM images were combined using Adobe Photoshop and digitally traced to mark out the position
282 of the slit sense organs. Visual inspection of slit length revealed a bimodal distribution and hence we
283 follow [Barth and Libera \(1970\)](#) and Barth and Stagl (1976) in classifying the isolated slits into small
284 isolated slits and large isolated slits, which also have subtly different morphologies.

285

286 Slit sense organ categories, adapted from Barth and Stagl (1976). [Examples of each of these categories](#)
287 [are shown in](#) (Figure 1):

- 288 1. Small isolated slits (Figure [1:D](#)).
- 289 2. Large isolated slits, with diffuse border (Figure [1:B](#)).
- 290 3. Groups of slits comprising 2 or more slits less than 100 µm away from each other (Figure [1:A](#)).
- 291 4. Lyriform organs consisting of 2 or more slits in an approximately parallel arrangement with a
292 distinct border (Figure [1:C](#)).

293

294 A full map of the right-hand legs was produced for a single individual of *Araneus* and *Trichonephila*.

295 We manually counted the number of each category of slit sense organ on each leg. [Using a method](#)
296 [where incisions were made in the centre of some leg segments could have led to a slight](#)
297 [underestimation of the total number of slits \(see above\), but would not have affected the distribution](#)
298 [of slits elsewhere on the legs](#). We did not duplicate the count of any slits that appeared on more than
299 one map from different angles. On the maps in Figures [3-6](#), individual slits will be shown from more

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315 than one angle and hence appear on more than one map. In Figures 3-6, individual slit sense organs
316 are shown in their accurate positions, traced from the SEM images, but are enlarged so that they are
317 visible on a figure of the whole leg. The outlines of the legs correspond to the shape of the leg
318 segments on the SEM images that the figures were traced from.

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319
320 Visual comparison with two other specimens of each species was used to verify that the overall
321 arrangement of slit sense organs (in terms of lines of single slits, and position of large slits, groups of
322 slits and lyriform organs) was the same between individuals. To quantify the extent of intra-specific
323 variation, we used full maps for a single leg segment (the metatarsus) of the third leg on the other two
324 individuals of each species to provide the number of small isolated slits (in each of the medial and
325 lateral lines), large isolated slits, groups of slits, extra slits and lyriform organs described in Table 2.

326
327 Cephalothorax width was measured by placing the spiders on a grid. Leg length was measured by
328 summing the length of each leg segment from Figures 3-6 with reference to the SEM scale bars in
329 order to obtain the total leg length when fully straightened.

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333 5. Results

334 3.1 Small isolated slits

335

336 3.1.1 Morphology of small isolated slits

337

338 The external morphologies of the small isolated slits in *Araneus diadematus* and *Trichonephila edulis*
339 are similar, consisting of a slit in the cuticle bordered by a raised “lip” on either side (Figure 1).
340 Nevertheless, whereas slit morphology is quite uniform in *A. diadematus*, there is more variation in *T.*
341 *edulis*, with morphologies ranging from long thin slits to sensilla with concave depressions around the
342 slits.

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Deleted: (Figure 1:6). The slits are oriented approximately parallel to the long axis of the legs. This is in contrast to the orientation of the slits in lyriform organs, which we found were frequently perpendicular or at an oblique angle to the long axis of the leg.

344 3.1.2 Number of small isolated slits

345

346 The total number of small isolated slits recorded in our full map of one *A. diadematus* specimen is 520
347 compared with 763 in our map of *T. edulis* (Table 1), which corresponds with the larger body size of *T.*
348 *edulis*. The numbers of slits on each leg ranks with the leg length for *A. diadematus*, whilst in *T. edulis*
349 leg 2 has fewer slits despite being longer than leg 1. In particular, the short third leg of both species
350 has far fewer slit organs (Table 1).

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352 3.1.3 Distribution of small isolated slits

353

354 Small isolated slits are widely distributed across the leg segments of both *A. diadematus* and *T. edulis*
355 with the exception of the coxa, which only has a few sparse slits in both species. Most of the small
356 isolated slits are arranged in lines parallel to the long axis of the leg. On the tarsus, metatarsus, tibia
357 and patella, the slits are arranged in two lines on the dorso-medial and dorso-lateral sides of the leg
358 segment. The femur of both species has a different arrangement to the rest of the leg. In *A.*

366 *diadematus*, there are 4 lines of slit sensilla in legs 1-3 and 3 lines on leg 4. In *T. edulis*, there are 4
367 lines of slit sensilla on the femur in all 4 legs (Figures 3-6).

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369 There are also a few slits located away from the main lines, which are referred to in Table 2 as "Extra
370 slits". We were unable to identify any consistent pattern in the location of these slits and they were
371 low in number.

373 3.1.4 Intraspecific variation in distribution of small isolated slits

374
375 Individuals of both species vary in the number and exact position of the small isolated slits (Table 2)
376 although the overall distribution (in terms of the number and position of the lines of slits and discrete
377 groups) is the same in all individuals (Figures 3-6). Individuals vary in the number of slits per line and
378 also the number of random extra slits situated away from the main lines. The total number of slits per
379 line correlates approximately with body size, here approximated using cephalothorax width, e.g. after
380 Olive (1980).

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382 3.2 Large isolated slits

383
384 In contrast to the small isolated slits, the large isolated slits are far fewer in number and occur in fixed
385 positions that do not vary between individuals. Two large slits, one anterior, one posterior, are present
386 on the underside of the distal end of the metatarsus, opposite the HS10 lyriform organs. The anterior
387 slit is located slightly closer to the prosoma than the posterior slit. There are also large slits on the
388 coxa of legs 2 and 3 in *A. diadematus*, but not *T. edulis*.

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390 3.3 Groups of slits

391

398 Groups of slits are located in fixed positions on the medial and lateral sides of the trochanter extending
399 towards the body from a protrusion of cuticle. Each group consists of up to 10 slits less than 100 µm
400 apart. The whole group is typically no more than 200 µm across. Most of the individual slits making
401 up the group would be classed as “large”, being similar in size to the large isolated slits, although there
402 are a few smaller ones.

403

404 3.4 Lyriform organs

405

406 The final category of slit sense organs, the lyriform organs, also occur in fixed positions on the leg
407 (Figures 3-6). There are 110 lyriform organs across all eight walking legs of *A. diadematus* and 108 in
408 *T. edulis* (Tables 3 and 4). Both species have either 12 or 13 lyriform organs per leg. The position of
409 lyriform organs in *T. edulis* is almost identical across all 4 walking legs, but legs 1 and 2 have an extra
410 lyriform organ on the ventral side of the tibia (Table 3).

411

412 In both *A. diadematus* and *T. edulis*, there is a lyriform organ embedded within the group of slits on
413 the posterior side of the trochanter (Figure 1:A). This whole structure could be considered
414 intermediate between groups of slits and lyriform organs – the organ itself is very simple, consisting
415 only of two slits, and is surrounded by tightly packed single slits forming the rest of the group. In some
416 cases, it is difficult to actually identify the organ. Although difficult to define, we have followed Barth
417 and Libera (1970) in considering this structure as a lyriform organ embedded within a group of slits.

418

419 In *A. diadematus*, there is an extra lyriform organ (consisting of two slits, similar to those on the
420 trochanter) on the ventral side of the coxa on legs 1 and 4, whilst on legs 2 and 3 this organ is replaced
421 by a single large slit. There is also an extra lyriform organ on the femur of leg 3, but aside from that,
422 the arrangement of lyriform organs is identical between legs (Table 4).

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427 In both species, the tibia was the leg segment most richly supplied with lyriform organs, followed by
428 the patella (Tables 3,4). This is in contrast to the distribution of single slits and other slit sense organs,
429 which were concentrated proximally.

430

431 6. Discussion

432 4.1 Comparison with other spiders

433

434 The main objective of the present study was to map the overall distribution of slit sense organs
435 (defined into categories of: single isolated slits, large isolated slits, groups of slits and lyriform organs)
436 on the walking legs of two species of mature female orb-weavers. In order to enable future research
437 that aims to explain patterns in the distribution of slit sense organs across large areas of the body (i.e.
438 entire legs), we particularly focused on the distribution of the understudied small isolated slits, which
439 are organised in lines along each leg segment – very different to the local measurements taken by
440 lyriform organs at specific sites. Our maps record the exact position and orientation of each small
441 isolated slit, which could be used as the basis for future comparative study.

442

443 Putting these findings in context, we find that the distribution of slit sense organs on the walking legs
444 of both *Araneus diadematus* and *Trichonephila edulis* supports what has been found for other species
445 described in the literature. Lyriform organs, large isolated slits and groups of slits are located
446 consistently near joints, whilst small isolated slits are distributed in lines along the length of the leg.

447 This suggests that slit sense organ distribution on the legs is tightly controlled by physical or
448 evolutionary constraints, which are heavily linked with morphology and body plan. We compare our
449 findings to a few species where distribution maps have previously been produced for at least one leg,

450 listed above in 1. Introduction. McIndoo (1911) produced a comprehensive survey of slit sense organ
451 distribution in 39 different species, which provides some useful context for this work. However, it is
452 difficult to use his study as a comparative tool as McIndoo did not identify many of the spiders to

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species level (and many of the genera have now been renamed and taxonomically split), did not produce distribution maps, and defined the slit sense organs in a different way to what is currently used in the literature (for instance, it is not clear whether his category of “simple lyriform organ” also includes loose groups of slits).

460

Our study found that intraspecific variation in slit sense organ distribution was low, which suggests that slit sense organ distribution is either functionally useful or constrained through development/body plan. The overall pattern of small isolated slits was the same in all individuals measured, as were the location of specific groups of slits and individual large slits – this supports what has been previously described in the literature (Barth and Libera, 1970; Barth and Stagl, 1976).

466

4.1.1 Small isolated slits

468

The external morphology of the small isolated slits is variable between species – they universally consist of a slit surrounded by a smooth protrusion, which in *Araneus diadematus*, *Trichonephila edulis* and *Argiope bruennichi* tend to be “lips” or flat C-shaped areas either side of the slit (Ganske and Uhl, 2018). In *Cupiennius salei*, the morphology is slightly different, with the slit being bordered by two elevated bulges (Barth and Libera, 1970).

474

The overall distribution patterns of small isolated slits we described, consisting of two lines of slits on the dorsomedial and dorsolateral sides of the tarsus, metatarsus, tibia and patella; multiple lines on the femur; and the proximal concentration of single isolated slits, are also found in other species of spider, such as the orb-weavers *Argiope bruennichi* (Ganske and Uhl, 2018) and *Larinioides sclopetarius* (Vogel, 1923), and the sit-and-wait hunter *Cupiennius salei* (Barth and Libera, 1970). In terms of explaining these conserved patterns, Barth (1976) suggested that the proximal concentration might be due to the increased number of muscles in this area, where the main back-and-forth

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500 movement of the leg is generated when walking. It is also possible that the lines of small isolated slits
501 correlate with the position of haemolymph channels. We therefore hypothesise that single slits are
502 coordinated in lines to effectively detect strains over a large area, such as the entire length of the leg
503 segment, rather than localised information at a point of interest such as a lyriform organ.

504

505 In contrast to these findings, the dwarf spider *Comaroma simonii* does not possess such a regular and
506 consistent distribution of small isolated slits – instead of discrete lines, they are grouped rather
507 sporadically on the walking legs (Kropf, 1998). This is also combined with a low number of single slits
508 (around 250) compared with the other species discussed above. These differences may be linked to
509 its much smaller body size – shorter legs may mean that detection of large-scale strains is not as
510 important as in larger spiders, whilst the magnitude of internal forces acting on the legs will also be
511 reduced due to low body mass.

512

513 Within the lines of small isolated slits, the exact location, size and orientation of a specific slit are
514 highly variable between individuals, as is the number of slits in each line and the number of random
515 slits away from the lines. We were unable to correlate these differences with any variation in
516 morphology, although it is probable that larger individuals have more slits.

517

518 4.1.2 Other slit sense organs

519

520 Two large slits are present on the underside of the distal end of the metatarsus, directly opposite the
521 HS10 lyriform organ, in both *A. diadematus* and *T. edulis*. These slits, have also been reported in *L.*
522 *sclopetarius* (Vogel, 1923), an orb-weaver which is closely related to *A. diadematus*. They were not
523 observed in any of the other species of spider to our knowledge.

524

Deleted: . A lack of slits on the trochanter and coxa of some species may be related to specific postures or levels of activity on the web that differ between these species – for example, orb-weavers that are comparatively more mobile than other orb weavers, may have these segments more richly supplied with slits. We speculate that the trochanter and coxa experience higher levels of cuticle deformation during locomotion as the entire leg pivots in both directions around these joints where it connects to the cephalothorax. Further research could investigate whether there are any sex specific differences in this area, as male orb-weavers are less sedentary than the females.

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Deleted: of muscle attachment points or

Deleted: (thus implicating a purely proprioceptive function), or potentially weak points of thinner cuticle which may be prone to catastrophic buckling (Parle et al., 2015)

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Deleted: The exact location of a specific small isolated slit is probably not crucial for mechanosensing, so long as the majority fall within the overall pattern of lines and groups.

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552 Groups of slits on the medial and lateral sides of the trochanter seem to be consistently present in *A.*
 553 *diadematus*, *T. edulis*, *C. salei* (Barth and Libera, 1970) and *L. scolopetarius* (Vogel, 1923). In *C. salei*,
 554 there is also a single lyriform organ in the middle of this group (Barth and Libera, 1970), whilst in *A.*
 555 *bruennichi* these groups of slits are replaced on legs 2-4 with lyriform organs (Ganske and Uhl, 2018).
 556 The distribution in *T. edulis* is similar but not identical in the closely related *Trichonephila clavata* –
 557 interestingly, *T. clavata* seems unusual in missing the HS10 metatarsal lyriform organ on leg 4 (Seo et
 558 al., 2020). *C. salei* has 15 lyriform organs in total on the leg, again in a similar arrangement, but with
 559 an extra two lyriform organs on the trochanter (Barth and Libera, 1970).

560
 561 The location of the lyriform organs within individuals of the same species appears essentially fixed.
 562 Previous research has shown that the morphology of each individual lyriform organ (such as the
 563 number, length and orientation of the component slits and the overall shape of the organ), changes
 564 between successive moults throughout an individual's development (Morley et al., 2016) and varies
 565 depending on whether a leg has been regenerated (Vollrath, 1995). For mature adults of the same sex
 566 on legs that have not been regrown, it has been reported that variation in lyriform organ morphology
 567 is very low (Barth and Stagl, 1976; Morley et al., 2016).

568 4.2 Comparison with other arachnids

570
 571 All arachnids utilise slit sense organs as their mechanoreceptors for sensing cuticular strain. Spiders
 572 are exceptional in the number of lyriform organs present on the legs, possibly due to increased
 573 reliance on sensing externally generated vibrations for hunting and courtship. Instead, these other
 574 arachnid groups tend to have more groups of slits and large isolated slits. Small single slits are more
 575 sparsely distributed in the other arachnid groups – the whip spider most closely resembles spiders in
 576 having a line of slits on the dorsomedial side of the leg (Barth and Stagl, 1976), but the others mainly
 577 have only loose groupings, or in the case of the scorpion just a profusion of slits covering the cuticle

Deleted: Different species of spider vary in the number and location of the lyriform organs. The distribution in *A. diadematus* is the same in the closely related *L. scolopetaria*, at least for the one leg illustrated (Vogel, 1923).

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Moved (insertion) [1]

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Deleted: , which has only 3 lyriform organs on the patella, but lyriform organs were not counted on the trochanter and coxa in this species

Moved up [1]: Interestingly, *T. clavata* seems unusual in missing the HS10 metatarsal lyriform organ on leg 4

Deleted: (Seo et al., 2020).

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¶ The fact that all the slit sense organs other than the small isolated slits appear in the same location between individuals of the same species indicates that this is important for their function. This may be due to predictable and relevant cuticle deformations occurring at these sites, unlike the more broadly distributed small isolated slits. ¶

Deleted: In comparison, only two are present in the harvestman *Amilenus aurantiacus*, one is present in the whip spider *Admetus pumilio* and the whip scorpion *Mastigoproctus brasiliensis*, and none at all in the scorpion *Androctonus australis* (Barth and Stagl, 1976; Barth and Wadepuhl, 1975).

604 (Barth and Wadepuhl, 1975). The fact that the overall, large scale distribution of the slit sense organs
605 in spiders is quite tightly organised (e.g. the long lines of small isolated slits along the legs) suggests
606 that the function of these organs is particularly crucial for spiders, especially when compared with the
607 somewhat sporadic and sparse distribution of these organs in other arachnids.

608

609 4.3 Comparison with other arthropods

610

611 The sort of questions that pertain to the distribution of arachnid slit sensilla apply equally to other
612 arthropods, in terms of the way in which the biomechanics of the animal's body influence cuticular
613 strains and the dynamics of mechanosensing – and by extension the distribution of embedded
614 mechanosensors across the animal's body. Insects detect strains in their cuticle using campaniform
615 sensilla, which are analogous to the slit sensilla of arachnids (Pringle, 1955). They consist of a flexible
616 cap innervated by a dendrite that responds to cuticular strain (Pringle, 1938). Several studies have
617 produced maps of insect campaniform sensilla, most notably on the cockroach *Periplaneta americana*
618 (Pringle, 1938), but also on the fruit fly model species *Drosophila melanogaster* (Dinges et al., 2020)
619 and the blowfly *Calliphora vicina* (Gnatzy et al., 1987). In all of these insects, the campaniform sensilla
620 tend to be distributed in fields (groups of slits) near the leg joints in a similar way to lyriform organs,
621 although there are also sparse single sensilla away from these main groups. As is the case with body
622 size in spiders, very small insects, such as the aphid *Mindarus*, possess a reduced number of
623 campaniform sensilla (Montagano and Favret, 2016). In addition, the observed concentration of slit
624 sense organs proximally on the leg in spiders is also apparent in the distribution of campaniform
625 sensilla in insects, suggesting that increased musculature in the proximal leg segments influences slit
626 sense organ distribution in both insects and arachnids (Pringle, 1938).

627

Deleted: Interestingly, the large isolated slits in the harvestman are oriented perpendicularly to the long axis of the leg, which deviates from the arrangement seen in most other arachnids. It is possible that this represents a different mode of slit stimulation where compression in the dorsoventral rather than proximal/distal plane is the crucial factor for mechanosensing (Barth and Stagl, 1976).

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¶ Overall, it can be seen that spiders possess an extensively developed mechanosensing system compared with other arachnids, with larger numbers of highly sensitive lyriform organs and slit sensilla arranged in consistent patterns.

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645 Therefore, it can be seen that some elements of the overall distribution of slit sense organs in insects
646 are broadly similar to spiders, although the organisation of small isolated slits in long lines appears to
647 be a spider-specific trait.

648

649 4.4 Further research/conclusion

650

651 Our study found that there are only minor differences in the slit organ distributions on the legs of *T.*
652 *edulis* and *A. diadematus*. Furthermore, we add these two species to a growing list of spiders that
653 seem to be remarkably similar in their arrangement of slit organs, despite different morphologies,
654 hunting strategies and evolutionary histories.

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656 The stand out feature of the observed slit organ distributions is that the single isolated slits are almost
657 always arranged in four lines along the leg. As the slit sense organs are sensitive to compression
658 perpendicular to the long axis of the slit, and most of the slits are orientated roughly parallel to the
659 long axis of the leg, this indicates that these lines function to detect expansion/contraction of the
660 cuticle or torsional forces in the leg around the central axis of the leg. Whether the distribution is
661 developmentally conserved, or constrained by underlying leg musculature or 8-legged body plan
662 shared by all spiders, remains to be investigated. Understanding the functional arrangement of this
663 slit organ arrangement, as well as its developmental pathway, are the first steps to potentially
664 providing insights into whether mechanosensing in spiders is modulated by evolutionary or physical
665 constraints.

666

667

668 Previous research has focused mainly on the function of the lyriform organs, and our understanding
669 of the function of the other slit sense organ types is limited. This question could be investigated

Deleted: Whilst the types of embedded mechanosensors found in different arachnid/arthropod groups may be different in structure, it is clear that the same basic underlying principles govern their distribution. The large isolated slits, groups of slits and lyriform organs are located in areas that experience high levels of cuticular strain – i.e. leg segments proximal to the body, and the areas bordering the leg joints. ...

678 through targeted ablation experiments, ~~neurophysiological recordings or describing the ultra-~~
679 ~~structural characteristics of the organs – e.g. dendrite morphology and receptor cell number.~~

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681 ~~The~~ overall distribution of slit sense organs (particularly the small isolated slits) may be particularly
682 useful in understanding how mechanosensing works on a whole-body scale for morphological
683 computation. ~~Morphological computation is where the body is used to process information before~~
684 ~~sensory transduction, thus reducing the total level of processing required in the central nervous~~
685 ~~system (Miller and Mortimer, 2020).~~ As the body of the spider acts as a transmission platform for
686 vibrational information, we might expect that the frequency content of a signal changes as it
687 propagates through the body. Frequency segregation certainly seems to occur in the legs of the spider,
688 with frequencies above 30 Hz attenuating significantly from the distal to the proximal leg segments,
689 and evidence from modelling suggests that this changes depending on posture (Mhatre et al., 2018).

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690 ~~It is possible that the slit sense organs are arranged tonotopically to reflect this – i.e. their frequency~~
691 ~~sensitivity may vary along the length of the leg. Assessing overall distribution may therefore be~~ crucial
692 in the context of morphological computation. Further research is ~~needed to uncover~~ potential factors
693 ~~that might explain the functional significance of the observed slit organ distribution. This could be~~
694 ~~investigated through finite element modelling of the legs of the spider, which would enable areas of~~
695 ~~strain concentration to be identified. It is unclear what factors, internal or external, explain and control~~
696 ~~this distribution, making this~~ a promising area for future research into arthropod proprioception and
697 haptic sensing.

Deleted: and that the slit sense organs are arranged tonotopically to reflect this.

Deleted: As each leg joint is tuned differently,

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Deleted: required to establish links between the observed pattern of slit sense organs and

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Deleted: For instance, how do the number and distribution of single slits change throughout development, and do these scale with the forces predicted to act upon the cuticle at different body sizes? ...

Deleted: Furthermore, what physiological features determine the distribution of small isolated slits along the long axis of the legs?

Deleted: whether this distribution is modulated by

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Deleted: perturbation (such as deflection of the entire leg due to unintended contact with another object, resulting in buckling...

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699 Author Contributions

700 TM wrote the first draft and prepared the figures. BM, GKT and TM edited the manuscript. BM and
701 GKT provided supervision for TM. All authors contributed to the article and approved the submitted
702 version.

703 Conflict of Interest

728 The authors declare that the research was conducted in the absence of any commercial or financial
729 relationships that could be construed as a potential conflict of interest.

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735

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846 **Figures and Tables**

847
848

849 Figure 1. Types of slit sense organ found on spider walking legs, illustrated on leg 1 of

850 *Araneus diadematus*. **A – group of slits (on the posterior side of the trochanter, also**
851 **containing a lyriform organ consisting of two slits in the middle).** B – two large isolated slits
852 (> 30 µm; on the ventral side of the distal end of metatarsus). **C – two lyriform organs (on**
853 **the lateral side of the distal end of the tibia).** **D – small isolated slit (< 30 µm; on dorsal side**
854 **of the tarsus).**

855

856 Figure 2. Comparison of the morphology of adult female *Araneus diadematus* and

857 *Trichonephila edulis*, with an explanation of positional terms used in Results.

858

859 Figure 3: Schematic map of upper portion of Leg 1 of *Araneus diadematus*. From left to right
860 – dorsal, prolateral, ventral and retrolateral view. The small isolated slits are enlarged to
861 increase legibility and show orientation – an indication closer to their true size is given in the
862 magnified view on the right (with small inaccuracies due to pixel sizes on SEM images).

863

864 Figure 4: Schematic map of lower portion of Leg 1 of *Araneus diadematus*. From left to right
865 – dorsal, prolateral, ventral and retrolateral view.

866

867 Figure 5: Schematic map of upper portion of Leg 1 of *Trichonephila edulis*. From left to right
868 – dorsal, prolateral, ventral and retrolateral view. The small isolated slits are enlarged to
869 increase legibility and show orientation – an indication closer to their true size is given in the
870 magnified view on the right (with small inaccuracies due to pixel sizes on SEM images).

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Deleted: A – small isolated slit (< 30 µm; on dorsal side of the tarsus).

Deleted: C – group of slits (on the posterior side of the trochanter, also containing a lyriform organ consisting of two slits in the middle). ...D
D

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884

885 Figure 6: Schematic map of lower portion of Leg 1 of *Trichonephila edulis*. From left to right

886 – dorsal, prolateral, ventral and retrolateral view.

887

888 Table 1. Total number of small isolated slits on the walking legs of *Araneus diadematus* and
889 *Trichonephila edulis*.

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Leg	<i>Araneus diadematus</i>		<i>Trichonephila edulis</i>	
	Leg length (mm)	Number of slits	Leg length (mm)	Number of slits
1	24.2	147	46.0	255
2	21.4	145	50.4	225
3	14.6	91	24.6	113
4	20.4	137	40.8	170
Total		520		763

891 Table 2. Number and distribution of small isolated slits (and extra slits situated away from
 892 the main lines of slits), large isolated slits, groups of slits and lyriform organs on the
 893 metatarsus of the third leg of three specimens of *Araneus diadematus* and *Trichonephila*
 894 *edulis*.

Species	No.	Cephalothorax	Medial line	Lateral line	Extra	Large	Groups of	Lyriform
		width (mm)			slits	slits	slits	organs
<i>A. diadematus</i>	1	5	10	7	2	2	0	1
	2	4.3	9	4	0	2	0	1
	3	4.6	13	8	0	2	0	1
<i>T. edulis</i>	1	5.8	12	16	0	2	0	1
	2	6.2	24	22	0	2	0	1
	3	7.4	24	33	2	2	0	1

895 Table 3. Number of lyriform organs on each walking leg in *Araneus diadematus*.

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Segment	Leg 1	Leg 2	Leg 3	Leg 4	Total
Tarsus	0	0	0	0	0
Metatarsus	1	1	1	1	4
Tibia	4	4	4	4	16
Patella	3	3	3	3	12
Femur	2	2	3	2	9
Trochanter	3	3	3	3	12
Coxa	1	0	0	1	2
Total	14	13	14	13	55

897 Table 4. Number of lyriform organs on each walking leg in *Trichonephila edulis*

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Segment	Leg 1	Leg 2	Leg 3	Leg 4	Total
Tarsus	0	0	0	0	0
Metatarsus	1	1	1	1	4
Tibia	5	5	4	4	18
Patella	3	3	3	3	12
Femur	2	2	2	2	8
Trochanter	3	3	3	3	12
Coxa	0	0	0	0	0
Total	14	14	13	13	54