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Further mechanistic insights into the trophic design of free-living mites

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ABSTRACT

Recent advances in the ecomorphological understanding of how gnathosomal features work as food processing tools relevant for astigmatan mites of economic importance and mesostigmatid predators are described. Engineering analysis is used. New unpublished acarine morphological results are included. Underbite and overbite in cheliceral chelae are exemplified and their function debated. Features for acarologists to search for in fluid handling are highlighted. The Rollplatte is re-evaluated. Designs for browsing, grazing and liquid feeding are discussed. Other topics covered include mites in cadavers, curve and hole cutting, sword-like designs, and prising open, cracking and tearing adaptations. A variety of tool types remain to be found in acarines.

Keywords Acari; agricultural implements; functional ecomorphology; gate latches; kitchen utensils; metal working; pincers; pliers; pollenophagy; snips; unguitractor; weaponry

Introduction

Heterotrophic animals must feed and within any one community will therefore potentially directly compete against each other. Their comparative design therefore matters. De Lillo *et al.* (1994, 2001) provide recent detailed micro-anatomical and histological accounts of various mite chelicerae building upon foundational work of acarologists stretching back to the 1800s. Adaptations for grasping, piercing/perforating, salivary injection and juice sieving/suction involved in prey and host processing are outlined.

This paper references unusual material for an acarological topic. Acarine examples will be linked to vertebrate ecology, the mechanical construction of 19th century objects to handle rainfall, human weaponry and even dinosaur palaeobiology. As Mark Purnell said on NBC News in 2009 (https://www.nbcnews.com/science/cosmic-log/how-dinosaurs-chewed-flna6c10404397):

“The more we understand the ecosystems of the past, and how they were affected by global events like climate change, the better we can understand how changes now are going to pan out in the future.”

Mites are useful ‘bellweather’ species in times of global change. Potential insights gained from acarine ecomorphological analyses are enhanced when the morphological variables measured can be interpreted in a clear functional context (Wainwright and Ricard 1995). It is essential to test form to postulated function relationships quantitatively (Lautenschlager *et al.* 2016). Mathematics and matching designs to physical macro-scale tools can help here for free-living mites (Bowman 2020, 2021, 2023a, 2023b, 2024a, 2024b). However, sometimes there may not be as a strong a relationship as first thought (e.g., beak shape and trophic function in birds, Navalón *et al.* 2019). Nevertheless, in selecting variables with clear functional consequences, interpretations of acarine morphology-diet relationships must be couched in terms of the behavioural capabilities of the animal concerned. After all any particular tool

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can be used in different ways according to the task in hand (although it just may not be very efficient at all of them).

Indeed, the morphology of the whole structures involved and not just only part of them needs to be considered to prove any posed functionality. How oral structures move as a whole, their integration and relationships with the other mouthparts needs careful evaluation especially if the posed movements of the mouthparts are the result of anatomic structures like the muscles which must assume certain arrangements. All aspects must not be forgotten in ascribing functions. This paper is a 'call to arms' for acarologists to pursue possibilities and seek proof of natural selection pressures.

Aim

Mites are an increasing focus of modern life, especially those controlling pests of human food production. So, accordingly, the opening question of this paper is:

"How do phytoseiid use tools to eat things?"

Exemplifying that they do this by

- Piercing and slashing things
- Sensing, cracking and tearing things
- Prising things open
- Opening things like a can
- Cutting curves in 'tough' things
- Snipping a hole in 'metal-like' things
- and, not 'dribbling'

Then, this paper widens matters to other acarines and asks:

"How can other mites attack things with other tools?"

Exemplifying that they do this by

- Levering things up and sawing
- Un-peeling things
- 'Trap-jaw snapping' on things and 'rearing up'
- and, locking onto things

Then, this paper asks:

"What about handling fluids?"

Exemplifying that this is done by

- Controlling the flow
- Feeding in fluids
- and, 'mopping up'

Before concluding with the question:

"What other tool types are there left to find in mites?"

Highlighting macro-scale tools for acarologists to search for and match to mite chelicerae such as:

- Tools for cutting into bodies
- Tools for cutting off legs
- Tools for cutting bodies up
- and, tools for grabbing, scratching and holding

To those ends, certain recently developed mite related topics will be discussed.

Results and discussion

"How do phytoseiid use tools to eat things?"

Piercing and slashing things

One might ask, to what extent are phytoseiid chelicerae designed like bladed weapons such as swords? Following Peter Saveliev's detailed explanation (see https://calculus123.com/wiki/What_shape_of_sword_is_best_for_cutting/%3F), curved swords (e.g., the shamshir, Figure 1 left) cut better than straight swords. This is true even of tools like a scythe (Figure 1 right) where the cutting edge is opposite to that of a downward striking sword blade.

The best sword shape is one where the curvature is decreasing towards the tip, i.e., the involute sword. The mathematical equation that describes this based upon a circle is $[x=r.(\cos(t)+t.\sin(t)),\ y=r.(\sin(t)-t.\cos(t))]$, $t>0$ and r=radius of circle. The path that this traverses is the same as an object connected to a string that wraps or unwraps around a circular post. In form it looks like an Archimedes spiral or a less expanding logarithmic spiral (found widespread in Nature).

Overall, do predatory mite moveable digits overall show such a form (i.e., a parallelism of blade location, with its 'propagation' and with its 'rotation' when occluding)? Certainly the Figures in Liu *et al.* (2017) suggest that phytoseiid mites probably do (but therein the quoted 'morphometric angle 15' values for the various phytoseiid feeding groups at around 30° are much higher than $60^{\circ}=\tan^{-1}\{y/((x-1))\}$, @ $t=1.57$ for the involute equation, $r=1$). Global rotation of the reference axes by around 10-15° does produce visual congruence on the SEMs shown in Flechtmann and McMurtry (1992b) (e.g., Figure 1 lower, and so consequently generate consilient lower final morphometric angle values). More work, of course, is needed. For instance, perhaps just the region from the tip to the first tooth could be also modelled in this way and compared to the ['gape':'bite/throat'] ratios of fishing hooks (of known different function already) found in Allen (1996) and in Beverly (2010)?

The involute shape has some interesting properties.

- From a fully closed chela, as the moveable digit opens (rotating in its condyle), a particular food morsel at first resting proximal to that condyle on the ventral surface of the moveable digit, will be continually pushed vertically downwards as the chela uniformly opens, as long as the moveable digit ventral surface can flow (in a relative sense) past it. That is, on rotation, "…the tangents to the involute having a given direction move in a uniform translation motion" (see the animation by Robert Ferréol of a cam at https://mathcurve.com/courbes2d.gb/developpantedecercle/developpantedecercle.shtml). So food material will be compacted, or an existing wound prised open, i.e., until the chela is fully open. Clearly, muscle arrangements and the relative power of adductors and abductors compared to any handling resistance of food material needs consideration here for this assertion to be definitive.

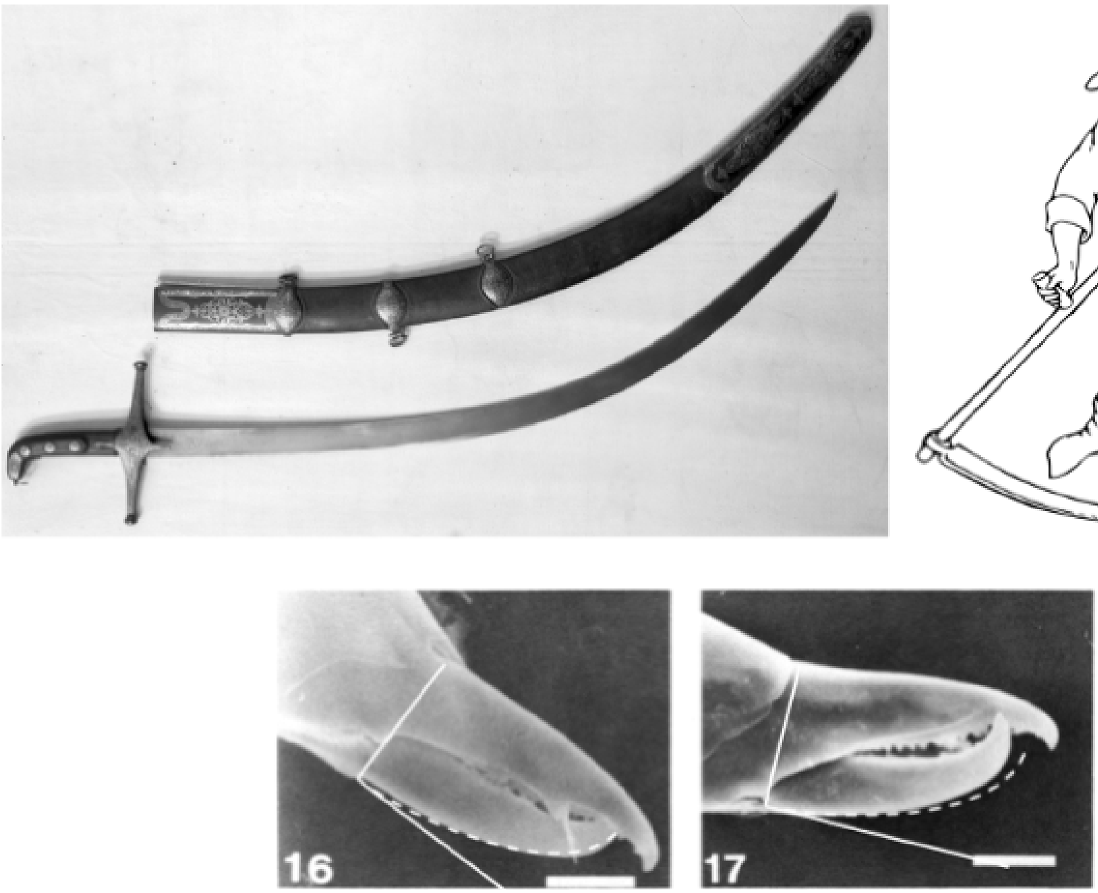

Figure 1 Curved blades. Upper left, Shamshir scabbard and sword. Unknown author - LSH 77113 (LN_A00689_000689), Public Domain, https://commons.wikimedia.org/w/index.php?curid=28898159. Upper right, Man using a scythe. In public domain (1980) https://commons.wikimedia.org/wiki/File:Scythe_user.png. Lower. Rotated involute function (dashed line with solid line reference axes) overlain on same *Amblyseius similioides* phytoseiid species as in Figures 2-7.

- Conversely, for a fully open chela (i.e., biting at a maximum gape), a particular food morsel at first resting on the dorsal surface of the moveable digit proximal to the tip, will be continually pushed vertically upwards as the chela uniformly closes, as long as the moveable digit dorsal surface can flow (in a relative sense) past it (until the chela is fully shut). A consequent slicing action is ensured for a narrow blade given high inertia in the food material. Forward facing teeth would of course prevent this smooth relative sliding of the digit surface against the food. Again, muscle arrangements and the relative power of adductors and abductors compared to any handling resistance of food material needs consideration here for this assertion to be definitive

Sensing, cracking and tearing things

In a later section, the design for pollenophagy is discussed in detail. For this (and other gripping tools), it would be advantageous to directly sense when the pollen grain (or food morsel) is successfully held on the inner side of the chelicera. The pilis dentilis, e.g., in *Amblyseius similioides* (Figure 2), as a sensory seta on the outside flank of the moveable digit is such a mechanism. Nuzzaci *et al.* (1992) and de Lillo *et al.* (1997) detail various other mouthpart sensilla in economically important mesostigmatids. Note that many melicharids which include

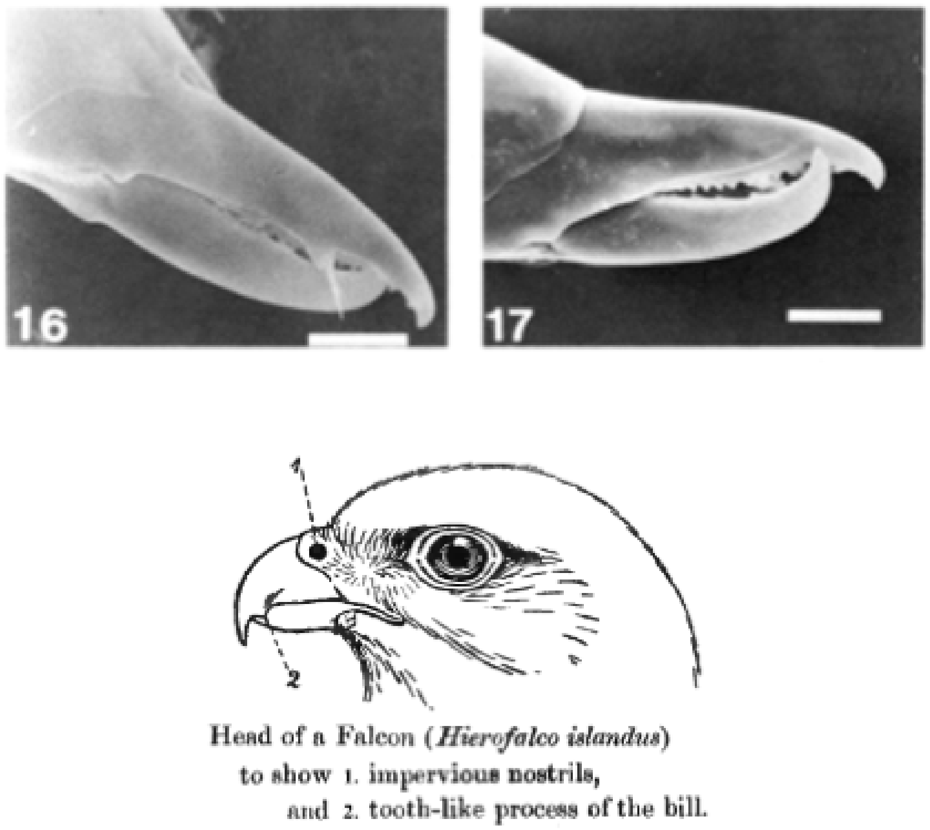

Figure 2 Sensing objects being held and cracking them. Upper. *Amblyseius similoides* (Phytoseiidae) chelicerae from Flechtmann and McMurtry (1992b) with author's permission. 16 = abaxial aspect (i.e., from outside the gnathosoma). 17 = adaxial aspect (i.e., from inside the gnathosoma looking laterally). Note seta on tubercle which would rest against the outside of a pollen grain. Lower. Falcon beak with tomial tooth (2) positioned to hold and dislocate the neck vertebrae of prey on occlusion as the lower mandible slices past the upper tomium (W R Ogilvie Grant 1921, Trustees of the British Museum, public domain illustration from https://en.wikipedia.org/wiki/Falcon).

several pollen specialists have their long pili dentili enlarged into membranous hyaline flang for fluid control or support (Lindquist and Hunter 1965, Masan 2022) They may also pick up other small objects like fungi which could be similarly sensed. Many other predatory mites also have the distal 'raptor' hook suitable for tearing at food (Figure 2). A SEM follow-up study is indicated.

Moreover the tubercle found here in phytoseiids may function like the tomial tooth of a peregrine falcon. This 'tooth' is also present in most celaneopsoid mites, (Seeman 2023, Seeman and Miranda 2024), where it is always the largest tooth.

The raptor-like hooked tip of chelal digits e.g., *Amblyseius similioides*, may facilitate tearing at prey flesh.

Prising things open

The crossed-over digit tips in some of the phytoseiids illustrated by other workers (e.g., Figure 2 top right) are reminiscent of the beak of crossbill birds (Jerry Krantz *pers.comm.*). These finches' unusual bill shape (see https://en.wikipedia.org/wiki/Red_crossbill) is an adaptation which enables them to extract seeds from pine cones by twisting their mandibles (see https://ebird.org/species/redcro9). For sure, if predatory mite digits were closed shut,

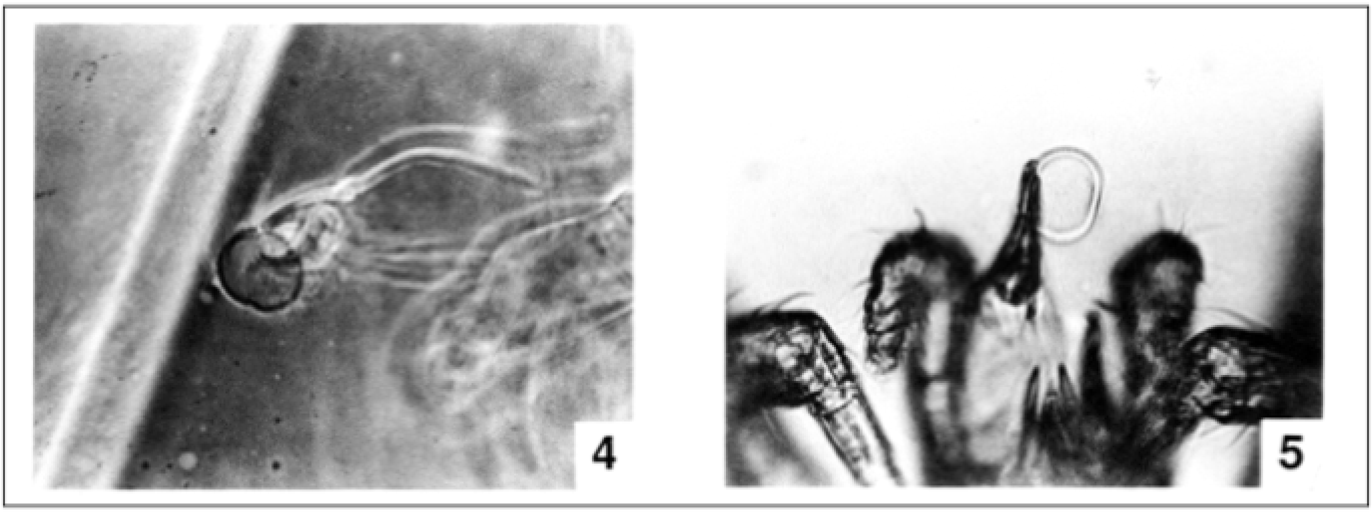

Figure 3 How pollenophagous phytoseiid mites hold pollen from Flechtmann and McMurtry (1992a) with author's permission. 4 = Protracted chelicera of *Euseius stipulatus* 'snatching' ice plant pollen grain. 5 = Ventral aspect of *Amblyseius similoides* chelicera holding ice plant pollen grain on its inner face. This requires an unusual chelal action.

this form would effectively widen the wound in any prey on cheliceral retraction (Bowman 2020).

For asymmetric-shaped prey like the snails attacked by the limpkin (https://en.wikipedia.org/wiki/Limpkin), beak shape needs to match the handedness of shell coiling to be maximally efficient. As each chelicera is a mirror image of the other so that both moveable digits swing 'inwards' i.e., there are not 'left-handed' mites and 'right-handed' mites only left-hand and right-hand chelicerae (within an individual). Mites by virtue of having two mirror image chelicerae (e.g. Figure 13 in Bowman 2020) thus can match either prey handedness. However, it is not clear how often predatory mites initially grab prey by 'shooting' both chelicerae out together in a tandem 'snap' versus a single chelicera being used in that first attack.

Opening things like a can

Flechtmann and McMurtry (1992a) describes a 'side-bite' mechanism by which a pollen grain is snatched and held by one chela and then ruptured by the other, all above the hypostome (Figure 3). How firmly the pollen grain is held during any fluid suction needs more clarity. However, if one focusses upon the stabbing moveable digit for such 'plant' feeders, the mode of action of a certain human kitchen utensil comes to mind here, i.e., the 'stab can-opener' (Figure 4) with an alternating rotating and piercing mechanism like in Figure 5. Indeed, Goleva and Zebitz (2013) show shrunken pollen with 'feeding holes' after phytoseiid attack. Of course each chelicera can swop their role interchangeably as they go along. The end result of the 'side-swipe' holding plus stabbing action of such a tool is that the pollen grain can be repeatedly punctured and sliced open held up over the hypostome fully releasing its contents for imbibition.

Cutting curves in 'tough' things

Is there a design that is consilient with other phytoseiids feeding where they are known to puncture prey legs and drain their body fluids (Flechtmann and McMurtry 1992a)? Their cheliceral form (Flechtmann and McMurtry 1992b) is more like Figure 6, suitable for cutting curves in tough material.

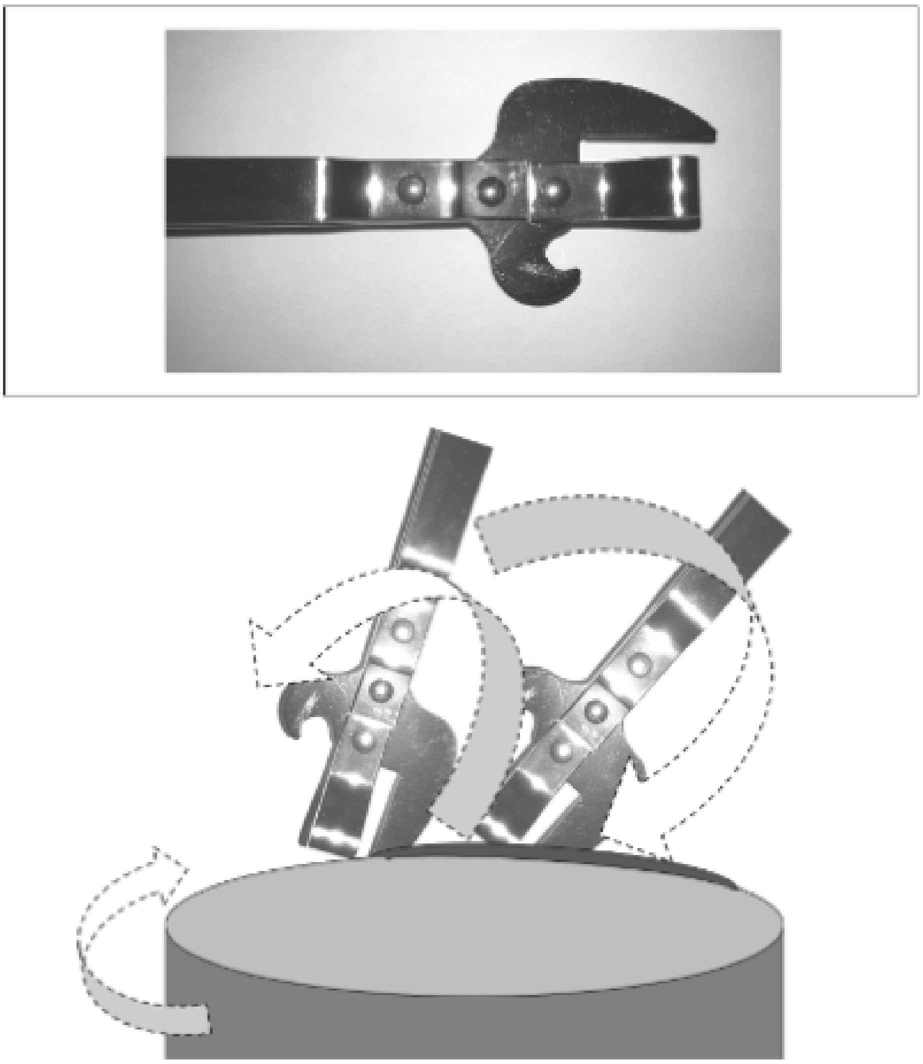

Figure 4 Steel 'Stab-can opener'. Upper. General form. Note heavy blunt central 'tang' (like acarine fixed digit). Small opposite hook used to deform and lever up metal caps on bottles. Lower. How a stab-can opener opens a tin. The tin is held against the central tang which is used as a fulcrum point for the pointed blade to pierce the lid. Then the tool is rocked back and forth so the blade slices the material, before the point is removed and the tin is repositioned to a new lever point. Then the blade slices again and the rupture is made longer. Note tang has a small central slot to engage with the edge of the tin.

There is an extreme design found in 'hawkbill cutters' used in podiatry and chiropody (Figure 7). This curved cutting style is necessary because metal (and keratin in nail) is stiff and heavy and does not move out of the way readily when cutting around a curve. Chitin is a laminated material like melamine, both of which can be stiff like metal. The respective styles of these pliers move such material out of the way when cutting in the direction that they are designed for. Mirror-image chelicerae with moveable digits formed accordingly would allow cutting in either direction.

Interestingly, estimating the moveable digit claw or hook angle (γ) and claw-length equivalent measures (see Bowman 2024a) for the phytoseiids illustrated in Adar *et al.* (2012) gives the following means per feeding style group: Group I-II: 126º, 13.4 µm, Group III: 127º, 13.8 µm, Group IV: 136º, 13.1 µm. This shows little differentiation between generalist and specialist predators and pollenophages for their ability to cut bent material without buckling it.

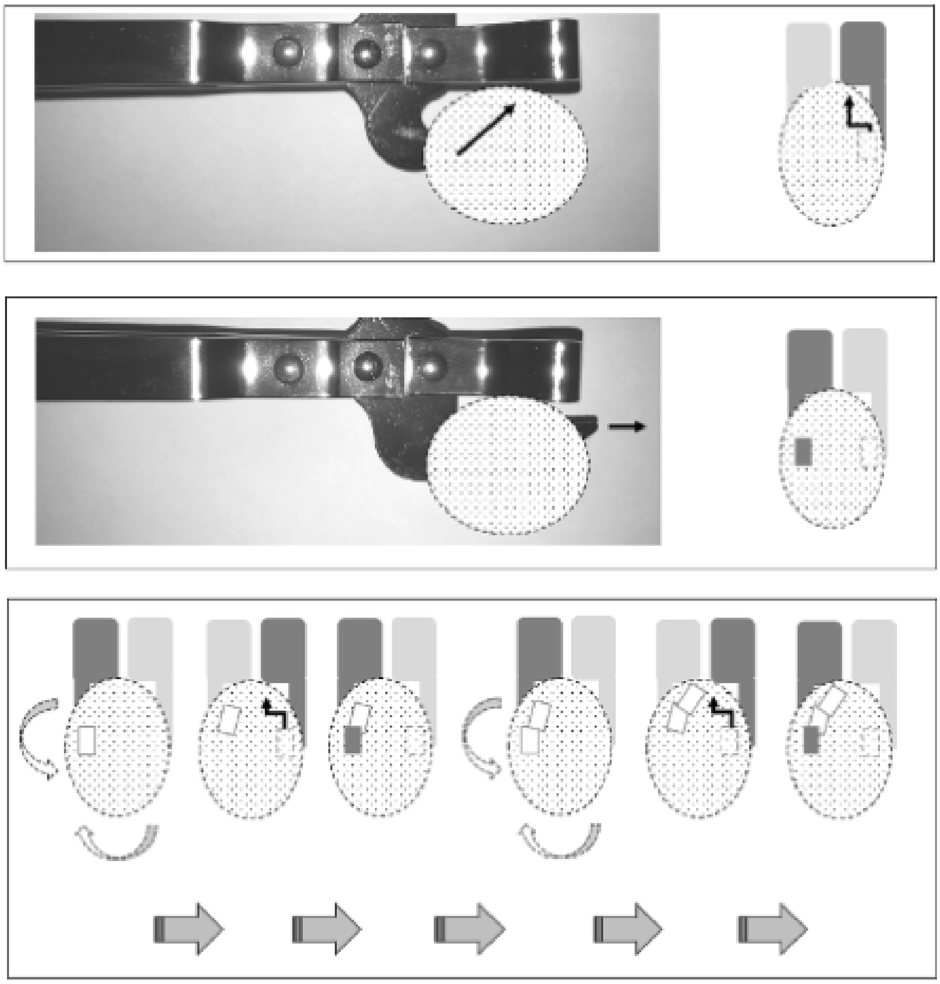

Figure 5 Stab-can opener mechanism for attacking a pollen grain. Dark = active chela. Upper. The pollen grain is 'bitten' in the side by the (dark) chelal moveable digit and held up against fixed digit. Paler chelicera retracted. Lateral and end-on view. Middle. Other chelicera becomes active, protracts and stabs rupturing the pollen grain. Lateral and end-on views. Lower. Cycle of action (end-on view, left to right as indicated by large arrows). Active chela retracted leaving rupture and pollen grain adjusted in order to give a new lever point for a (dark chelicera) side-bite to hold the grain again and the pollen is ruptured anew etc., etc. following the action in Figure 4. If a prey leg could be rotated with respect to the gnathosoma by body counter-movements a similar result would be achieved.

Snipping a hole in 'metal-like' things

'Aviator snips' which come in left-cutting and right-cutting versions are used for cutting tight curve holes in pipes. The shape of the blades allow for sharp turns without buckling flat sheet metal that they are also used for. Arthropod cuticle is tough. Again the mirror-image form of acarine chelicerae allow cutting curves in either direction (i.e., clockwise or anti-clockwise). Aviator snips blades are usually serrated to prevent material slippage, just like phytoseiid digits. Note that teeth serrations apparently do not affect stress dissipation during feeding (at least not in herbivorous dinosaurs, Reichel 2010). Blunt curved pliers as opposed to such cutters are also known being usually called curved jaw or bent nose pliers.

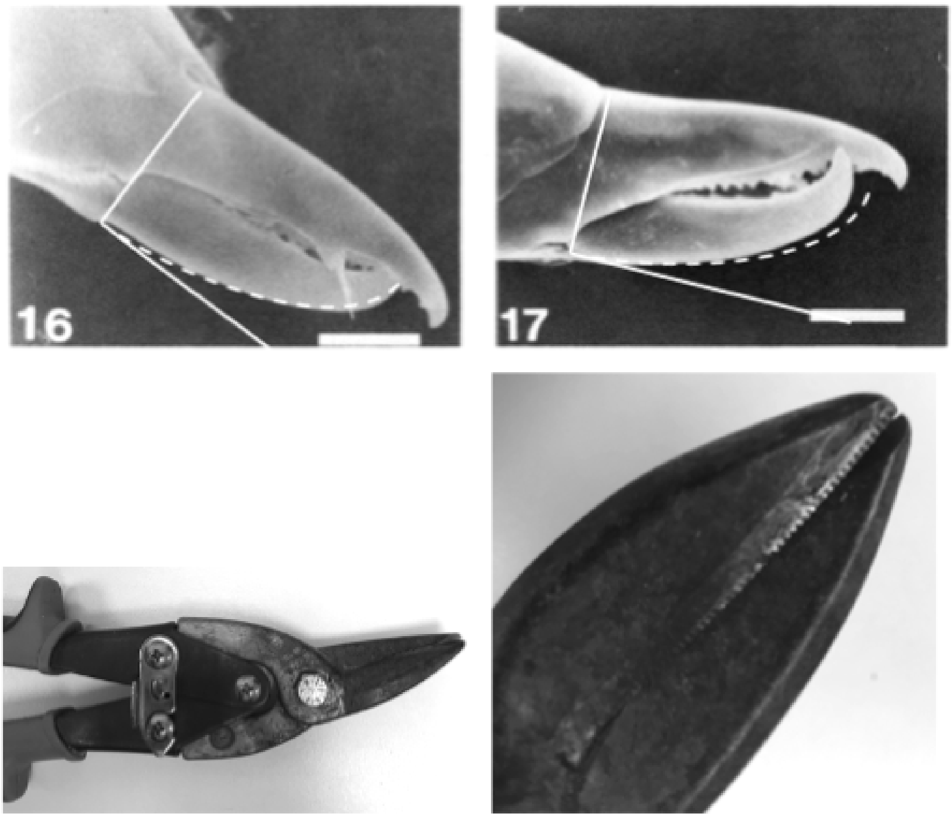

Figure 6 Design for cutting a hole. Upper. Pollenophagous *Amblyseius similoides* (Phytoseiidae) chelicerae from Flechtmann and McMurtry (1992b) with author's permission. 16 = abaxial aspect (i.e., from outside the gnathosoma). 17 = adaxial aspect (i.e., from inside the gnathosoma looking laterally). Note overbite of fixed digit and how moveable digit swipes slightly sideways and occludes on the internal fixed digit face. Lower. Aviator or aviation snips (red right-handed version). Note asymmetric slicing curved blades and serrate edges near tips.

And.. not 'dribbling'

Many vertebrate animals have cheeks. Could mites have anything similar (recall the hyaline flange of *Proctolaelaps* and some other melicharids), and are there unusual actions related to them?

Pergamasid mesostigmatids have been observed to drink from droplets (despite the challenges of viscosity at that scale, Bowman 2023b). Humming bird flower-inhabiting mites handle nectar not just pollen, depleting flower stocks significantly if in large population numbers. Various subsidiary structures are described to facilitate fluid feeding in some phytoseiids (Flechtmann *et al.* 1994). How do these function? Some clues as to unusual fixed digit actions in some phytoseiid mites are the location of apparent cuticular extensions to the sensory dorsal proprioreceptive lyrifissure on some species (e.g., in euseiids, Flechtmann and McMurtry 1992b). These augmentations extend laterally around the digit shaft. The lyrifissure functions as a strain gauge for fixed digit cuticular flexing under moveable digit occlusion against foodstuffs in mites. These extra cuticular folds suggest a degree of movement outwards (i.e., obliquely sidewards) on chewing as the moveable digit slides against the upper fixed chelal teeth. This is consilient with the side-bite action discussed above. It also is much like the action (Weishampel 1984) arising from the unique 'hinge' between the upper jaws and the rest of the skull in ornithopods (which compensates for the lack of a flexible lower jaw joint prevalent in modern day mammalian herbivores) and also in the beaks of crossbills.'Cheeks'

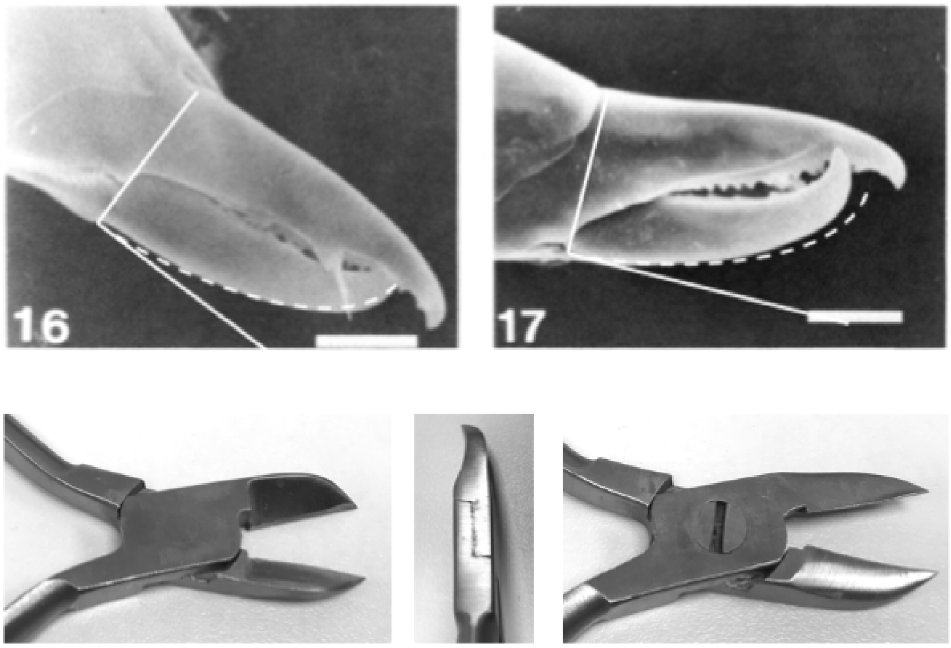

Figure 7 Design for cutting curves. Upper. *Amblyseius similoides* (Phytoseiidae) chelicerae from Flechtmann and McMurtry (1992b) with author's permission. 16 = abaxial aspect (i.e., from outside the gnathosoma). 17 = adaxial aspect (i.e., from inside the gnathosoma looking laterally). Note curved blade-like digits. Lower. Hawkbill clippers used to slice tough toenails leaving a curved profile. Note sharp blades on front (left), curved profile from above (middle) and clear curved digit depth (right).

would hide this action during chewing (Williams and Purnell 2008).

Hamsters are of course well known for sequestering foodstuff in their cheek pockets. Indeed, fluids released from pollen by some phytoseiid mites can be channelled (much like how a straw functions) between the chelicerae by the exterior lobes on the chelae (Figure 8). Such lobes are functioning like how the duck-billed hadrosaur cheeks (Galton 1973) did in keeping food within the oral area. Of course, any lengthening of the distance liquids have to flow before entering the pre-oral food channel and being imbibed by mites may affect feeding efficiency. However, prevention of loss by stopping overflow 'spilling' may be a selective advantage. Just as a cheek-delimited 'pocket' retaining material for the continual intensive mastication and further extraction of fluids would too. Such lobes appear in other taxa (e.g. trigynaspids) – so perhaps *Proctolaelaps* solved this problem by modifying the pilus dentitlis, while others modified other structures like the membranes where the moveable digit connects with the fixed digit.

"How can other mites attack things with other tools?"

Levering things up and sawing

Underbite in a chelicera occurs when the length of the moveable digit is more than that of the fixed digit i.e., $VP_{md} > DP_{fd}$ (Adar *et al.* 2012). In contrast, overbite occurs when the length of the moveable digit is less than that of the fixed digit i.e., $VP_{md} < DP_{fd}$. Both such malocclusions can be adaptive. What biomechanical consequences might they have?

An example of underbite is the chelicera of certain mesostigmatids (Figure 9). Here the long serrate moveable digit may be used to lever up between the joints of millipedes scales (Seeman 2022*)* lifting them up so that the mite can access its host's body fluids after sawing into the underlying tough cuticle. Note that the 'tomial' tooth seems to be secondarily lost in

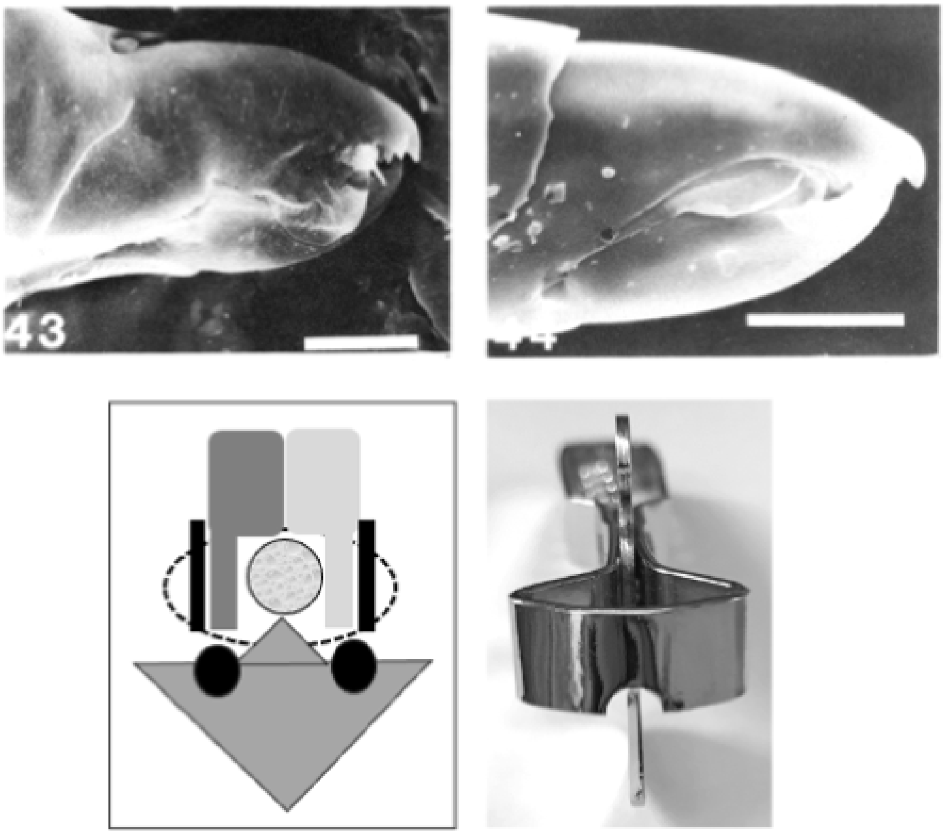

Figure 8 ‘Cheeks’ and notches. Upper. *Euseius stipulatus* (Phytoseiidae) chelicerae from Flechtmann and McMurtry (1992b) with author’s permission. 43 = abaxial aspect (i.e., from outside gnathosoma). 44 = adaxial aspect (i.e., from inside the gnathosoma looking laterally). Note gripping apparatus on tip of moveable digit (c.f. central slotted tang of stab-can opener) and flap-like lobes between the fixed and moveable digit. Lower. Left. Schematic cross-section of gnathosoma. Each chela flanked by lobes (in black) that seal the tube-like portion of fluid between them above the hypostomal labrum. Dashed line pollen remnants. Black circles = supportive corniculi. Lower. End-on view of a stab can-opener showing notch analogous to the divided features on the end of fixed digits in the euseiid chelae that could engage with pollen exine crenelations.

Terrogynium weatherwaxae unsurprisingly (Figure 9).

Overbite is a feature of many uropodoid mites (e.g., *Cilliba cassidea*). Here the length of the fixed digit is visually approximately 125% that of the moveable digit (Athias-Binche 1977). Such ‘small-headed’ mites may still have a powerful chelal crunch force as the adductive muscles can be stored well back in the larger cheliceral base segments within the gnathosoma. The third baso-basal segment in some species may increase such muscle power even more, making them designed ‘track nuts’.

In the gamasines, Adar *et al.* (2012) found that plant feeding phytoseiids had $\frac{DP}{VP} > 1.0$ compared to non-plant feeders at $\frac{DP}{VP} < 1.0$, i.e., there is a degree of overbite in the (facultative) herbivores (or conversely a degree of underbite in the predators). Liu *et al.* (2017) found that pollen feeding phytoseiids had fixed digit dorsal profile perimeters greater than their moveable digit ventral perimeters (i.e., $\frac{DP}{VP} > 1.0$) compared to generalist and specialist predators (who showed the opposite i.e., $\frac{DP}{VP} < 1.0$). All phytoseiids illustrated by Flechtmann *et al.* (1994) and Flechtmann and McMurtry (1992b) appear to have overhanging fixed digits in lateral SEM pictures of the chelicerae. Overbite can be useful for a ‘can-opening’ action (see above). For sure, to the author’s knowledge there is no evidence for a supernumerary process on mite moveable digits (like the predentary bone in ornithischian jaws (Nabavizadeh and Weishampel

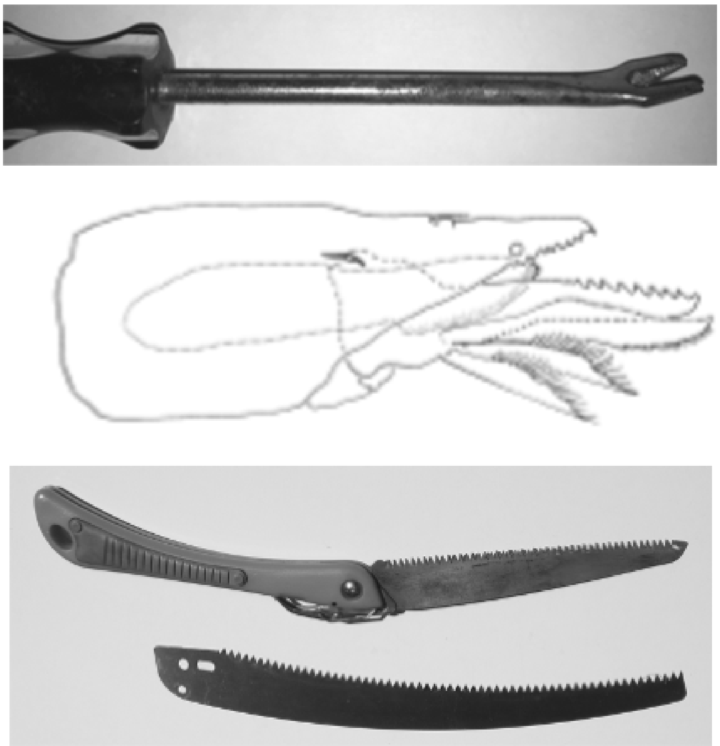

Figure 9 Underbite. Upper. Tack-lifter tool used to prise open joins (like a crow-bar) and to remove nails and fasteners from surfaces. Middle. Schizogyniid female *Terrogynium weatherwaxae* chelicera from Seeman (2022) Fig 3a with author's permission. Note plumose setae to act like 'mops' and collect consequent host fluids. Lower. A Japanese-style folding saw that cuts on the pull stroke together with a spare saw blade for a giraffe- or pole-saw used in tree pruning (amended from StromBer 29 April 2008 https://en.wikipedia.org/wiki/Polesaw under Creative Commons Attribution-Share Alike 2.0 Germany license).

2016)) to compensate for any overbite.

Un-peeling things

Are certain chelicerae designed for browsing or designed for grazing? A question that can be often asked of herbivorous and saprophagous mites. There is already the same long-standing debate regarding such in different hadrosaurs amongst palaeontologists. So, what are the key design features of each modality?

For essentially tubular animals, metazoans accessing terrestrial material has its challenges (Wassenbergh *et al.* 2006). Mites with their anterior gnathosoma and oral opening above a hypostome need to get food up and into their gut. Grazers (like vertebrate sheep or cows) feed on vegetative material close to the ground and are morphologically adapted accordingly (i.e., by bending their necks down and cropping food). Browsers (like vertebrate deer or giraffes) consume higher growing material (such as leaves and twigs) and are designed differently. Indeed what are the micro-scale equivalents of trees, bushes, twigs and leaves for mites? Some chelae are designed not just to crop but also to unpeel material (Figure 10).

For sure, the former near-ground grazer habit requires a klinorhynchid pose or an ability to access material essentially underneath the main axis of a mite's idiosoma. Uropodoids certainly have adaptations for this (with effectively teeth on the end of a long snout like in weevils). Just what might be the micro-equivalent of grasslands like the Serengeti for mites? Browsing is facilitated by a long flexible neck on an airorhynchid pose or the ability of an animal to rear up (especially onto rear legs like for instance *Brontosaurus*). Are there such mite analogues? More

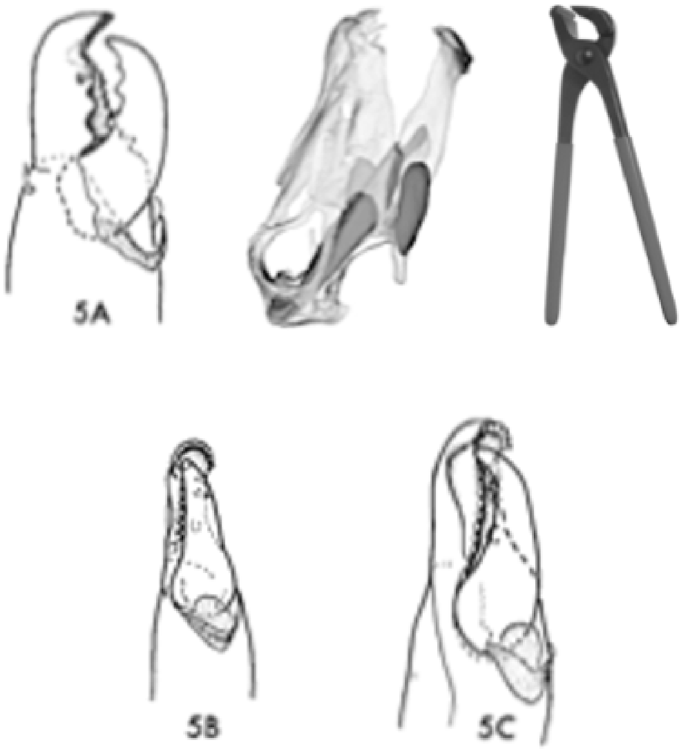

Figure 10 Overbite. Upper. Overbite in female blattisociid *Hoploseius comerta* chela (amended from Lindquist (1963) with author's permission). Upper. Left. 5A = lateral view. Middle. *Diplodocus* skull lateral view with jaw musculature amended from Button *et al.* (2014) under Creative Commons Attribution License 4.0. Note serrate front edge to upper mandible and spike-like profile of lower mandible. Right. No. 2795 STUBAI Seam opening pliers for metalworking (amended from © https://www.stubai.com/en/n-2795-stubai-seam-opening-pliers/ under 'Fair use'). Note curved 'digit' opposing laterally flattened 'digit'. Lower. Female *Hoploseius comerta* chela 5B = ventral view, 5C ventrolateral view showing commonality of design with the dinosaur and pliers.

detailed observations of certain free-living astigmatan and mesostigmatid feeding in the wild are needed to see if either behavioural modality is observed to match their cheliceral design.

For sure, a rasping type of overbite (Figure 10) is found in the form of the blattisociid *Hoploseius cometa* fixed chela (Lindquist 1963). This species shows a blunt apical end to the fixed digit with a curved row of small teeth along the apical margin, plus a sharp 'normal' moveable digit. In general form this looks like a version of a mini-top cutter, however, where one 'digit' surface remains curved while the other is flattened out, like Stubai standing seam opening pliers. The latter are used to open up seams on metal roofs (see https://www.stortz.com/product/standing-seam-opener-364-a/). This serrate broad snout matches the upper mandible of *Diplodocus longus*, itself like the shape of a horse's head. This dinosaur is posed to be a branch stripper, smoothly gleaning foliage from such stems or cropping soft water plants as the animal's head moved backwards. Other camel-like gleaning hadrosaurs like *Edmontosaurus* share the same distal design. *Hoploseius* is associated with shelf and bracket fungi (and drosophilids therein, Lindquist 1963). Its ecology is not clear. However, these multiple notches on the mite's digit of course would also engage with material for the moveable digit to act like a can-opener blade - another example of a polyfunctional composite tool.

In bee-hive living astigmatans, gleaning was associated with chelae like 'pliers' (Bowman 2024b) and browsing with saw-like moveable digits (Bowman 2024a), the latter design also having a greater occlusive chelal force against foodstuffs (Bowman 2021). Amongst herbivorous dinosaurs, *Stegosaurus* had a more powerful bite than its peg-like teeth would suggest (although this is a lot less than what its five ton body weight might suggest, Lautenschlager *et al.* 2016). Is this true also of mites in general? Indeed why are there seemingly no powerful jawed herbivorous mesostigmatids (or even spiders for that matter) designed like a Giant Panda (Bowman 2020)? Indeed, why have no non-acarine chelicerates figured out how to stab plants with their fangs and feed upon phloem (like aphids do)? Why are there no large uropodoids (in the micro 'rainforest' environment of temperate soils) matching the equivalent damp niche of extinct land-based giant turtles like *Carbonemys* (Cadena *et al.* 2012) with its relatively massive jaw? Is it that such trophic opportunities are dominated by oribatids which effectively exclude other acarine competitors? What is it about Acariformes that make them successful herbivores? Where are the predatory mite equivalents of snake-necked turtles (like *Chelodina*)? Is it that tracheal respiration effectively restricts activity in flood-able environments so that active predators need significant plastrons (like in mesostigmatids)? Can oribatids actually ever be truly predatory in design (as opposed to be just opportunistic or facultative zoophages)? Many questions remain.

Indeed, is it that a very long chelicera (as in uropodoids) is an energy efficient adaptation for these mites to browse across wide swathes of potential food without moving much as posed for sauropods (and they are not indeed 'crevice feeders')? Could such uropodoids live in semi-sedentary, slow-moving herds (or flocks)? Could the trophic niche of uropodoids simply be equivalent to that of dry habitat ostriches (i.e., extant ratites) or even ornithomimosaurians (Barrett 2005)? But then, why are there seemingly no high speed moving and kicking uropodoids? For sure, the uropodoid strategy seems to be based around limpet-like protection (their pedofossae are significant, letting them pull their legs under their body and then they 'hunker down', Evans 1972). Some uropodoids are also cryptic, covering themselves with grit etc., so running and kicking probably needs a big change in life strategy. Indeed, kicking itself is not commonly reported in mites (usually it is males kicking other males while engaged in precopula).

Much previous work in oribatids examined the degree to which different feeding styles are reflected in gnathosomal morphology (e.g., Perdomo *et al.* 2012). This can, like in dinosaur assemblages (Mallon and Anderson 2014), explain co-existent species in communities. However, Bowman (2024a) makes the point that at least in some astigmatans, chelae are composite (i.e., not of a single function) tools. Indeed Bowman (2024b) illustrates how for *Carpoglyphus lactis* the moveable digit may be simultaneously both a picker, a fluid slicer and a hyphal cutter/crusher (much like 'long nose' cutting pliers). Similarly, *Tyrophagus putrescentiae* may both grip and crush fungal and nematode food as well as strip (like 'slip joint pliers') conidia and spores off of the hyphal stalks. Is this an analogue of how some Serengeti ungulates perform? As the conclusion of Klunk *et al.* (2023) shows for insect mandibles, it is the active use of morphology, not just its static form, that matters.

'Trap-jaw snapping' on things and 'rearing up'

Bowman (2020) offered a variety of functions for the 'Rollplatte' in the chelicerae of uropodoid mites. Such mites have elongate chelicerae acting almost like an elephant's trunk. The unguintractor in the leg pre-tarsi of other arthropods may help in understanding which of the posed functions is more likely.

Gorb (1966) discusses the functional design of the insect leg pre-tarsus (a strongly modified structure originating from the crustacean dactylopodite with only a flexor muscle). The pre-tarsus connects to the terminal segment of the tarsus by a sclerotised plate called the unguitractor (or unguitrador plate). This attachment structure (Ditsche and Summers 2014) has long been used as a taxonomic feature in insects (e.g., Ruiter 2004). The unguitractor (plate) is an insertion point of the claw flexor internal muscle. This system is interpreted as an energy-saving unit that fixes the claws in the grasping position and can vary ecomophologically (Matsumura *et al.* 2022). In Diptera, Coleoptera, Hemiptera (Rebora *et al.* 2021) and Hymenoptera (Asperges *et*

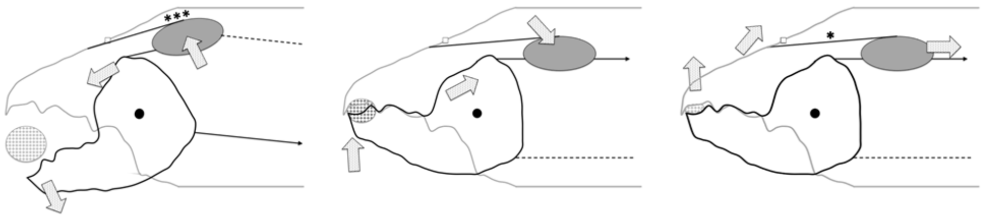

Figure 11 Schema of how a Rollplatte might work like an 'internalised' unguitractor plate (*sensu* Gorb 1966) or a falcon's claw tendon locking mechanism. Cheliceral profile based upon astigmatan *Tyrolichus casei* simply for ease of illustration (N.B. Rollplatten are a mesostigmatid only feature). Black circle = rotation point at condyle. Small open square = dorsal lyrifissure. Hashed arrows indicative movements when masticating food. Left. Chela opened by abductor tendon. Rollplatte pulled forward and up (effectively rotating around near lyrifissure by passive tension on adductor tendon) to engage with inside of cheliceral shaft where friction (***) prevents moveable digit over-extending. Whole chelicera ('jammed open') can be moved forward like a 'snow-plough' to engage with foodstuff. Tension may build in adductive tendon by further adductive force F1. Middle. Standard (or 'snapping') occlusion of previously ploughed material by adductive muscle force. Rollplatte disengaged. Tense tendon may recoil to accelerate digit 'snap' given suitable ('cocking'/unlocking) condylar geometry. Right. Continued pulling on adductive tendon could rear up whole chela head (rotating it - see Bowman 2020) reinforced by the indirect pull on * (= continuing 'unguintractor tendon') , as chitinous exoskeleton of fixed digit buckles.

al. 2017) the roughened surface plate is semi-external to the body to facilitate insect attachment by adhesion.

If the seemingly internalised Rollplatte in uropodoids acted with the same ratchet-like function (except here the van der Waals forces-mediated adhesion is not to the external substrate surface as in insect claws, but to the internals of what was the ancestral tarsal shaft), then Figure 11 indicates its likely role. This would mean that the adductor muscle would not need to resist the over-opening forces of an open chela being moved forward plough-like into the foodstuff (thus saving muscle energy in maintaining the orientation of its moveable digit mastication surface, teeth and blades with respect to foodstuffs). This fits with idea of the chela being used like a mechanical shovel-bucket digger or bulldozer (Bowman 2020).

The idea of an internalised plate is not so fanciful. In the claw of the midge *Chironomus riparius*, the unguitractor is recessed so deeply into the cuticular pocket of the tarso-pre-tarsal joint membrane that even when the pre-tarsus is extended it does not reach the walking surface (Seifert and Heinzeller 1989). Follow-up acarological work is needed to look for scaly (Gladun 2008) or micro-trichial roughed surfaces on Rollplatten (and their corresponding cheliceral base engagement surfaces like in Plecoptera, Nelson 2009) using scanning electron microscopy of freeze-dried fractured chelicerae. However, it can be difficult to demonstrate physical contact between such surfaces (Gorb *et al.* 2019).

A similar internal mechanism is found in the tendon locking mechanism (TLM) of falcon (and parrot) claws (Einoder and Richardson 2006). There, a ventrally located tubercle pad on the tendon interacts with a stationary plicated sheath (and the phalangeal bone) to keep the claw closed with less continual muscle effort. Of course, the exact movement of the acarine fixed digit in this scheme will depend upon the geometry of the articulating condyle (or equivalent flexible cheliceral sheath) as well as the exact location of the tendon junctions with the fixed digit (see Bowman 2024a for a discussion on coronoid process design margins).

More morphological and embryological work is needed to regularise what parts of mite chelicerae might be related to the arci, arolia (Federle *et al.* 2001), auxilliae, empodia, manubria, planta and pulvilli found in arthropod claws (https://en.wikipedia.org/wiki/Arthropod/_leg) and the precise way that they interact (e.g., see Gladun 2008). For sure there are known phylogenetic, body size and ecological correlates of the TLM in birds (Einoder and Richardson 2006). Could the sizes of Rollplatten be informative too?

Instead, could some uropodoids be considered as 'arthrodires' (https://en.wikipedia.org/

wiki/Arthrodira)? That is, if the fixed digit of the uropodoid chela is rapidly pulled up and backwards at the same time as the moveable digit opens (sabre-tooth like as Bowman 2020 suggested), then it is possible at a very local micro-scale to produce a tiny suction effect (much like at the macro-scale the extinct apex predator *Dunkleosteus terrelli* skull functioned). Such would bring material into the chelal occlusion area. Is this sudden dorsal flexure what the jointed basal third cheliceral segment might be able to achieve for the chelal head in uropodoids? It is worth pointing out that suction feeding in the analogous aquatic very long-necked hunting placoderm *Dinocephalosaurus* (Spiekman *et al.* 2024) has not been universally accepted (https://en.wikipedia.org/wiki/Dinocephalosaurus).

Moreover, this "jointed-neck» placoderm had another possible commonality with these mites - the armoured fish lacked distinctive teeth, using instead strengthened edges of a bony plate on their bony jawbone as a biting surface. The exposed upper and lower jaw plates came together to form a scissor-like cutting edge that would also self-sharpen every time the fish jaws opened and closed. Uropodoid moveable digits simply by virtue of their smallness must consiliently have rather small thickness especially distally (thus approximating such bony 'edges'). Indeed, the left inferognathal anterior in the largest currently known individual (CMNH 5936) of *D.terrelli* (Engelman 2023) looks very much like the typical moveable digit dentition of some soil living oribatids (e.g., *Steganacarus magnus*).

Finally, if there were special condylar modifications that would allow not just pivoting, but also 'slip joints' or 'cocking slip joints' (Kaji *et al.* 2018) in the chela, then chela in uropodoids with Rollplatten could function as ultrafast 'snapping claws' like in shrimps or have a trap-jaw snapping action as in some ants (https://en.wikipedia.org/wiki/Odontomachus). Here, from an open jaw 'cocked' position with the Rollplate 'anchored' (Figure 11 Left), tension is accumulated in the adductive tendon. This continues, until suddenly the joint slips un-cocking the digit with an attendant release of the inner adhesion of the Rollplatte (Figure 11 Middle). The energy stored in the stretched spring-like tendon is released, slamming the digit shut and continuing into the upper flexing action of the chelal head (Figure 11 Right). In this way, the mite 'ploughs' (deep into the substrate), and the moment sensory receptors on the fixed digit tip detect something - the mite instantly grabs it (before it can move even a tiny bit away) and tears the morsel up and out from its original location all in one scheme. Nano-computerised tomography and confocal microscopy is needed in follow-up work to check for such joint architectures.

Locking onto things

A further unusual action is the possible 'latch' mechanism (Figure 12) in the diplogyniid *Weiseronyssus mirus*, an associate of scarabaeid beetle larvae (Zhang *et al.* 2024). In this species an object hitting the large tooth may be cut or sliced by it, but almost certainly drives the moveable digit open as it rises up the sloping surface until it transverses the zenith of the mastication surface and drops into the nadir where membranous excrescences seal around it. A novel idea is to suggest that the trapped material is the chitinous exoskeleton of the beetle larva and the various membranes are to channel host fluids into the oral area while the mite is stuck fast on its food source. Eventually courtesy of the short output moment arm, any held-fast material can be easily crushed. As a polyfunctional tool, the chela of course is also able to stab, grip and crush other foodstuffs (like acarid mites or nematodes) more distally in line with these mesofaunal predatory scavenging mites typical habits.

"What about handling fluids?"

Preventing 'dribbling' has been already discussed above

Controlling the flow

Daggerboards are a feature of historical UK railway station canopies (many having been built in the Victorian era -

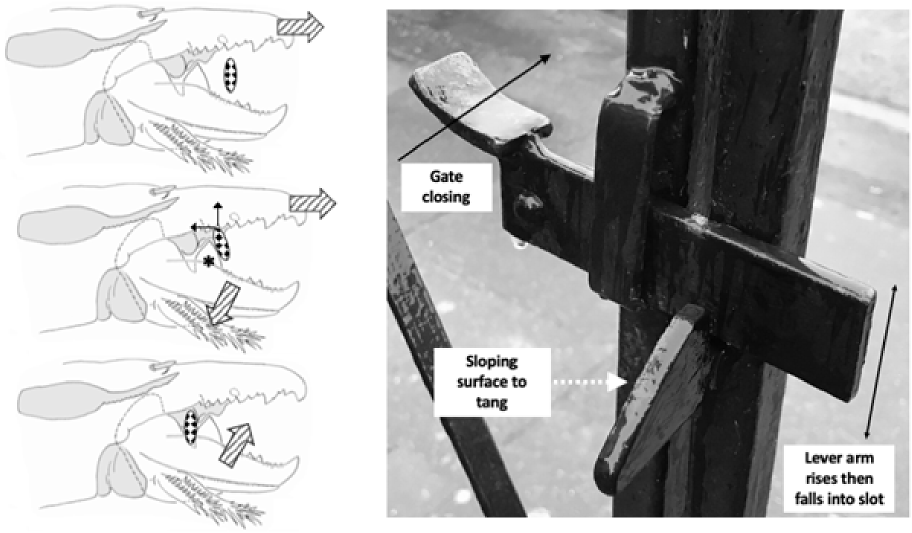

Figure 12 Proposed mechanism by which a chelicera, here of a female mesostigmatid *Weiseronyssus mirus* (Diplogyniidae), functions as a gate-latch. The object (dotted oval) acts like the main body of the 'latch-arm' of a gate-catch which hits the tang on the 'receiver/strike'. Left. Gate open. Second row. The object engages with the major proximal tooth (*) as the whole chelicera is moved forward (striped arrow, ≡ gate closing), the object is forced upwards (small black arrows) along the oblique curved surface (≡ the tang). Unlike a gate where the latch arm has unrestrained upwards movement, the moveable digit is forced open instead (striped arrow), Third row. Finally the moveable digit snaps shut (striped arrow, ≡ gate closed) and the chela holds the object firmly locked into the gully behind the tooth (surrounded by grey membraneous features). Amended from an illustration in Zhang *et al.* (2024) with the author's permission. Right. Garden gate latch. Note that here the latch arm is pivoted, not the tang, but the 'catch' principle is the same.

https://roofingtoday.co.uk/the-distinctive-designs-of-railway-station-canopy-roofs/. Such crenelations facilitate rain handling directing the fluid downwards. Are there similar bladed structures in mites?

Efficient fluid handling whether of prey/host liquids or coxal gland debouched (Nuzzaci *et al.* 1999) material during feeding (Bowman 2014, 2017a, 2017b, 2019) is important in efficient mesostigmatid feeding (Bowman 2023b) not just via gnathosomal grooves and channels but also through using droplet 'depots' and distributive 'points'. Surface characteristics are the key (Figure 13). A good example of controlling fluids with 'depots' at a macro-scale, are the gaps between Victorian vertical flat daggerboards (Figure 14) on the margins of old UK railway station roofs. Since fluids try to form a surface of minimal energy, surface tension will suck water films along the edges of adjacent daggerboards (near their base) and accumulate rain on the surfaces in the spherical depot areas, which when sufficiently full will collapse (due to gravity) and flow down towards the sharp drip point.

Indeed the constriction (even in an open channel like this) of flowing down the narrow slots will induce a Venturi effect by which there will be a reduction in fluid pressure and an increase in fluid speed. The cupped wing profile of diving peregrine falcons also increases air flow speed via a similar effect (Ponitz *et al.* 2014). This may be the reason why in places the mesostigmatid deutosternal groove in cross-section is concave. One would be most intrigued to see if dagger boards are more effective in shifting rainfall if the edges facing the previous/next board are routed out into a shallow central groove.

Daggerboard drip points distribute the rain away much like the various fimbriate excrescences and tips of internal male on a mesostigmatid mite's hypostome (albeit at a different scale and by an edge crawling mechanism). If the tips were (super)hydrophobic, subsequent droplet formation and loss by gravity would be facilitated. Some canopies can have a string of depots too (just like the localised deutosternal differentiations first categorised by Karg 1965).

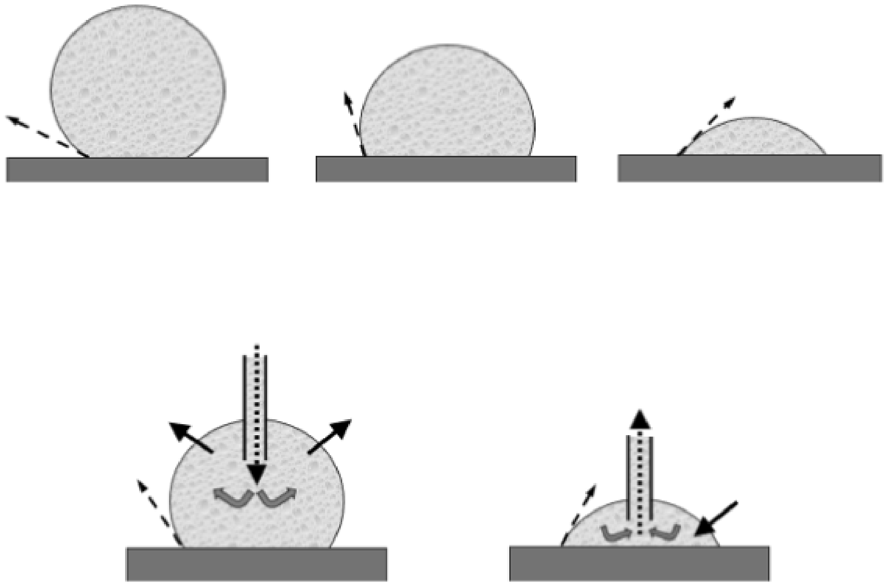

Figure 13 Surface tension determines droplet spread on a surface, its shape and whether the fluids move into or out of the droplet from another reservoir (‘static’ equilibrium contact angle Θ, Bowman 2023b, shown as arrowed dashed lines, fluid movement as dotted lines). Upper left to right: Superhydrophobic surface $\Theta>150^\circ$, Hydrophobic surface $\Theta>90^\circ$, Hydrophilic surface $\Theta<90^\circ$. Lower left: Fluid entering into droplet on a (super)hydrophobic surface from an open reservoir showing advancing angle (= maximum static contact angle) as droplet grows (solid arrows). Lower right: Fluid being drawn out of droplet on a hydrophilic surface to an open reservoir showing receding angle (= minimum static contact angle) as droplet shrinks (solid arrows).

Figure 15 illustrates the mapping between daggerboards and the forward flow of gnathosomal fluids on the ventral surface of the mesostigmatid hypostome. Further examples with the same topology can be seen in various Uropodina (e.g., Figs 3 and 11 of Bal 2006, Fig 3A of Bal and Özkan 2007, Fig 5 of Gwiazdowicz *et al.* (2023), Fig 4D of Kazemi and Klompen (2022), etc.,).

Depots can have another possible function. Addition of a surfactant or an oil into the depot can cause effective unidirectional movement driven by changes in surface tension. This is the mechanism that can propel a flat floating toy boat with soap, or a flat paper fish by a droplet of oil (see Dev Vries 1974) over a water surface. Sugar secretion will have the opposite effect removing water from surface depots. This is all mediated by the flat boat or fish surface sitting on the fluid and a change in wetting angle (Figure 13) which can have dramatic effects upon droplet shapes and flows. Looking for secretory pores and ducts leading to acarine fluid depots whether hypostomal or idiosomal is needed in follow-up morphological work.

Of course, on mite surfaces fluids move, advancing and receding within the gnathosoma, according to a scheme summarised in Bowman (2023b). Indeed, Jiang (2021) gives a nice recent review of how oscillatory mechanisms can move fluids in unexpected ways. The advancing (wetting) angle of a fluid is thought to be more sensitive to hydrophobic components of the solid surface. The receding (de-wetting) angle has been shown to correlate well with the adhesion force between the solid and the liquid. The difference between the two is called contact angle hysteresis (Eral *et al.* 2013). It is widely accepted that practically all real surfaces exhibit contact angle hysteresis arising from chemical and topological heterogeneities (e.g., roughness of the nanometer scale and chemical heterogeneity as small as 6-12 nm can contribute to this contact angle hysteresis). Narrow rectangular planes (like for example a deutosternal groove) alters advancing and wetting behaviour (Hong *et al.* 2013). Fluids can be pinned (and thus de-pinned) when advancing and receding (Chou *et al.* 2012), phenomena

Figure 14 Canopy crenelations at Platform 4, Maidenhead Great Western Railway station UK. Note 'drip-tips' and circular reservoir between each pair of boardings hanging vertically down from roof. Twyford GWR station has pairs of daggerboard examples each with two vertically arranged 'depots'.

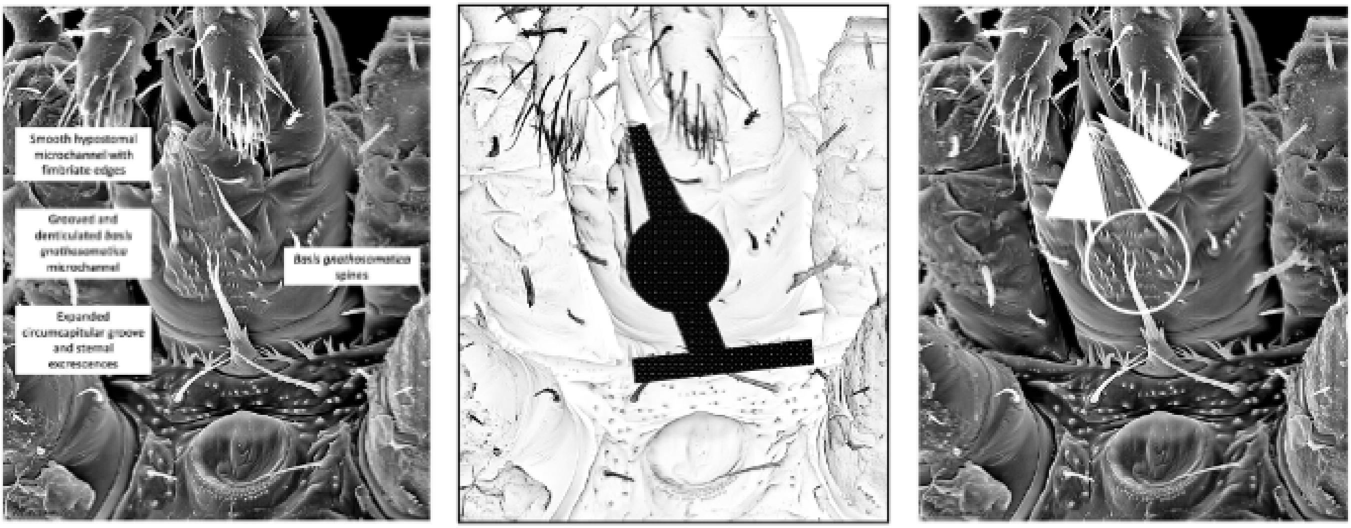

Figure 15 Daggerboard design superimposed upon venter of the gnathosoma of a male sejid. Amended from photograph of male *Epicroseius* sp. ex An Empty Shell (April 25, 2015) by Dave Walter at https://macromite.wordpress.com/2015/04/25/an-empty-shell/ with permission. Left, schema. Middle, negative showing liquid volume in (black) circum-gnathosomal and deutosternal channels matching daggerboard design. Right, sub-triangular 'drip tips' of hypostomal flanks and internal/external malal excrescences (in white) matching daggerboard apices. Circular reservoir or 'depot' highlighted centrally in deutosternal groove

which may occur at the deutosternal ridges. Indeed, wettability is a complex topic. Dorrer and Rühe (2006) is a useful entry point to the literature.

Although not obviously crenelated, there are a variety of other flat membraneous structures within the gnathosoma of some mites other than the 'cheeks' discussed above. All Celaenopsoidea and Megisthanoidea have two 'membranous flanges' on the inner surface of the fixed digit, the base of which itself is a broad membranous area Owen Seeman *pers.comm.*). It is not yet clear exactly how these work when the chelicerae are working back and forth, but when together these membranous areas would certainly appress channelling fluids accordingly. They are not 'pukka' cheeks as they are on the inner surface, true cheeks need to be on the outside. An SEM follow-up study is needed.

Feeding in fluids

Astigmatans exemplify different design solutions for feeding in fluids. For example, if carpoglyphids do not 'skim' fluids (Bowman 2024a) for nutrition, how else might they feed?

Putting aside histiostomatids (and probably *Hericia*) for the moment, who access and filter essentially 'planktonic' particulate material, the chelicerae of some carpoglyphids are designed in such a way as to be effective in skimming for food through fluids if necessary (Bowman 2024a). This is a limnetic style of feeding (McGee *et al.* 2013). However, this relies upon them (or at least their cheliceral bases or gnathosoma) being propelled forward through very wet food. Perhaps the mites are very motile and march their idiosoma forward continually with their gnathosoma tilted obliquely down when feeding? More detailed observations in the wild are needed.

If skimming does not occur,

- Is there any actual evidence that carpoglyphid mites collect or pick *specific* material from the fluid's benthic surface (McGee *et al.* 2013)? Biting and manipulating such material is often not needed (such for example does not occur in wrasses, Ferry-Graham *et al.* 2002). However, the ability to bend the oral apparatus down (like in the evolution of terrestrial vertebrates, Wassenbergh *et al.* 2006) is needed.
- Is there any actual evidence of these mites striking forward or 'ramming' (Wasiljew *et al.* 2022) and attacking aquatic-based food material episodically (like an ice-spear, as posed in Bowman 2024a)? For sure there are a diversity of food capture styles, different behaviour and mechanical solutions to the problems of feeding in water shown in snakes (Alfaro 2002). Aquatic strikes are less successful (Vincent *et al.* 2005) presumably in part due to the resistive thickness of the medium compared to moving through air. Could fast moving aquatic micro-prey be efficiently stabbed by carpoglyphids during feeding (freshwater rotifers can be as small as 50 μm)?
- If there was a suction mechanism driven by some sort of rapid pharyngeal or gut expansion mechanism, could soft food specialist mites be striking straight-on into food with some sucking action like fish jaws to engulf food?

Manipulators (Higham 2011) need not necessarily move forward nor rely upon moving foodstuff by pressure changes. Indeed, can astigmatan bite size (estimated by Bowman 2023a) be validated by using scanning electron microscopy to measure the actual surface area removed from say (micro-sized) standardised gelatine blocks (John *et al.* 2020) at various hydration levels?

Fish can be categorised as 'grabbers' versus 'engulfers' (Mihalitsis and Bellwood 2021). Are stenophagous carpoglyphids therefore engulfers compared to the euryphagous biting acarids and glycyphagids who may grab drier food and manipulate it? What does the gut contents of wild-collected carpoglyphids actually look like?

However astigmatan feeding in fluid is done, (most) mites are visually blind (although *Carpoglyphus* do have structures called 'eyes'). Could carpoglyphids have pressure sensors in the tips of their cheliceral digits (much like those in Kiwis and those purported to have been found in pterosaurs Martill *et al.* 2021). For sure, there is no distal complicated sensory apparatus as in some uropodoids.

Returning to the derived histiostomatids whose feeding is very distinct (Wirth 2010). Can the equivalent filter feeding apparatus as that found in baleen whales or Mesozoic marine reptiles (Fang *et al.* 2023) be found in mites? More SEM studies are needed.

'Mopping up'

Paramegistids are medium to large (0.48 - 1.65 mm long), circular mites whose adult life stages have a penchant for long, thin slippery animals like millipedes or snakes (Baker and Seeman 2008). Their biology is poorly known but there are reports of them feeding on their hosts' external secretions, organic particulates and fluids. Lawrence (1939) took them to be spermatophagous. They have various derived characters like an enormous pilus dentilis and paddle-like ventral setae (Owen Seeman *pers.comm.*). Do such sequester fluids?

Neomegistus remus from an Australian millipede has an unusual chelicera and membraneous corniculi on its conical hypostome (Figure 16). This matches the design of a 'cloth mop' and its 'wringing out' apparatus. The very long moveable digit with its long membranous excrescence, finely toothed inner margin and many fine hairs distally on its external margin could 'suck up' liquids when it is dipped in by surface tension onto itself. Such 'mops' are also found in Fedrizzioidea where they are used to clean out the insides of dead arthropods (Seeman 2007) and in Parantennuloidea (Seeman 2025). In *Micromegistus* it is the cheliceral seta that is extraordinary rather than the pilus dentitlis. In both groups 'beaded' filamentous excrescences help mop up fluid. Fluid feeding Diptera use a similar mechanism to lap-up nutrients. Indeed, Brazilian bearded capuchin monkeys use their long slender furry tails to dip into water stored deep in tree holes - the wet tail is then run through their mouths to extract fluids (Castro *et al.* 2017). Fluids in the mite excrescences can be similarly squeezed out as the chelicera is retracted and compressed between the gnathotectum, palp coxae and the fimbriate hypostomal floor. Fluids could be prevented from leakage by the membraneous corniculi sealing the gnathosomal 'tube' and then the fluids being subsequently imbibed much like the strainer functions in a mop bucket when a liquid laden mop is pressed into it.

What other tool types are there left to find in mites?

Tools for cutting into bodies

At one level the moveable digits of *Carpoglyphus lactis* look like needle-nosed pliers (with the three small teeth acting like the pliers' transverse striations in order to facilitate grip Bowman 2024a). However, acarine exemplars of many other macro-scale tool types remain to be found (see Figures 17-19).

Are there gleaner-habit mites who preferentially use their chelal tips distally like wire-stripping pliers (Figure 17 bottom row) rather than proximal digit mastication surface notches (like *Tyrophagus putrescentiae*, Bowman 2024b) to strip material? Even a single digit with a distal notch would catch onto linear material (like a farm gate catch does, Figure 17 bottom row) and enable the stripping of say conidia from a hypha.

A possible analogy (in part) to the leverage of the fencing plier design (Figure 17 middle row) might be the unexplained function in *Katydiseius* (see Fain and Lukoschus 1983) and *Berlesia* chelae (Lindquist *et al.* 2020). The 'jaws' are at the end of elongate chelicerae (weevil-like). However, here the exact internal arrangement of tendons and the apparent inverted position of the fixed digit compared to the bladed moveable digit awaits further detailed micro-investigation. At one level, the sharp robustly toothed moveable digit could saw and slice like a can-opener blade, but it seemingly has nothing to press the food material against in order to laterally grip such. Rather than a chelate fixed digit, there appears to be an offset pointed outgrowth of the distal cheliceral segment comprising it. This perhaps could stab, root into or lever material. A detailed discussive scheme for how it might work (comparing it to

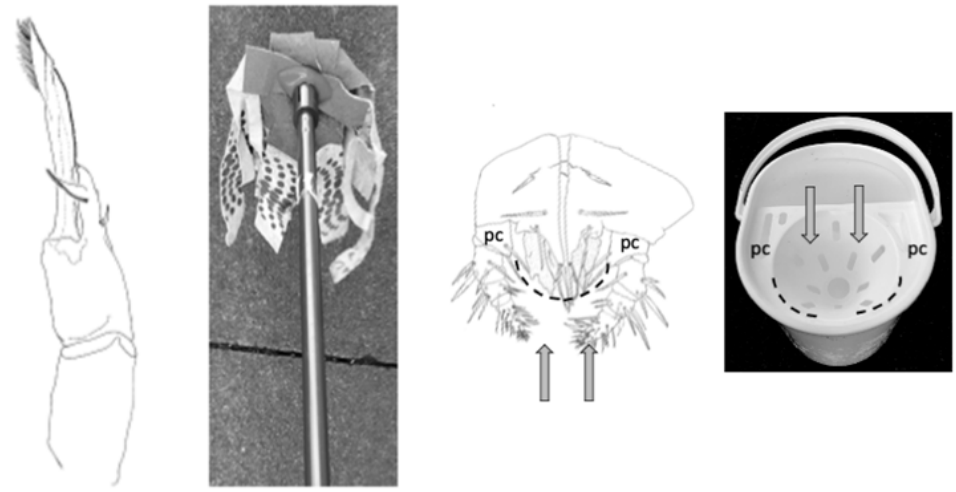

Figure 16 *Neomegistus remus* female gnathosoma may function like a mop and bucket to collect and strain fluids. Amended from Baker and Seeman (2008) with author's permission. Left. Hirsute extended chelicera (on left) compared to cloth mop head on elongate handle (to right). Right. Left. Ventral view of hypostome (anterior down the page). Heavy arrows show chelicerae being retracted laden with liquids above hypostome. Margins of membraneous corniculi exaggerated with dashed black lines. Right. Dorsal view of corresponding bucket. Note pressure of mop into the strainer releases fluids into the bucket (labelled like the hypostome). The tubular mite gnathosoma (with pc = palp coxa) is posed to act similarly

Varroa and ixodid ticks) is given in Lindquist *et al.* (2020). A SEM follow-up study is needed to better understand the chelal geometry exactly in these laelapids (which were previously in the Otopheidomenidae).

Rhagidiids like *Robustocheles* may have a fixed digit that works like a wire-stripper and a moveable digit acting like hawkbill pliers or diagonal/side-cutters (see Zacharda *et al.* 2012). Diagonal cutting or side-cutting pliers (Figure 19 top and second row) have heavy blades sharpened at their edge and excavated on one side. They are ideal for cutting medium and medium-hard wire close to the surface. Could this design (like plastic pipe cutters) be the optimal form for the chelae of nematode feeding mites or mites rupturing dipteran larvae, enchytraeids etc.?

Tools for cutting off legs

Steel electric cable wire cutters (Figure 19 third row) have specially shaped shearing surfaces designed to slice through very tough material. To my knowledge phytoseiids have not been observed cutting off legs. However, could this be the chelal design for other predatory mites to attack heavily armoured tube-like material like arthropod legs at the junction with their bodies?

Tools for cutting bodies up

If deep digit blades were flattened and curved like scimitar-shaped plates one obtains the form of umbilical cord scissors (Figure 19 fourth and bottom row). These are smoothly rounded for safety when delicately inserted amongst tissues, and specifically designed to easily cut tubes (≡ nematodes for a mite). Are there any mite chelae like this? *Lardoglyphus zacheri* can be found in surface or shallow-buried dead bodies (where the species is active in the 'bloated' and 'dry' stages of decomposition)? *Lardoglyphus zacheri* has an extreme cheliceral design position amongst the microsaprophagous free-living astigmatans. Inspection of Figure 18 upper, shows it to be one of the most westerly and north-westerly located taxon in the lower group of the gnathosomal design space of Bowman (2021).

Figure 17 Three tools types yet to find mite chelal exemplars. Top row. Mini-top cutting or end-cutter pliers, full scale {left}, obliquely end-on {right} showing deep width like a rhinoceros or hippopotamus jaw (≡ *thick* parameter for acarine chelae in Bowman 2023a). Middle row. Fencing pliers with hammerhead 'digit' and other 'digit' with large ventral tang (highlighted in dashed white circle) in order to lever wire and staples. Bottom row. Wire stripping pliers full scale (left) and obliquely end on (middle). Note both 'digits' have terminal notches to grip and strip material (like a gleaner). Farm gate catch (right). Note how the notch retains protruding parts of the chain keeping the gate (to which it is attached) closed

Indeed, lardoglyphids have a distinct flesh-slicing cheliceral form (Figure 18 lower). For the scale of its chelal velocity ratio (being like that of the more centrally located *Acarus siro*, A10b), the cheliceral base of *L.zacheri* has a relatively more elongate shape than expected. Or for that relatively elongate shape of its cheliceral base (like that of the more centrally located *Tyrophagus putrescentiae*, T13) its chela has a higher velocity ratio than expected. The former inference suggests lardoglyphids (like *Lardoglyphus konoi* categorised as a surface-living, potential crevice feeding/excavating specialist consuming only small and soft food morsels, Bowman 2021), feeds on more easily available resources than the 'demolition-feeding' storage acarid also found in cadavers (which excavates into material Bowman 2021). The latter inference, suggests an ability to tackle relatively tougher surface material than the mycophagous *Tyrophagus putrescentiae*. However, either way it has a feeble chelal crunch force for its body size indicating a soft flesh slicing habit. Whether its moveable digit ascending ramus indicates

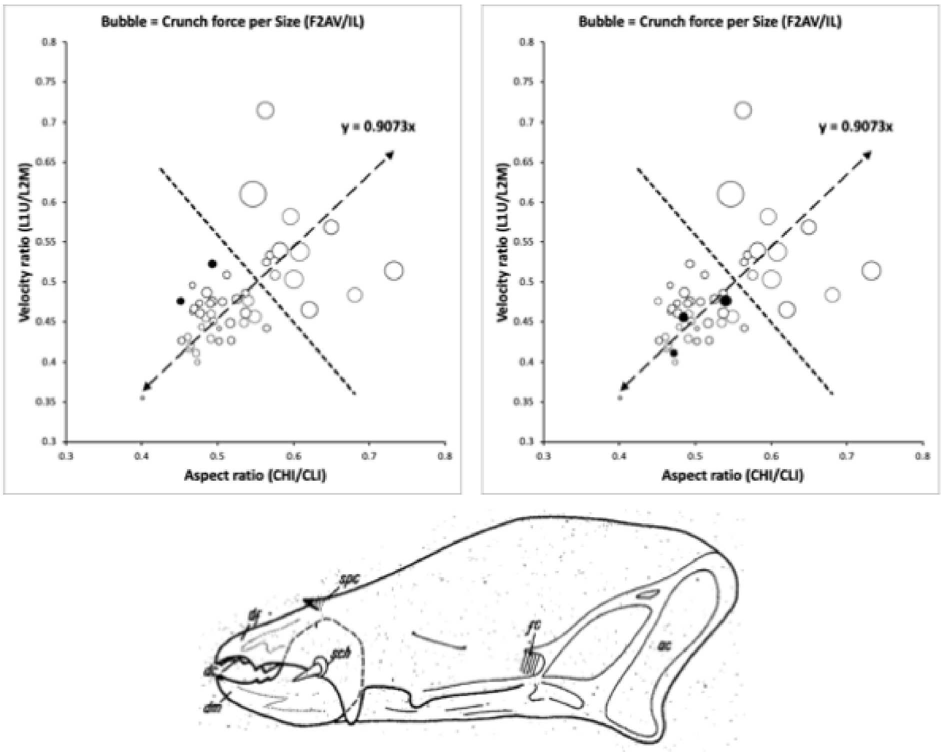

Figure 18 Lardoglyphids and geometric similarity design space for free-living astigmatan chelicerae (Bowman 2021). Upper. Left black circles = *Lardoglyphus konoi* L1 (in upper location), *Lardoglyphus zacheri* L3 (in lower location). Upper. Right black circles = other species found in (non-sequestered) cadavers *Acarus siro* A10b and A15, *Tyrophagus putrescentiae* T13. Note the latter are less derived and more central near the overall regression line. Lower. Chelicera of *Lardoglyphus konoi* (with original abbreviations from Akimov 1985 with permission). Note few if any teeth and elongate base shape. *L.zacheri* L3 is very similar in digit design.

that it could function like a 'stitch unpicker' as in *Carpoglyphus lactis* (Bowman 2024b) awaits investigation.

This taken all together with the fact that lardoglyphids have few if any cheliceral teeth (e.g. *Lardoglyphus konoi*, Figure 18 lower), marks them out more like a weak-jawed extinct ankylosaur (Haas 1969) which had small leaf-shaped teeth to aid in stripping and pulping soft leaves from plants rather than breaking up large material or grinding such. This match to a non-selective low-browse cropper, suggests that lardoglyphids are likely to be consiliently consuming relatively soft non-abrasive material. This matches the conclusion of Bowman (2021) where they are archetypal feeble effort, small food material, little morsel biting, tiny mouthful feeders. For sure, *L.zacheri* neither shows clear heterodonty, nor the single kind of tooth for instance found in dolphins or porpoises that deal with grasping slippery or evasive prey (Das *et al.* 2023). Given that lardoglyphids are not armoured like ankylosaurs (or even uropodoid mites), this poses the question - what is their defence mechanism against predation from mesostigmatids also known in cadavers for instance? Is it that they 'outbreed' their opponents (they are not high speed movers who could flee) or do they just rely upon tough skinned hypopal stages to 'weather any storm' (Iverson et al 1996)? Do they produce noxious oily secretions? More work for forensic acarologists beckons.

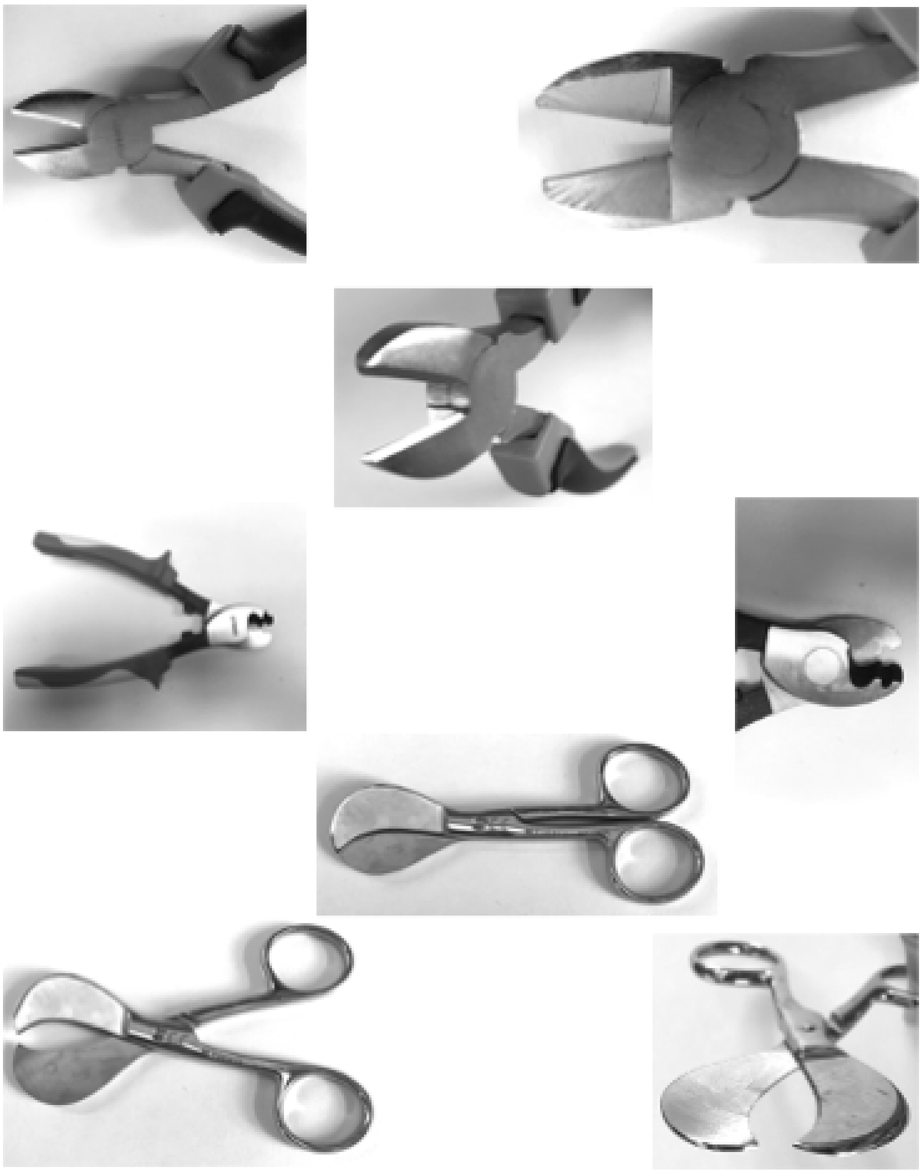

Figure 19 Three more tools types yet to find mite chelal exemplars. Top and Second row. Diagonal cutting or side cutting pliers. Front, rear and obliquely end-on. Note inclined cutting edge and excavated rear surfaces (equivalent to an intracheliceral space for possible fluid pooling and collection). Third row. Steel-electric cable wire cutters (≡ arthropod 'leg-cutters'?). Full scale and view from other side. Note asymmetric 'digits' with mirror image shearing surfaces. Fourth and Bottom row. Umbilical cord scissors used in midwifery. Closed, open and obliquely end-on

Tools for grabbing, scratching and holding

Are there wide-mouthed mites designed like a white rhinoceros (https://en.wikipedia.org/wiki/White_rhinoceros) or a hippopotamus (https://en.wikipedia.org/wiki/Hippopotamus) that match end-cutter pliers (Figure 17 top row)? If the illustrated mini-top cutter design is blunted and made much larger one obtains the form of traditional carpenter's pincers, which are used to grab, grip and extract nails without damaging the surface of the substrate. Are there mites that pull their foodstuffs out like this?

Rather than an 'unpeeling' design (Figure 10), if both the upper and lower cutting edges of a mini-top cutter design were flattened out (into smooth mastication surfaces), then one forms flat welding pliers, glass breaking pliers, canvas and sheet metal pliers. Do any mite chelae grab and grip such wide flat surfaces to snap material off?

Do mites use digit excrescences to lever up or grub up material or root about in the substrate so material could be levered out like how fencing pliers (Figure 17 middle row) are used? This is how extinct tusked deinotherids may have grabbed and fed even on trees and bushes (https://en.wikipedia.org/wiki/Deinotheriidae). Indeed do saprophagous mites hoe? More live observations are needed.

'Dual chain catches' (Figure 19 bottom row) may perhaps be useful in phoretic species? The large proximal tooth in *Weiseronyssus mirus* (Figure 12) could function like the setscrew in the upper jaw of the wire-stripping pliers illustrated in Figure 17 (Jerry Krantz *pers.comm.*) as it would preclude complete digit closure unless socketed into the fixed digit (see Bowman 2024a for discussion on effective gape and tooth position).

Many trophic modalities need acarologists to search for mites designed appropriately.

Conclusion and Future challenges

Any one mite species might do one or all the feeding actions discussed above at once!

Applied acarologists are asked:

”Which of your species are designed as

- A specialist feeding tool ?
- A generalist feeding tool ?”

and,

“What might that mean for your success in biological control against different pests?”

The discussions above rely upon fixed structures within and between identified taxa (recall that the bizarre chelicerae and membranous or modified corniculi of several trigynaspid mites only develop in the adult stage indicating that the adults are doing something different to the juveniles). However, could there be acarine gnathosomal polymorphisms driven by living conditions? Round-worms can develop into a wide-mouthed predator or a narrow-mouthed bacteria eater (Ragsdale *et al.* 2013) controlled by their environment. When the animals were starved or when too many worms crowded the Petri dish, the researchers observed the increased development of the wide-mouthed variant. Can acarologists find similar mite examples?

What about 'fasteners' and not just tools? Ixodid tick mouthparts with their jagged hypostome inserted into host epidermis mimic dry wall anchors, and with the palps splayed out during feeding bear a strong resemblance to plaster-board spring-loaded fasteners. Are there parasitic mites with structures like hollow-wall fasteners, cavity-wall or butterfly anchors, rag- or through- or 'molly'- or toggle-bolts etc.? Many challenges await future acarologists - mite chelae or gnathosomal parts like all of these macro-devices might exist.

Finally, perhaps there are acarologists out there who can draw together the scattered diverse literature to compile for all mites the equivalent of the recent book on dinosaurs i.e., Nabavizadeh and Weishampel (2023)? However, even though the parallelism and comparison with other phyla is intriguing, doing this is not just to categorise different species but to crucially relate their evolutionary forms to feeding guilds unequivocally determined in the wild using isotopic ratios (as done in mesostigmatids and oribatids by Perdomo *et al.* (2012), Díaz-Aguilar and Quideau (2013) etc.,. That would be truly impressive.

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Author contributions

All aspects were solely carried out by CEB.

Declarations

Conflicts of interest

The author declares that they have no known conflicts of interest. No competing claims are known.

Human or animal rights

This article does not contain any studies with human participants or vertebrate animals performed by any of the authors.

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