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## Research

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# How ticks get under your skin: insertion mechanics of the feeding apparatus of *Ixodes ricinus* ticks

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The tick *Ixodes ricinus* uses its mouthparts to penetrate the skin of its host and to remain attached for about a week, during which time Lyme disease spirochaetes may pass from the tick to the host. To understand how the tick achieves both tasks, penetration and attachment, with the same set of implements, we recorded the insertion events by cinematography, interpreted the mouthparts' function by scanning electron microscopy and identified their points of articulation by confocal microscopy. Our structural dynamic observations suggest that the process of insertion and attachment occurs via a ratchet-like mechanism with two distinct stages. Initially, the two telescoping chelicerae pierce the skin and, by moving alternately, generate a toehold. Subsequently, a breaststroke-like motion, effected by simultaneous flexure and retraction of both chelicerae, pulls in the barbed hypostome. This combination of a flexible, dynamic mechanical ratchet and a static holdfast thus allows the tick to solve the problem of how to penetrate skin and also remain stuck for long periods of time.

## 1. Introduction

In contrast to other blood-feeding ectoparasitic arthropods, hard ticks parasitize vertebrate hosts for several days or more, and they must attach firmly enough to their host's skin to remain in place in spite of mechanical perturbations associated with various activities, including grooming of the host. This strategy appears to favour infection by particular vector-borne pathogens, for example the agent of Lyme disease, which is transmitted typically not before the second day of the blood meal with a transmission efficiency that increases strikingly with feeding duration [1]. Indeed, the Lyme disease spirochaetes adhere quiescently to the midgut wall of the questing tick and become activated only upon feeding of the tick, crossing into the haemocoel, and aiming for the salivary glands, whence they are finally pumped into the host [2]. Thus, understanding how ticks remain attached for long periods of time is important to explain the efficiency of transmission of tick-borne pathogens.

As attachment is associated with the tick mouthparts, we start by considering the feeding apparatus which comprises two structures: the ventral hypostome, a plate armed ventrally with rows of spine-like denticles; and the chelicerae, a pair of telescoping, articulated structures armed with hook-like barbs. Morphological analyses of the mouthpart structures have inferred their function of insertion and attachment based on anatomical appearance [3,4]. The cheliceral teeth are thought to be adapted to cutting as well as holding [5,6], and ticks are said to 'cut', 'saw' or 'push' their way into the skin of their hosts [7–9]. During the blood meal, the inserted mouthparts of many ticks remain in place by means of a prominent feeding cone, formed by a cement-like substance that is produced by the ticks' salivary glands [10]. This structure provides passive attachment and simultaneously

would overcome the reversibility of the cutting action used to insert the feeding apparatus. In *Ixodes ricinus* ticks, however, cement appears not to be present [11], raising the paradox of how structures adapted for piercing or cutting can also serve to firmly anchor the mouthparts of a tick in the skin of its host.

To understand how the mouthparts of these ticks become inserted into the elastic skin matrix and how they remain anchored firmly without much effort, we recorded the sequence of insertion events of these structures by means of cinematography and correlated these observations with scanning electron microscopic observations designed to interpret function from form as well as confocal microscopic analyses of the cheliceral digits designed to identify their points of articulation and direction of movement.

## 2. Material and methods

To record the movements of the feeding apparatus of a tick when penetrating the skin of its host, we permitted nymphal *I. ricinus* ticks to attach to the ears of euthanized hairless mice. The sequence of events was viewed using a camera (Sony DXC-950p, one-half inch chip) equipped with a Macro-Elmar-R objective (1:4/100, Leitz) and recorded digitally using the Pinnacle DC 2000 system. The film sequence was edited using the ADOBE PREMIERE 6.0 software.

To describe the structure of the mouthparts, we prepared ticks for scanning electron microscopy according to the method by Dixon *et al.* [12]. Ten nymphal and 10 adult female *I. ricinus* ticks were preserved in 70% ethanol in individual glass vials and dehydrated by two 1 h changes in absolute ethanol. Adult ticks were then held overnight in anhydrous acetone and sonicated in xylene for 15 min (Sonorex TK52, Bandelin, Berlin, Germany). Nymphal ticks were incubated in xylene for 1 h and sonicated for only 5 min. Ticks were washed in two 1 h changes of acetone. The *basis capitulum* of each tick was removed from the *opisthosoma* by gentle traction and was mounted on a stub by means of conductive carbon cement (Leit-C, Neubauer Chemikalien, Münster, Germany) either whole or with the stylets dissected free. Specimens were spattered with gold palladium and viewed in a scanning electron microscope Cam Scan CS44 (Gresham Cam Scan Ltd, Cambridgeshire, UK).

To determine the articulation of the mouthparts, the auto-fluorescent properties of the cuticle were exploited for confocal microscopy. The *basis capitulum* was gently removed from larval or nymphal *I. ricinus* ticks by means of forceps in a drop of gum damar diluted in xylene, transferred to more viscous gum damar and coverslipped. Chelicerae of other nymphal ticks were dissected free of the *basis capitulum* by means of minuten needles, transferred to gum damar and coverslipped. Specimens were viewed in a confocal microscope SP2 (Leica, Bensheim, Germany) using 20× and 40× oil objectives. Virtual z-sections of about 0.2 μm thickness were acquired using an excitation of 476 and 488 nm, an emission of 500–600 nm, and a pinhole of 1.00 airy. Images were scanned with 1024 × 1024 pixel at 8 bits. Each series of z-sections was rendered three-dimensional using VOLOCITY v. 2.5 software (Improvision Deutschland, Tübingen, Germany), which permits opaque as well as transparent renderings. Three-dimensional renderings were prepared as movies for display online.

## 3. Results

### (a) Anatomical description of the mouthparts

The hypostome (hy) of the *I. ricinus* tick (figure 1a(i)) is fixed immovably to the ventral surface of the *basis capitulum*

(figure 1b). Its dorsal surface resembles a shallow basin and is fringed by rows of prominent, recurved denticles (figure 1a(ii)). The broad groove lying at the centre of this basin is positioned to channel the flow of food into the oral opening of the tick and, vice versa, of tick saliva into the skin of the host. The ventral surfaces of the cheliceral shafts roof this groove dorsally such that a 'tube' is formed. The numerous hypostomal denticles on its ventral side do not articulate. The hypostome serves to stabilize and anchor the tick's mouthparts in the skin of its host and to channel the exchange of fluids.

Each of the paired chelicerae comprises a tubular shaft (c), tipped by a bundle of digits (cd) (figure 1c). The cheliceral shaft is retractable into an extended limb of the dorsal surface of the *basis capitulum* and joined to it by a thin membranous sleeve (cm), also known as the 'inner cheliceral sheath' [13], riding over it and sealing the cheliceral shaft. The doubled membranous sleeve covers about half the length of the exposed cheliceral shaft, which permits that shaft to retract completely within the *basis capitulum* or to extend telescope-like almost twice its length protracting the tips of the digits beyond the tip of the hypostome. When the telescope-like cheliceral shafts are fully retracted, only their digits remain exposed (figure 1d). The rows of minute spines that cover the extended surface of the *basis capitulum* project dorsally and caudally.

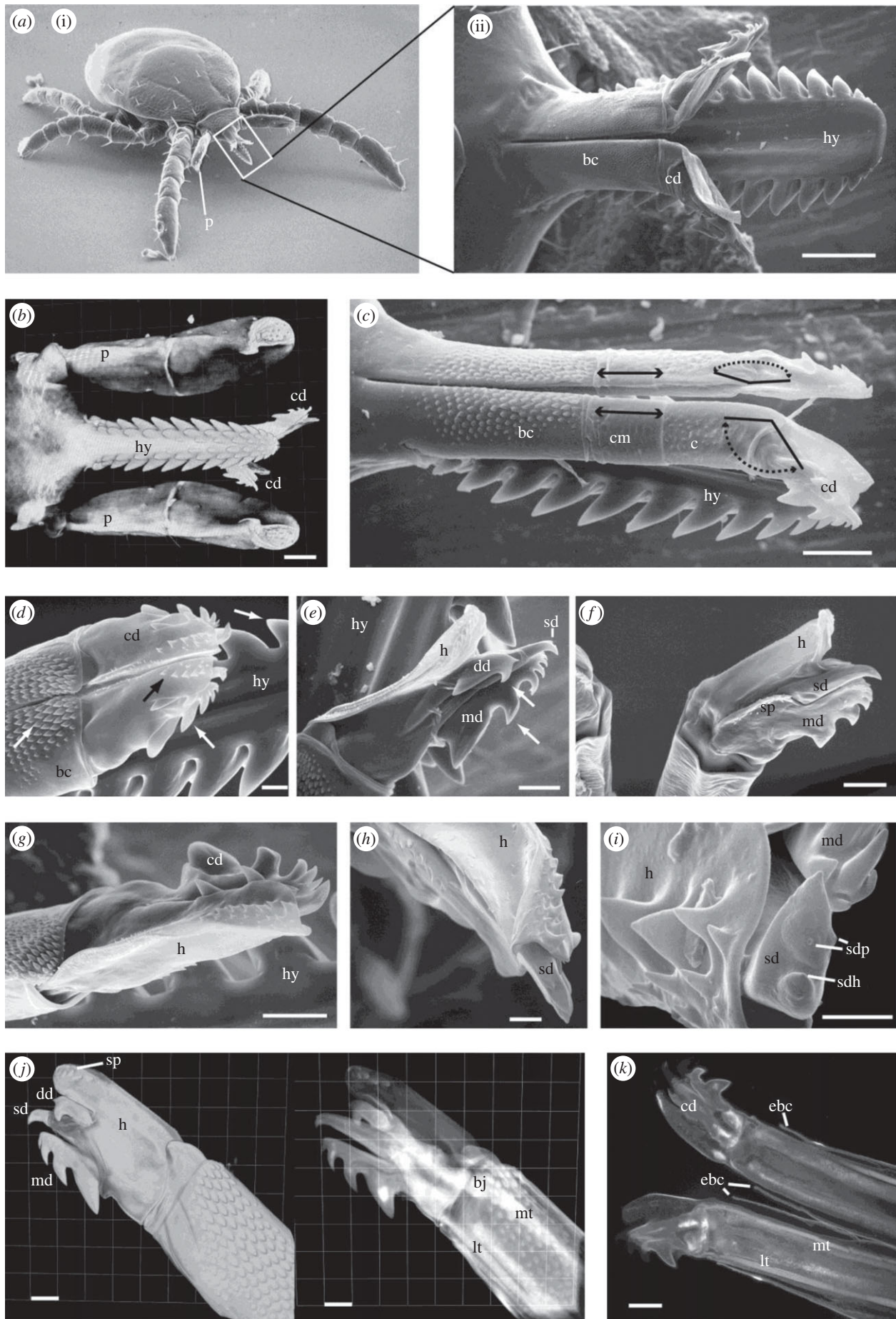
A hood-like structure (h) that ornaments the end of each cheliceral shaft appears continuous with the surface of the shaft (figure 1e (dorsal) and f (ventral)). It encloses the hooked digits medially (figure 1e,g). This recurved plate appears to articulate only slightly so that the digits appear somewhat external to the hood (figure 1f). A diaphanous veil originating in the margin of the hood encloses two of the hooked digits, basally (figure 1e). The heavily cuticular line of barbs on the hood projects in parallel with the axis of the cheliceral shaft (figure 1e). This hood-like structure protects the cheliceral digits and may stabilize the tick's mouthparts against the skin of a host.

The single-hooked digit (sd), also known as the 'internal article' or 'inner digit' [13], extends more anteriorad than the other relatively robust digits, continues the line of the shaft and is the lead digit touching the host's skin (figure 1e). This slender stylet tapers to a particularly sharp point (figure 1h) so that relatively little force is required in order for it to gain a point of purchase (in contrast to the hypostome). Its anterior end bears a small hooklet [14], mounted above an indented pit (figure 1i). Besides puncturing the host's skin superficially when coursing its surface, it gains chemical and proprioceptive information with its sensilla [3,14].

The most laterad is the stout multi-hooked digit (md), also known as the 'external article' or 'outer digit' ([13]; figure 1e,f). Its hooks are aligned in a row, with the largest placed caudally. The most anterior of its hooks is surrounded by three hooklets (figure 1i). The ventral margin of this digit is armed with a row of minute forward-facing spines (figure 1f).

The hooks of the double-hooked digit (dd) lie at an acute angle to the plane of the other digits and this digit bears a prominent apical spine (figure 1e). In contrast to the single- and multi-hooked digits, which oppose the cheliceral shaft at a broad base, the double-hooked digit tapers to a fine stalk that is inserted into a circular opening anterior to the base of the digital bundle, about equidistant between the ball-joint and the insertion point of the large lateral tendon (figure 1j). The slender stalk of the double-hooked digit appears to articulate slightly within its insertion.





**Figure 1.** (Caption overleaf.)

The 'hinge point' is evident as a prominent 'ball-joint' located close to the medial angle of the cheliceral shaft (figure 1j; electronic supplementary material, movie S7).

The bundle of digits, thereby, is free to rotate laterad through an arc representing an acute angle. The anterior margin of the cheliceral shaft slants in a manner that facilitates this

**Figure 1.** (*Overleaf.*) (a) Larval *I. ricinus* tick (i) splaying its palps (p) exposing the mouthparts (insert). Dorsal aspect of mouthparts of a female *I. ricinus* tick (ii, scale bar, 100  $\mu\text{m}$ ) consisting of the hypostome (hy), paired tubular extensions of the *basis capitulum* (bc) with retracted cheliceral shafts and flexed cheliceral digits (cd). (Scanning electron micrographs.) (b) Ventral aspect of the hypostome (hy), cheliceral digits (cd) and palps (p) of a nymphal *I. ricinus* tick. One of the chelicerae is extended and its digits flexed; scale bar, 37.6  $\mu\text{m}$ . (Confocal microscopic rendering.) (c) Dorsolateral aspect of the chelicerae of a nymphal *I. ricinus* tick. Each of the paired chelicerae comprises a tubular shaft (c), tipped by a bundle of digits (cd). The cheliceral shaft is retractable (black arrows) into an extended limb of the *basis capitulum* (bc) and joined to it by a thin membranous sleeve (cm) riding over it and sealing the cheliceral shaft. The doubled membranous sleeve covers about half the length of the exposed cheliceral shaft, which permits that shaft to retract completely within the *basis capitulum* or to extend telescope-like almost twice its length, protracting the tips of the digits beyond the tip of the hypostome (hy). Each of the paired bundles of cheliceral digits flexes laterally; scale bar, 30  $\mu\text{m}$ . (Scanning electron micrograph.) (d) Dorsal aspect of fully retracted cheliceral shafts and hierarchy of barbs and hooks (see arrows) of different sizes and shapes on the mouthparts of a nymphal *I. ricinus* tick. The small-sized barbs on the hood (h) of the digital bundle and on the tubular extensions of the *basis capitulum* (bc) serve to provide a shallow anchor. The hooks on the cheliceral digits serve the ratchet-like action and the numerous hooks on the hypostome (hy) serve as deep anchor; scale bar, 10  $\mu\text{m}$ . (Scanning electron micrograph.) (e) Dorsal aspect of the bundle of cheliceral digits, comprises the multi-hooked (md), the double-hooked (dd) and the single-hooked digit (sd) as well as the hood (h) of a female *I. ricinus* tick. The flexed bundle of digits has partially emerged from the hood; scale bar, 30  $\mu\text{m}$ . (Scanning electron micrograph.) (f) Ventral aspect of the bundle of cheliceral digits of a female *I. ricinus* tick. The multi-hooked digit (md) is armed with a row of forward-facing spines (sp); scale bar, 30  $\mu\text{m}$ . (Scanning electron micrograph.) (g) Medial aspect of the cheliceral hood (h) enclosing the cheliceral digits (cd) of a female *I. ricinus* tick; scale bar, 30  $\mu\text{m}$ . (Scanning electron micrograph.) (h) Anterior aspect of the single-hooked digit (sd), sheathed by the hood (h), of the chelicera of a female *I. ricinus* tick; scale bar, 10  $\mu\text{m}$ . (Scanning electron micrograph.) (i) Anterior aspect of the single-hooked digit (sd) and multi-hooked digit (md) of the chelicera of a nymphal *I. ricinus* tick. The tip of the single-hooked digit is armed with a hooklet (sdh) and two indented pits (sdp); scale bar, 3  $\mu\text{m}$ . (Scanning electron micrograph.) (j) Opaque and transparent renderings of the articulation of the cheliceral digits within a chelicera of a nymphal *I. ricinus* tick. The digits articulate on a ball-joint (bj) in response to forces applied by the lateral (lt) and medial tendons (mt). The spines (sp) arming the anterior-medial margin of the hood (h) lie in the same plane as the tip of the single-hooked digit (sd). The plane of the double-hooked digit (dd) differs from that of the multi-hooked digit (md); scale bar, 10  $\mu\text{m}$ . (Confocal microscopic rendering.) (k) Section of the chelicerae of a nymphal *I. ricinus* tick. The lateral (lt) and medial tendons (mt) are inserted into the basal corners of the bundle of cheliceral digits (cd). Note the position of the anterior extensions of the *basis capitulum* (ebc); scale bar, 10  $\mu\text{m}$ . (Confocal microscopic rendering.)

movement. A prominent tendon, extending the length of the cheliceral shaft, is inserted into the angle formed by the densely cuticular, lateral base of the digital bundle (figure 1*k*). A slender tendon, running medially along the length of the cheliceral shaft, is inserted into the medial base of the bundle. The insertion point of the lateral tendon is about three times as far from the ball-joint as is that of the more slender medial tendon. The position of the digital tendons relative to that of their joint is consistent with deep lateral movements alternating with slight movements oriented medially. The cheliceral digits articulate laterally in a specimen that was fixed with the *basis capitulum* intact (figure 1*b*; electronic supplementary material, movie S5). The digits of the right fully extended cheliceral bundle appear as if engaging in a ratchet action.

### (b) Cinematographic observations

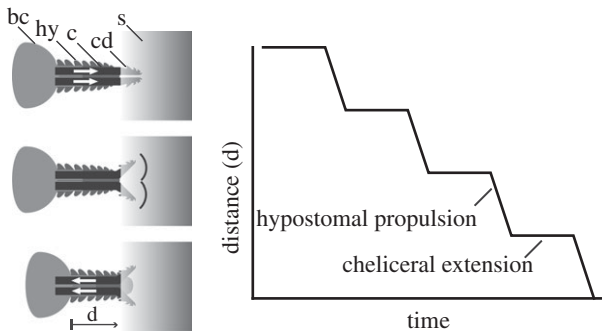
By means of cinematography, we observed five nymphal *I. ricinus* ticks as they inserted their mouthparts into the skin of hairless mice. These movements, divided into a set of four phases, appeared not to vary between individual specimens and were recorded in a representative filmed sequence (see the electronic supplementary material, movie S1). (i) The first phase ‘surface coursing’ commenced when the tips of the chelicerae first came in contact with the host’s skin while the palps splayed slightly toward each side. Each of the paired chelicerae, which extended beyond the tip of the hypostome, alternately moved sideways over a short period (see also the electronic supplementary material, animation movie S2), forming a small divot. (ii) During the second phase ‘superficial attachment’, the tips of both chelicerae remained stationary but were accompanied by subtle twitching. (iii) The third phase ‘cheliceral insertion’ commenced when the chelicerae moved by flexing at their hinge. These movements were initially of an alternating nature (see also the electronic supplementary material, animation movie S3), and then switched to a simultaneous shearing nature. Each sweep

buried the cheliceral bundle deeper into the skin. After about 30 such movements, the tips of the chelicerae were inserted to the depth of their articulation. (iv) Finally, the fourth phase ‘hypostomal envelopment’ commenced by the simultaneous retraction of the flexed cheliceral bundles via a breaststroke-like movement that caused both cheliceral shafts and their hinges to flex into a V-like form. This action caused the ventrally barbed hypostome to enter the skin of the host. With each cycle of simultaneous linear cheliceral extension and flexural retraction, the hypostome was drawn ever deeper (see also the electronic supplementary material, animation movie S4; figure 2). Full retraction of the cheliceral shafts was also discernible in the *opisthosoma*, within the body of the tick. After about six such ratchet-like extensions and retractions of the chelicerae, the entire feeding apparatus was enveloped by the skin.

## 4. Discussion

To understand these observations, we take a physical approach to the problem [15] that addresses the different components associated with (i) piercing, (ii) burrowing and (iii) passive attachment without components for example muscle. Attachment to soft substrates, for example skin, requires deep penetration beyond the epidermis. However, penetrative cutting alone is not sufficient as it provides no anchoring mechanism. The combined requirements of deep penetration and anchoring are strong constraints on any solution and can be satisfied by a flexible mechanical ratchet [16], as shown in figure 2 (and in the electronic supplementary material, animation movie S4), wherein cyclic movements of the chelicerae translate periodic linear motion of the chelicerae into irreversible anteriorad motion of the hypostome.

The cheliceral digits curve in the direction of their articulation and have barbs which allow for rectification of cyclic movement, and thus confer anteriorad irreversibility



**Figure 2.** Schematic of ‘hypostomal envelopment’ via a ratcheting mechanism. A two-step process starting with cheliceral extension that actively propels the cheliceral bundles (cd) into the skin (s). This is followed by simultaneous retraction of the flexed cheliceral bundles via a breaststroke-like movement that causes both cheliceral shafts (c) and their hinges to flex into a V-like form, thereby causing the ventrally barbed hypostome (hy) to enter the skin of the host. This alternate ratchet-like motion allows for a decomposition of the task into dynamic and static components with specialized structures.

(figure 1e; electronic supplementary material, movie S5). Protraction of the telescope-like cheliceral shafts derives from hydrostatic pressure, its retraction is effected by extrinsic muscles that originate at the posterior margin of the scutum and extend into the ends of the cheliceral base [17]. Intrinsic muscles in the bulbous cheliceral base and extending into the digits by means of asymmetrically placed tendons serve to articulate the cheliceral bundle (figure 1j,k; electronic supplementary material, movies S6 and S7). Muscle contraction affecting the larger tendon flexes the digits laterally, whereas contraction affecting the smaller tendon extends the digital bundle medially (figure 1c). Alternating contractions of the muscles that control the large lateral and the small medial tendons result in sweeping movements that allow superficial entry of the mouthparts into the skin, but permit the cheliceral digits to penetrate only to their point of articulation. Deep penetration of the skin is effected by the simultaneous activity of both chelicerae. After the cheliceral shafts telescope anteriorad to their full extension in a concerted action, the digits of both chelicerae flex owing to a powerful contraction of the intrinsic muscles connected to their large tendons. Simultaneous contraction of the extrinsic muscles causes the cheliceral shafts to withdraw (figure 1a(ii),c). As a result, the hypostome is pulled into the skin. This mechanism is reminiscent of a marionette where the digits (limbs) are controlled by forces applied distally and mediated by flexible tendons (strings).

Ratchet-like motility [16] is an example of convergent evolution across multiple scales, spanning the molecular to the macroscopic, and operates in a variety of different environments; in the context of molecular motors [18], polymerization engines [19] and botanical structures, for example wheat awns [20]. A recent article proposing to

mimic porcupine quills for potential biomimetic injection devices [21] suggests that here, too, a ratcheting effect may be at play; indeed the asymmetry of the scales on the quill combined with the contractions of muscles explains how the quill moves unidirectionally in tissues [22]. In another analogy, the two interlocked valves of the wood-drilling wasp’s ovipositor equipped with backward-pointing pull-teeth are sequentially pushed and pulled in reciprocal motion which facilitates and stabilizes the insertion with virtually no net force [23–25]. The subsequent development of microtextured surfaces for deep-brain stimulation electrodes inspired by the wasp’s ovipositor demonstrates that this design not only facilitates the insertion process, but also enhances gripping and anchoring of the device [25]. In the context of the tick, the ratchet-like motility of the flexible chelicerae allows the tick to penetrate a soft substrate, pulling in the rigid anisotropic hypostome that favours robust attachment to soft substrates without active force.

The barbs of various sizes and shapes on the cheliceral digits, the cheliceral shafts and the hypostome (figure 1d) may serve several functions. If some of them function analogous to barbs on porcupine quills, they may facilitate insertion of the feeding apparatus into the tissue by stress concentration near the barbs, thereby reducing the penetration force [21]. Simultaneously, just as sets of barbs on porcupine quills cooperatively enhance tissue adhesion force [21], particular barbs on the tick’s mouthparts might serve to anchor the feeding apparatus firmly in the tissue. However, in contrast to the rigid barbs on porcupine quills, barbs localized on the articulated chelicerae of ticks can interact flexibly and dynamically with the host’s tissue fibres resulting in sufficient friction to propel the barbed hypostome forward, followed by a disengagement of the cheliceral barbs from the surrounding tissue to gain a new and deeper foothold for a subsequent shove.

Each of these ratchet actions by itself, penetration, deformation and anchoring, can be seen in other organisms [26–28]. But *I. ricinus* ticks may uniquely combine these ratchet actions by using dynamic burrowing as well as passive attachment implemented via the different mouthpart structures. It shows how a combination of functional requirements and physical constraints lead to the evolution of a solution that might well have arisen multiple times and further serves as an inspiration for biomimetic designs.

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