

Research Article

Ovipositor Internal Microsculpture in the Relic Silverfish *Tricholepidion gertschi* (Insecta: Zygentoma)

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The microsculpture on the inside surface of the ovipositor of the relic silverfish *Tricholepidion gertschi* (Wygodzinsky, 1961) (Insecta: Zygentoma) was studied with scanning electronic microscopy for the first time. Both the first and second valvulae of *T. gertschi* bear rather diverse sculptural elements: (1) microtrichia of various shapes and directed distally, (2) longitudinal ridges, (3) smooth regions, and (4) scattered dome-shaped sensilla. As in several other insects, the distally directed microtrichia most likely facilitate unidirectional movement of the egg during egg laying. Involvement of the ovipositor internal microsculpture also in the uptake of male genital products is tentatively suggested. From a phylogenetic point of view, the presence of internal microsculpture appears an ancestral peculiarity of the insect ovipositor.

1. Introduction

The “living fossil” *Tricholepidion gertschi* Wygodzinsky, 1961, is the sole extant member of the silverfish family Lepidotrichidae, which inhabits small isolated regions of coastal redwood forests in southern Oregon and northern California [1]. It has been formally placed in the insect order Zygentoma by the author of the first description. However, the phylogenetic position of *T. gertschi* has been subject to debate because of a unique combination of plesiomorphic and apomorphic morphological characters in this species. *T. gertschi* has often been recognized either as a sister group of the Dicondylia (the Zygentoma plus the Pterygota) (e.g., [2–4]), as the basal-most group of Zygentoma (e.g., [5, 6]), or as a close relative of certain zygentoma subgroups (e.g., Nicoletiidae by [7, 8]; see also review in [9]). Molecular evidences have not fully resolved the phylogenetic position of *T. gertschi* (see [10], but also see the results and discussion by [11]). Thus, the relationships of *T. gertschi* (and, therefore, of the whole family Lepidotrichidae) within the basal hexapod lineages constitute one of the most debated issues in hexapod phylogeny. Moreover, “*Tricholepidion* is the most promising candidate for a new insect “order” (or, in other words,

the only insect species whose ordinal classification remains uncertain)” [12, Page 220].

The ovipositor that comprises gonapophyses of the 8th and 9th abdominal segments is considered a synapomorphy of the Insecta (e.g., [14]). The winged insects, the Pterygota, use their ovipositors mainly for transporting the eggs outside the body and placing these within or onto oviposition substrates. Microsculpture of the internal walls of the ovipositor is almost ubiquitous among insects, and it is thought to facilitate the movement of eggs along the ovipositor [15]. Ovipositor internal microsculpture has been recorded so far in the Odonata, Hemiptera, Orthoptera, aquatic Coleoptera, Hymenoptera, and Raphidioptera (see [13, 15–20] and references therein). The morphology of cuticular microtrichia inside the ovipositor has been studied most precisely in several wasps; in fact, it has been suggested to be a source of phylogenetically informative characters at several levels within the Hymenoptera (e.g., [21–30]). Nevertheless, ovipositor internal microsculpture still remains practically undescribed in more basal, and evolutionarily more intriguing, hexapod orders, the Microcoryphia and the Zygentoma. This study was performed as the initial stage of a wider study of ovipositor internal microsculpture in apterygotous

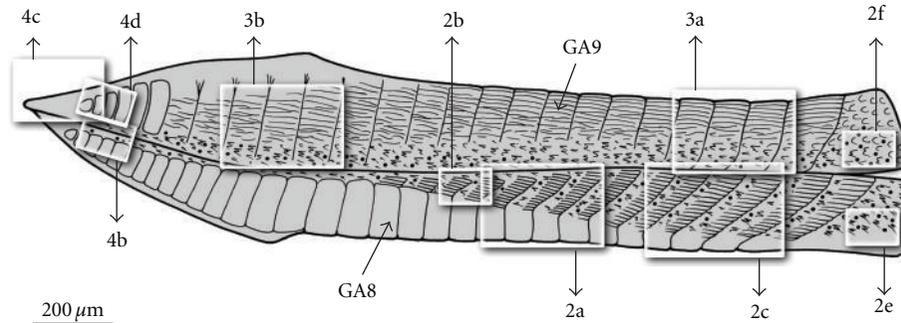


FIGURE 1: General organization of microsculpture on the inner surface of the ovipositor in the silverfish, *Tricholepidion gertschi*, diagrammatically. Rectangles indicate relative locations of the SEM micrographs given in the next figures (except Figures 2(d), 3(c), 3(d), and 4(a)). Black dots indicate the ovipositor parts with dome-shaped sensilla. GA8 and GA9: the gonapophyses of 8th and 9th segments, respectively.

insects. Its aim was to describe the microsculpture of the ovipositor inside surface in the relict silverfish *T. gertschi* and to discuss it from functional and phylogenetic standpoints.

2. Materials and Methods

One female of *Tricholepidion gertschi* was collected in the Heath and Marjorie Angelo Coast Range Reserve (Northern California, USA) into 100% ethanol by Markus Koch (Freie Universität Berlin, Germany). In order to be used for scanning electron microscopy (SEM), the female postabdomen was washed in water, dissected, and then macerated for 10–12 h at room temperature in 10% KOH. The macerated cuticular parts were thoroughly washed in distilled water, dehydrated in graded ethanol series and acetone, dried at the critical point (OM CPD 7501), mounted onto a stub, coated with gold-palladium (OM-SC7640), and examined with a Zeiss EVO-50 SEM (Museum of Zoology, Natural History Senckenberg Collections Dresden, Germany). To study the underside of sensilla, the ovipositor valves were afterwards lanced with a small insect pin, sputtered with metal for the second time, and again examined under the SEM.

3. Results

The proper ovipositor of *T. gertschi* is conspicuously compressed laterally, blade-shaped; it comprises two pairs of valvulae, gonapophyses of the 8th abdominal segment (ventral valvulae) and gonapophyses of the 9th segment (dorsal valvulae) (Figure 1). All gonapophyses are free at their bases and not fused into pairs. The 8th gonapophysis and 9th gonapophysis at each body side are connected with a groove-and-tongue articulation (the olistheter), so that they can slide along each other. The ventral, groove-like component of the olistheter (the aulax) is located on the dorsal margin of the 8th gonapophysis (Figures 2(b)–2(d)). The dorsal, tongue-like component of the olistheter (the rhachis) is situated on the ventral edge of the 9th gonapophysis (Figures 3(a), 3(c), and 3(d)). The apical part of each valvula is spear-shaped and pointed. Most of the surface (both external and internal) of each gonapophysis is sculptured with a metameric, annulated pattern of transverse fields.

In the middle part of the 8th gonapophysis each such field consists of an oblique dorsal part and a straight ventral part (Figure 2(a)). The dorsal part bears parallel longitudinal ridges, 4 to 8 μm apart, in its anterior half, and distally directed microtrichia up to 4 μm in length in its posterior half (Figures 2(b) and 2(c)). The ventral part of the field is smooth. Towards the tip of the ovipositor, the smooth ventral parts expand progressively, while the dorsal sculptured parts progressively shrink (Figure 1). The apical broadening of the 8th gonapophysis is sculptured with entirely smooth fields (Figures 1, 4(a), and 4(b)). The narrow dorsal stripe immediately bordering the aulax lacks any trace of transverse annulation and bears distally directed microtrichia (Figures 2(b) and 4(b)). The basal-most region of the 8th gonapophysis is covered with spine-bearing scales and dome-shaped sensilla (7.5–10 μm apart) (Figure 2). Some sensilla are also scattered between distally directed microtrichia throughout the entire length of the 8th gonapophysis (Figure 2(b)). The ventral-most portion of each transverse field bears one or two oblique wrinkles, running in the dorsoanterior-to-ventroposterior direction throughout most of the length of the 8th gonapophysis (Figure 2(a)); near its apex the wrinkles reverse their direction or run parallel to its ventral edge (Figures 2(a) and 4(a)).

The internal surface of the 9th gonapophysis is also distinctly and diversely sculptured (Figure 1). The basal-most region bears distally oriented squamous microsculpture with scattered sensilla (placed ca. 8–11 μm apart) and lacks any trace of transverse annulations (Figure 2(f)). The rest of the inner surface is sculptured with transverse fields, which are more distinct in its dorsal half. The microsculpture here comprises longitudinally directed parallel ridges and wrinkles, placed ca. 5.5–7 μm apart (Figures 3(a) and 3(b)). The ventral half of the valvula bears spineless squamous scales, gradually replaced more ventrally and apically with spine-bearing scales and then with dense microtrichia ca. 2–2.5 μm in length; dome-shaped sensilla (placed 15–30 μm apart) are scattered among the scales (Figures 3(b) and 3(c)). The apical-most microsculpture is represented by sharply outlined tablet-like smooth fields and, more ventrally, with relatively sparse short spines ca. 1–1.5 μm in length (Figures

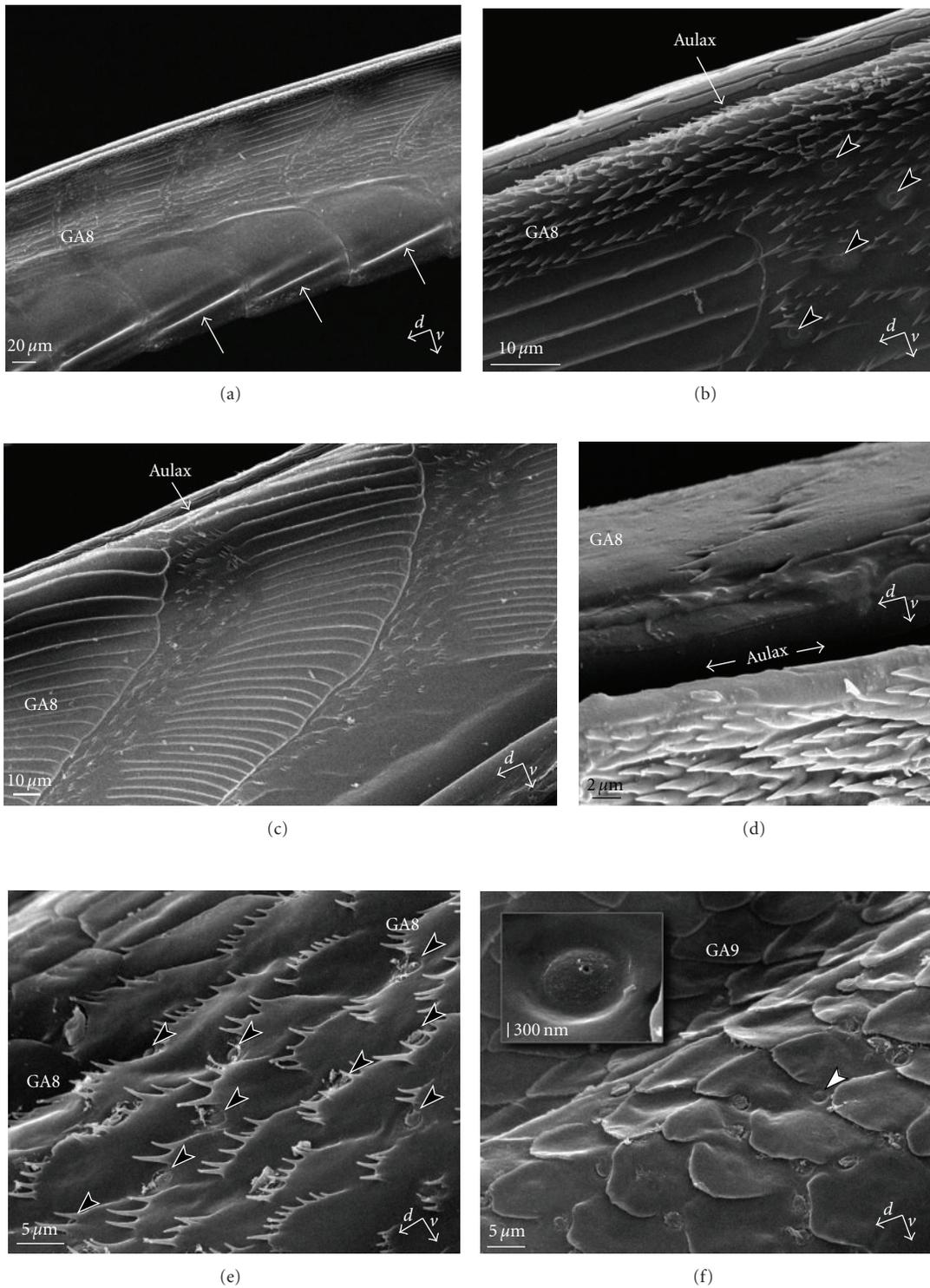


FIGURE 2: SEM micrographs of the inside surface of the gonapophyses in *Tricholepidion gertschi*: (a) middle part of the 8th gonapophysis; (b) dorsal margin of the 8th gonapophysis showing microtrichia, sensilla, and longitudinal ridges; (c) one transverse sculptured field of the 8th gonapophysis; (d) aulax; (e) basal part of the 8th gonapophysis with spine-bearing scales and sensilla; (f) basal part of the 9th gonapophysis with squamous microsculpture and sensilla (one sensillum is enlarged in inset). Arrowheads indicate uniform dome-shaped sensilla, externally identical to the campaniform sensilla with a central moulting pore on the ovipositor of the glassy-winged sharpshooter, *Homalodisca coagulata* [13, Figure 4]. Arrows indicate ventral corrugations of the 8th gonapophysis. GA8 and GA9: the gonapophyses of 8th and 9th segments, respectively. *d* and *v*: distal and ventral directions, respectively.

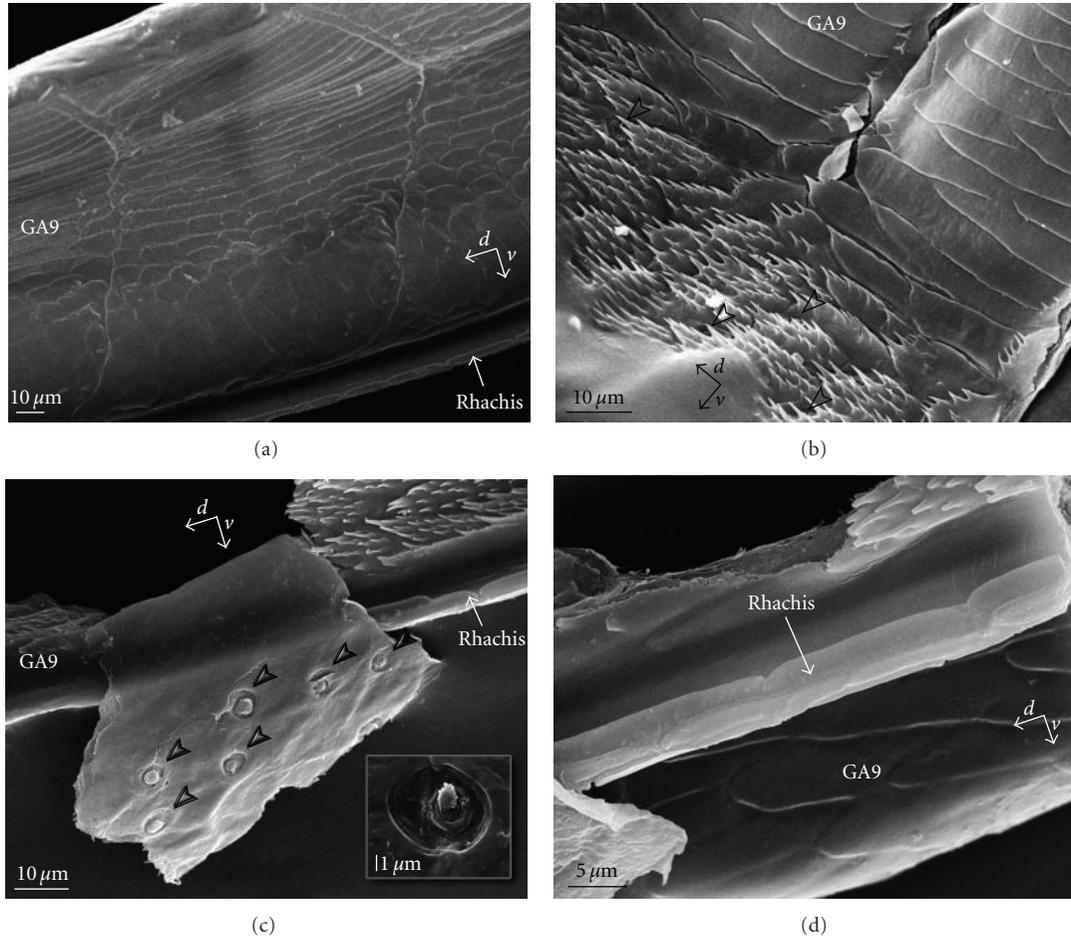


FIGURE 3: SEM micrographs of the inside surface of the 9th gonapophysis of *Tricholepidion gertschi*: (a) transverse sculptured field in the middle part of the gonapophysis, with longitudinal ridges and wrinkles dorsally and squamous microsculpture ventrally; (b) transverse sculptured field in the subapical part of the gonapophysis, with longitudinal ridges and wrinkles, ventrally replaced by spine-bearing scales and microtrichia; (c) fragment of the integument turned inside out to show the density of dome-shaped sensilla (underside surface of the sensillum is enlarged in inset); (d) rhachis. Arrowheads indicate dome-shaped sensilla. GA9, the gonapophyses of the 9th segment. *d* and *v*: distal and ventral directions, respectively.

4(c) and 4(d)). The rhachis is slightly corrugated in both longitudinal and transverse directions (Figure 3(d)). All the dome-shaped sensilla are uniform (ca. $2.0\ \mu\text{m}$ long, $1.7\ \mu\text{m}$ wide), with a central pore or depression.

4. Discussion

The well-developed ovipositor of insects mostly functions as a penetration organ adapted to egg laying into the oviposition substrate. The primitive oviposition of insects is presumed to be endosubstratic egg deposition [31] (cryptozoic oviposition, following Hinton's terminology [32]), when the ovipositor places the egg into a preexisting hole or fissure in a substrate without cutting the latter [33]. More typically, the insect penetrates plant tissues with its ovipositor, which often possesses specialized structures like denticles or serrations, and then places the egg into the resulting slit (endophytic oviposition, after [32]). As an exceptional case, the insect can use its well-developed ovipositor for egg deposition onto the

surface of a plant or another exposed substrate (exophytic oviposition, after [32]; see examples below). In all cases the egg is moving along the ovipositor's inner walls, which form the egg canal.

The egg canal is typically furnished with microsculpture and can bear sensilla (see review in [15]). Egg canal microsculpture varies in shape and arrangement among studied insect groups. Austin and Browning [15] have discussed possible correlations between the shape of the ovipositor microsculpture and the egg-laying behaviour of some insect groups, focusing mainly on the mechanical properties of the oviposition substrate. Since the microtrichia are always directed distally, several authors suggested their importance for the unidirectional movement of the egg along the ovipositor [15, 19, 34–37]). Direct mechanical manipulation of anaesthetized crickets has provided strong evidence for this hypothesis [15].

Very little is known about how the Microcoryphia and *Zygentoma* lay eggs in nature. A few direct observations

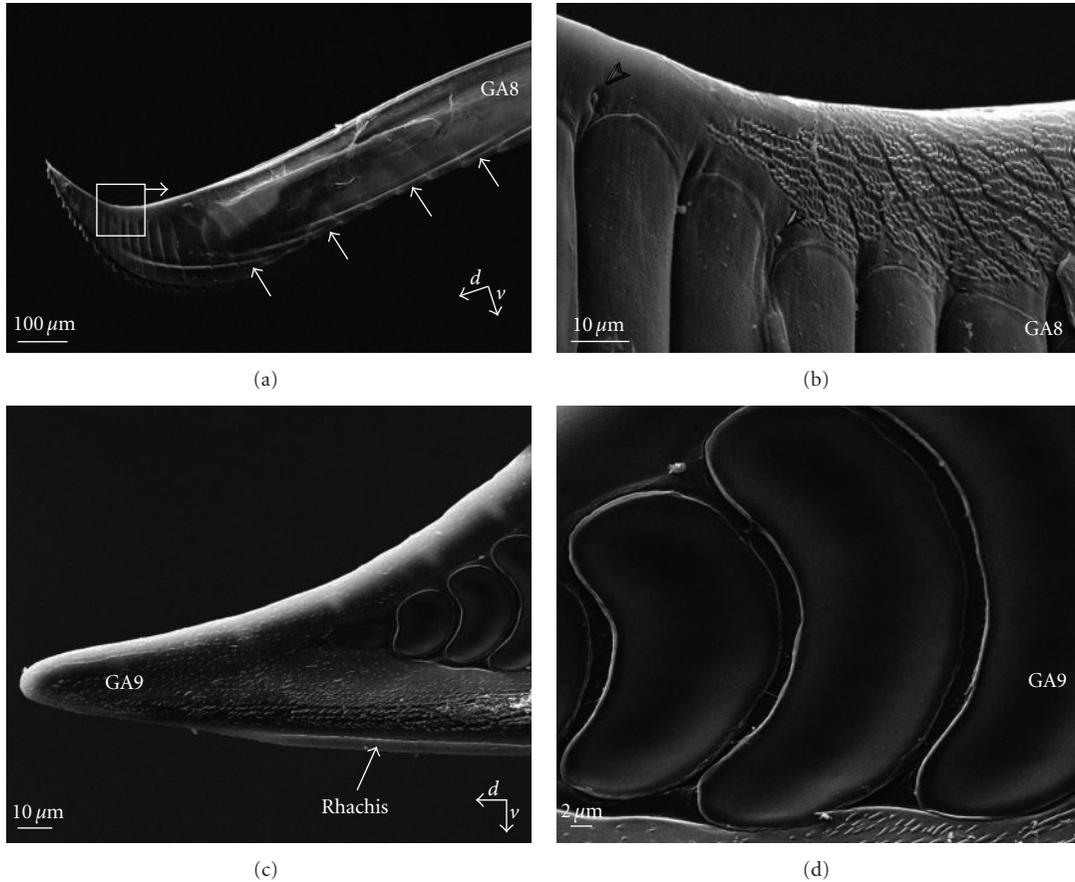


FIGURE 4: SEM micrographs of the inside surface of gonapophyseal apices in *Tricholepidion gertschi*: (a) distal part of the 8th gonapophysis (inset is enlarged in (b)); (b) dorsal margin of the 8th gonapophysis showing smooth tablet-like fields and short microtrichia above; (c) apical part of the 9th gonapophysis with tablet-like fields and short microtrichia below; (d) subapical part of the 9th gonapophysis showing smooth tablet-like fields. Arrowheads indicate dome-shaped sensilla. Arrows indicate ventral corrugations of the 8th gonapophysis. GA8 and GA9: the gonapophyses of 8th and 9th segments, respectively. *d* and *v*: distal and ventral directions, respectively.

focused mainly on the Microcoryphia: their relatively large eggs (over 1 mm in diameter) were always deposited without cutting of the substrate into preexisting fissures and depressions of rocks and stones (=endosubstratic oviposition) or rarely onto plants and wood (=exophytic oviposition) [38]. Representatives of the genus *Machilis* (Microcoryphia, Machilidae) have been observed to clean and enlarge suitable depressions in oviposition substrata with the ovipositor [38–40]). Current knowledge of the oviposition behaviour in *Zygentoma* derives almost entirely from laboratory cultures of anthropophilic *Thermobia domestica* Packard, *Lepisma saccharina* L., and several species of the genus *Ctenolepisma* (*Zygentoma*, Lepismatidae). The eggs of these species are typically laid, in batches or singly, onto the substrate surface or into highly porous substrate like cotton [41, 42]. *Nicoletia phytophila* Gervais (*Zygentoma*, Nicoletiidae), a cosmopolitan species that inhabits greenhouses and often reproduces parthenogenetically, laid the eggs free and unattached to the substrate. This is remarkable because the Lepismatidae are known to attach their eggs to the substrate [43]. However, the egg-laying behaviour of *Tricholepidion gertschi* has never been observed. The highly sclerotized and strongly laterally

compressed valvulae of this species led Wygodzinsky [1] to suggest that the females may oviposit into decaying wooden tissues, abundant in the habitats of *T. gertschi*. This assumption receives new morphological support from my results. Specifically, the dome-shaped sensilla within the egg canal of *T. gertschi* are superficially identical to the campaniform sensilla with a central molting pore, of a presumed mechanosensory function, found on the ovipositor inner surface of the glassy-winged sharpshooter, *Homalodisca coagulata* (see [19, Figure 4]). The presence of numerous such campaniform sensilla indicates that the ovipositor may be subject to considerable mechanical stress during penetration of a relatively dense substrate.

The internal surface of the egg canal in *T. gertschi* reveals surprisingly diverse microsculpture. Following the assumption by Austin and Browning [15], mentioned above, scales and microtrichia oriented in the distal direction may facilitate one-way movement of eggs within the ovipositor of *T. gertschi*. Similar sculptures have been frequently recorded within egg canals of various insect groups (e.g., in the snakefly *Raphidia* spp. by [16]; in several orthopterans and hymenopterans by [15]). Longitudinal ridges occur much

more rarely (e.g., on the ovipositor valves of the caddisfly *Philanisus plebeius* (Trichoptera: Philanisidae), after [15]). Besides *T. gertschi*, a microsculptured rhachis (the dorsal component of the olistheter interlocking mechanism) has been described in several insects (e.g., in the honeybee, *Apis mellifera* L. (Hymenoptera, Apidae) by [44]; in the digger wasp *Bembix rostrata* (Fabricius) (Hymenoptera, Crabronidae) by [45]; in the damselfly *Lestes macrostigma* (Eversmann) (Odonata, Lestidae) by [20]). It most likely serves to prevent adhesion between the sliding ovipositor valves by reducing their area of contact. The presence of ravioli-like wrinkles along the ventral edge of the 8th gonapophysis is also remarkable. Morphologically and topographically similar structures have been recorded in dragonflies [20, 46, 47]. Those structures are placed slightly asymmetrically between the left and right 8th gonapophyses, probably forming a device which locks the valvulae together. It remains unclear whether the ventral corrugations of the 8th gonapophyses in *T. gertschi* function in a similar way.

Reproductive behaviour of apterygotous insects is characterized by several primitive features. Unlike the absolute majority of winged insects, representatives of Microcoryphia and *Zygentoma* studied in this regard have never been observed in a true act of copulation, exhibiting instead indirect sperm transfer (see review in [38]). The male produces a sperm droplet or a spermatophore and leaves it generally on carrier threads or on the substrate. Then the female has to gather the male products with her ovipositor. Thus, the ovipositor of apterygotous insects seems to have additional functions of taking up the male genital products and possibly also of searching for and identifying these. Specifically, a male *T. gertschi* produces secretory threads, on which a roundish spermatophore, ca. 1 mm in diameter, will be deposited [48]. Then the female bends her abdomen ventrad and takes up the entire spermatophore by means of her ovipositor. The mechanism of absorbing male genital products by the female ovipositor remains obscure. Possibly the sperm flows in under the action of capillary forces acting within the thin gap of the opened ovipositor. If this is so, the ovipositor internal microsculpture (especially the longitudinal wrinkles and ridges) may facilitate the capillary flow of sperm by serving as “slide rails” directing it to the sperm storage organs.

Apart from this work, there currently exist only two records of egg canal microsculpture in apterygotous insects. Distally directed microtrichia have been discovered on the inner surface of the 8th gonapophysis in two microcoryphians, *Petrobius brevistylus* [38] and *Petrobiellus tokunagai* [49]. In the latter case, unusually large (ca. 40–50 µm long) rod-shaped “microtrichia” differed notably from microstructures recorded in other insects, including *T. gertschi*. In the absence of more detailed studies, it is not possible to prove the function of egg canal microstructures in apterygotous insects or explain their observed morphological variation. TEM examination, biomechanical and electrophysiological studies are needed to verify the hypothesized functions of both the microsculpture and sensilla. Additional live observations of ovipositors in action, accompanied with detailed morphological descriptions, are also essential. The

presence of microsculpture inside the insect ovipositor should be tentatively considered an ancestral character state, but the homologies of ovipositor microstructures within and between different insect groups remain to be studied.

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