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THE SCLERITE COMPOSITION OF THE FEMALE GENITALIC REGION IN AN ENIGMATIC SILVERFISH *TRICHOLEPIDION GERTSCHI* (INSECTA, ZYGENTOMA)

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The sclerite composition of the female genitalic region in an enigmatic silverfish *Tricholepidion gertschi* (Insecta, Zygentoma). Matushkina, N. — *Tricholepidion gertschi* (Lepidotrichidae) has an unresolved phylogenetic position, being placed as sister group to Dicondylia (Zygentoma + Pterygota) or within Zygentoma, making it the only insect species whose ordinal status remains uncertain. In this work, the sclerite composition of the female postabdomen of *T. gertschi* was investigated using scanning electron microscopy. A transverse sclerotized bridge between the gonangula, interpreted as a derivative of sternite 9, was found. Comparative analysis with published data shows that the presence of distinct sternal sclerotisations in segments 8 and 9 of *T. gertschi* is a plesiomorphic condition that has not been found in Zygentoma so far. This finding confirms the unique morphology of this species. It is suggested that transverse sternal sclerotisations in *T.gertschi* enhance mechanical stabilisation of the ovipositor during egg laying in hard substrates such as wood.

Key words: cuticle, SEM, insect morphology, homology.

Introduction

Insects exhibit a particularly intricate organisation of the postabdomen were genitalia are developed (Scudder, 1961; Klass & Ulbricht, 2009; Matushkina & Stetsun, 2025). This region includes the venters of abdominal segments 7 (posterior part only), 8, and 9 (Snodgrass, 1933; Scudder, 1961; Rousset, 1973; Bitsch 1974 a; Klass 2008; Klass & Matushkina, 2012, 2018). The ovipositor which consists of valves is the principal structure of the female external genitalia (Matushkina & Stetsun, 2025).

The overall complexity of the region is largely attributable to the sclerites surrounding the bases of valves and an elaborate musculature.

The extant species *Tricholepidion gertschi* Wygodzinsky, 1961 — regarded as a 'living fossil' by Wygodzinsky (1961) and some authors listed below — is the sole surviving representative of the silverfish family Lepidotrichidae Silvestri, 1913, which was previously known only from Eocene fossils. Although originally assigned to the order Zygentoma in the original taxonomic description, the phylogenetic position of *T. gertschi* has long been contentious owing to its distinctive combination of plesiomorphic and apomorphic morphological features (Engel, 2006). Competing hypotheses recognize *T. gertschi* as the sister group of the Dicondylia (i. e., Zygentoma + Pterygota) (e. g., Bitsch & Bitsch, 2000; Staniczek, 2000), as the basalmost lineage within Zygentoma (Kristensen, 1981; Koch, 2003; Engel, 2006), or as closely related to certain zygentoman subgroups (e. g. Nicoletiidae by Smith, 1998; Nicoletiidae + Ateluridae by Dallai et al., 2004, see discussion therein). Molecular data have yet to resolve the placement of *T. gertschi* unambiguously (Giribet et al., 2004; see also Nardi et al., 2003), leaving the relationships of *T. gertschi* — and by extension the entire family Lepidotrichidae — among basal hexapods one of the most debated issues in hexapod phylogeny. Moreover, *Tricholepidion* was considered as a "the most promising candidate for a new insect 'order' (or, in other words, the only insect species whose ordinal classification remains uncertain)" (Zrzavý, 2008: p. 220).

In the present study, the sclerite composition of the female genitalic region in *T. gertschi* was analyzed using scanning electron microscopy (SEM). By comparing these original observations with published morphological data for Archaeognatha and Zygentoma, homologous elements were identified and the structural organisation of the female genitalic region was clarified. This comparative approach aims to refine the understanding of female genitalic evolution at the base of the insect tree of life and to contribute to ongoing discussions about the systematic placement of *T. gertschi*.

Material and Methods

A single female postabdomen of *Tricholepidion gertschi* was provided by Markus Koch (University of Bonn, Germany) with the following label information: Heath and Marjorie Angelo Coast Range Reserve, Northern California, USA (M. Koch leg). The materials were preserved in 100% ethanol.

For scanning electron microscopy (SEM), the postabdomen of the specimen was rinsed with water, dissected with fine tweezers and microscissors, and then macerated in 10% KOH solution for 10–12 h at room temperature. The resulting cuticular fragments were thoroughly washed in distilled water, dehydrated through a graded ethanol and acetone series, and dried using a critical-point dryer (OM CPD 7501). Dried cuticle parts were mounted on the stub probe holder using an adhesive tab, sputter-coated with gold–palladium (OM-SC7640), and examined using a Zeiss EVO 50 SEM (Museum of Zoology, Senckenberg Natural History Collections, Dresden, Germany).

The nomenclature of abdominal sclerotisations is based on conditions recorded from Archaeognatha (Klass & Matushkina, 2012, 2018; Matushkina & Klass, 2020). Abbreviations: BS (+ number) = basal sclerite of coxal vesicle, topographically ho-

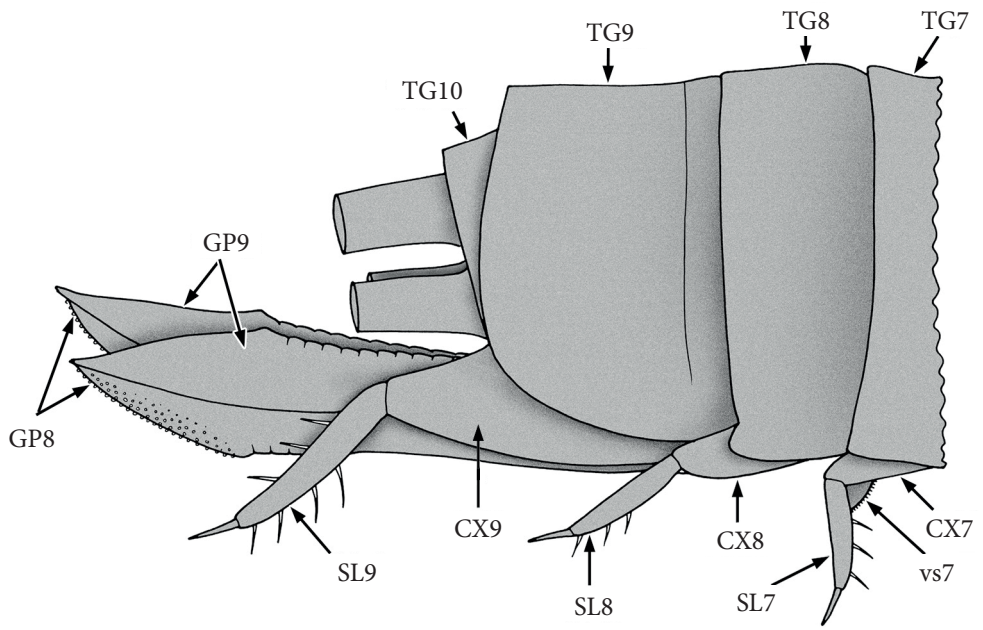

Fig. 1. Female postabdomen of *Tricholepidion gertschi* (Zygentoma), semi-diagrammatic lateral view with caudal appendages partly removed. Abbreviations of abdominal structures are given in Materials and Methods

mologous with basal sclerite of the gonapophysis (number = segment); CX (+ number) = coxa/−ite (number = segment); GP (+ number) = sclerotisation of gonapophysis (number = segment); LC9 = laterocoxa/−ite of segment 9 (number = segment); SL (+number) = stylus (number = segment); ST (+number) = sternum/−ite (number = segment); TG (+number) = tergum/−ite (number = segment); vs (+ number) = coxal vesicle (number = segment).

Results

The female postabdomen of *T. gertschi* is cylindrical, with a laterally compressed true ovipositor consisting of the ventral valves of the 8th abdominal segment (gonapophyses 8) and the dorsal valves of the 9th segment (gonapophyses 9) (Fig. 1). All gonapophyses remain unfused at their bases (Fig. 2, *a*, *b*). The basal part of gonapophysis 8 (= basal sclerite) is separated from the remainder of the gonapophysis by an annulation and differs in its microsculpture, which more closely resembles the setose microsculpture of the adjacent coxite 8 than the essentially smooth surface of the distal gonapophysis 8 (Fig. 2, *c*). The basal region of the gonapophysis 9 is morphologically indistinct, showing no peculiarities in microsculpture.

Coxites 8 are separated medially. The approximately triangular laterocoxites 8, which adjoin the anterolateral margins of coxites 8, are connected medially via a narrow transverse sclerite (= sternite 8) that is clearly visible both externally and internally (Fig. 2, *a*). Coxites 9 form the third valves of the ovipositor, covering the base of the true ovipositor laterally. Anterolateral to coxites 9 lie the lon-

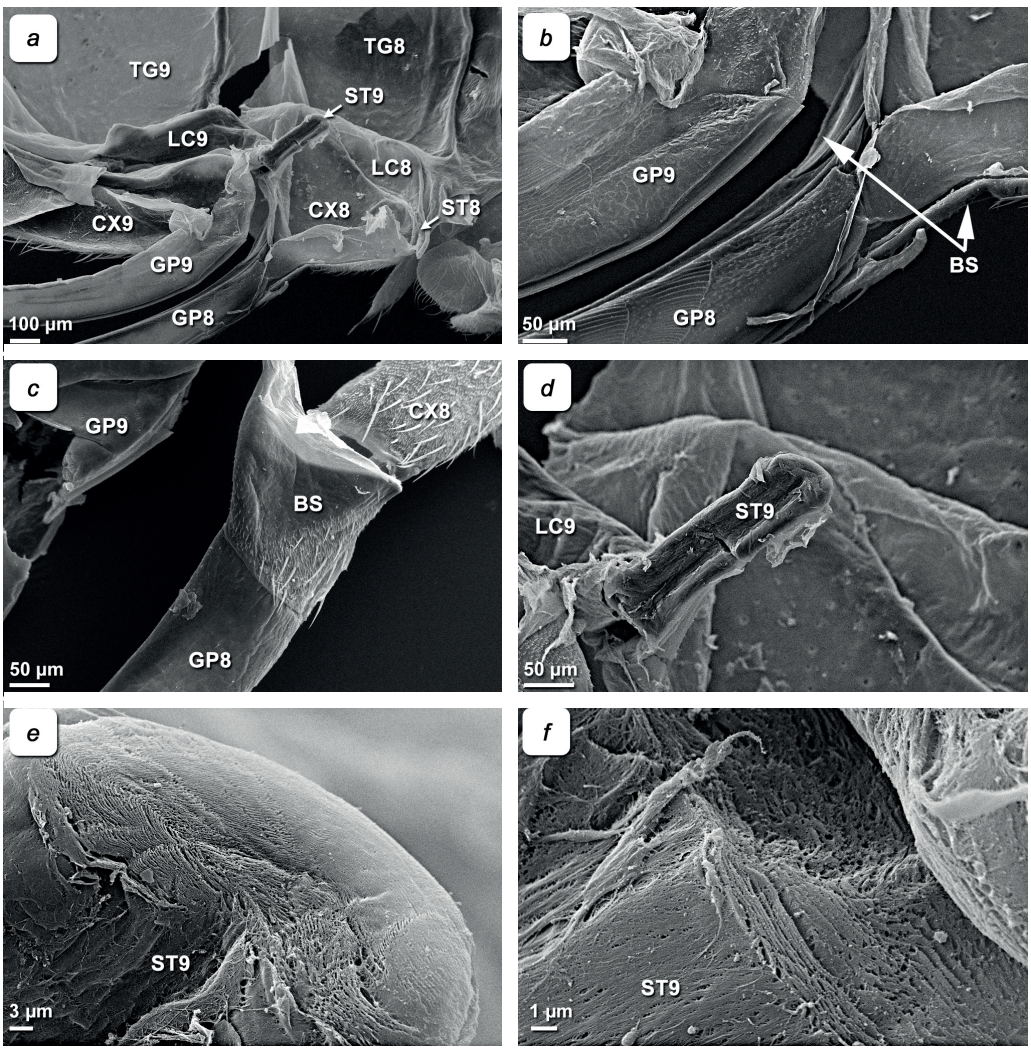

Fig. 2. Microstructure of the basal part of the ovipositor of *Tricholepidion gertschi* from the inside (*a*, *b*, *d–f*) and outside (*c*), SEM: *a* — base of the ovipositor; *b* — base of gonapophyses 8 and 9; *c* — base of gonapophysis 8 and its basal sclerite; *d–f* — transverse sclerotized bridge between gonangula at different magnifications, note layered cuticle consisting of fiber network. Abbreviations of abdominal structures are given in Materials and Methods

gitudinally elongated sclerites — the gonangula (laterocoxites 9). Each gonangulum articulates with tergite 9 via its anterior lateral margin, with the gonapophysis 8 via its ventral medial margin, and with coxite 9 via its posterior margin. A rod-like sclerotized transverse bridge lies between the medial surfaces of the two gonangula, deepening in the space between gonapophyses 8 and gonapophyses 9 (Fig. 2, *a, d*). This bridge is completely hidden under gonapophyses, and thus not visible externally. In cross section the bridge is semicircular and composed predominantly of distinctly layered cuticle with clear fiber network (Figs 2, *e, f*). According to the principles of topographic homology, this transverse bridge is interpreted as a derivative of sternite 9.

Discussion

Wingless insects (Archaeognatha and Zygentoma) share a plesiomorphic morphology of the generalized abdominal segment. In Archaeognatha, a typical pregenital segment bears a tergite, as an entire U-shaped sclerite, dominating the dorsal surface, and a set of ventral sclerotisations of varying size, including one or two median sternal sclerotisations, paired coxites (with styli and, in anterior segments, eversible vesicles), and paired laterocoxites (sclerites anterolateral to coxites) (Fig. 3, *a*) (Sturm & Machida, 2001; Klass & Matushkina, 2012). In the female postabdomen, where the ovipositor develops, the eversible vesicles on the coxites are replaced by gonapophyses (ovipositor valves), the coxites become more widely spaced (coxite 9 is also enlarged), and the sternal sclerotisations either fuse with the adjacent coxites (segment 8) or are weakly sclerotized (segment 9) (Klass & Matushkina, 2012).

The female postabdomen of Zygentoma conforms to this general pattern but exhibit a more consolidated ventral region and a flatter tergite. The sclerite composition of the female postabdomen in Zygentoma has been originally described in detail for two species: *Thermobia domestica* (Packard, 1837) (Lepismatidae) and *Nicoletia* sp. (Nicoletiidae) (Rousset, 1973). In *T. domestica*, the seventh abdominal segment bears a single ventral sclerotisation encompassing both the sternal and coxal regions, referred to as the coxosternite. The ventrum of the eighth segment displays

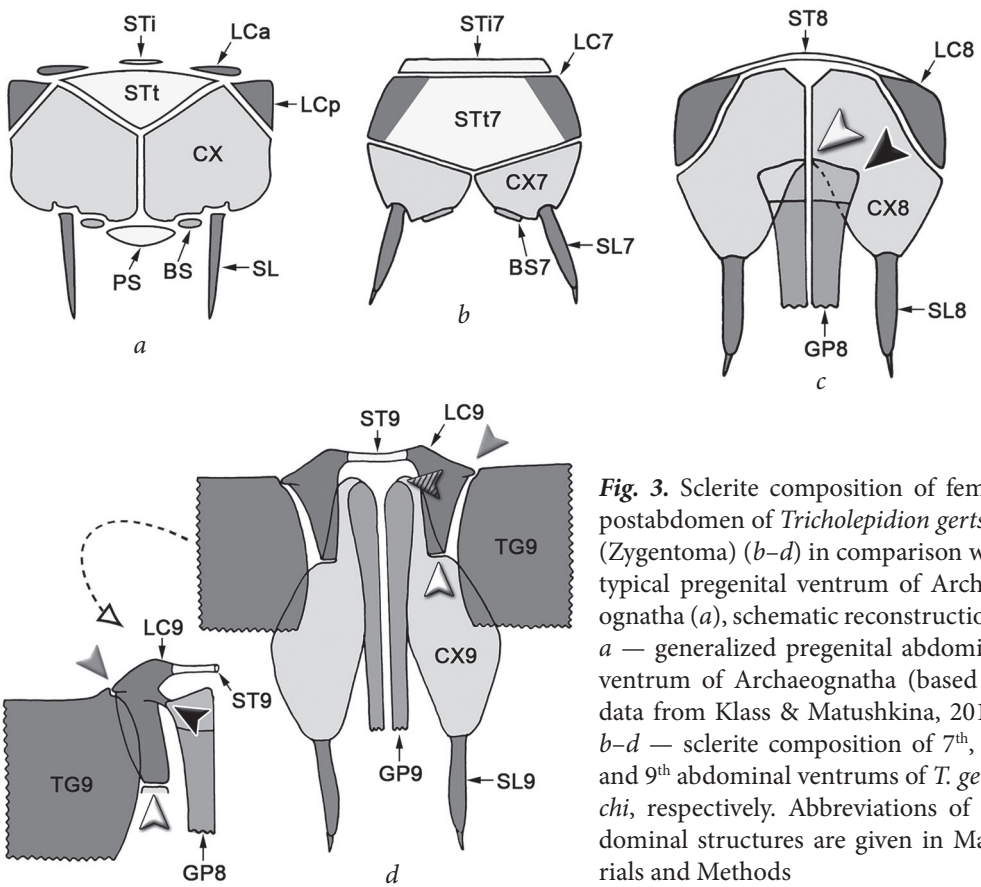

Fig. 3. Sclerite composition of female postabdomen of *Tricholepidion gertschi* (Zygentoma) (*b–d*) in comparison with typical pregenital ventrum of Archaeognatha (*a*), schematic reconstructions: *a* — generalized pregenital abdominal ventrum of Archaeognatha (based on data from Klass & Matushkina, 2012), *b–d* — sclerite composition of 7th, 8th, and 9th abdominal ventrums of *T. gertschi*, respectively. Abbreviations of abdominal structures are given in Materials and Methods

two separate bilateral sclerotisations — the coxites (each bearing a stylus and a coxal vesicle transformed into a gonapophysis) — whereas the ninth segment, in addition to the coxites, gonapophyses, and styli, also bears an elongated laterocoxite 9, the gonangulum. This sclerite articulates anteroventrally with gonapophysis 8, anterodorsally with tergite 9, and posteriorly with coxite 9. Distinct sternal sclerotisations are absent in the eighth and ninth segments.

By contrast, the composition of female postabdominal sclerites in *Nicoletia* more closely resembles that of Archaeognatha. The ventrum of the seventh segment bears a trapezoidal median sternal sclerotisation (the (eu)sternite after Klass & Matushkina, 2018), surrounded by paired lateral regions (the coxites) each containing an eversible vesicle and a stylus. Anteriorly, there is a transverse presternal sclerotisation (the intersternite after Klass & Matushkina, 2018) and, on each side, a small laterocoxal sclerite. The ventrum of the eighth segment in *Nicoletia* does not differ in composition from that in *Thermobia*. In the ninth segment, sternal sclerotisations are absent, and the very large gonangulum partially substitutes the coxal sclerotisation, being separated from it by a membrane rather than a joint (this condition was erroneously interpreted by Rousset as the gonangulum is "not separated from the coxite").

Compared with these taxa, the composition of female postabdominal sclerites in *Tricholepidion* is unique within Zygentoma studied in this respect, as it retains distinct sternal sclerotisations connecting the laterocoxites in segments 8 and 9 (Figs 3, *c*–*d*). The presence of sternal sclerotisation(s) in segment 8, characteristic of Archaeognatha, can — given the well-established sister-group relationship between Archaeognatha and Dicondylia (e. g., Misof et al., 2014) — be interpreted as a plesiomorphic condition. However, sternal sclerotisation in segment 9 represents a feature not reported in any other representative of wingless insects. This transverse sclerotisation, forming a seemingly rigid cuticular bridge, may restrict the movements of the separated right and left gonapophyses 9 relative to each other. Notably, in the studied representatives of Archaeognatha (Klass & Matushkina, 2018: *Petrobiellus takunagae*), as well as in *Thermobia* and *Nicoletia* (Rousset, 1973), gonapophyses 9 show varying degrees of fusion, whereas gonapophyses of *Tricholepidion* are free at their bases (Matushkina, 2011). Thus, *Tricholepidion* displays a unique adaptation for mechanical stabilisation of the bases of gonapophyses 9. In terms of serial homology, presence of sternal sclerotisation of the 9th abdominal segment considered a plesiomorphic state as it occurs in unspecialized pregenital segments of Archaeognatha and pregenital and 8th abdominal segments of some Zygentoma.

In a functional context, this peculiar sclerite composition of the female genital segments in *Tricholepidion* may relate to oviposition in relatively hard substrates such as wood, as suggested by the presence of a blade-like, pointed, denticulated ovipositor (Wygodzinsky, 1961; Matushkina, 2011; Matushkina & Stetsun, 2025). The present observations confirm considerable variation in consolidation of ventral sclerites within Zygentoma, with *Tricholepidion* retaining several plesiomorphic features and thus representing a unique condition among wingless insects. Although this pattern appears consistent with a shift from a multi-elemental to a more integrated configuration, the actual direction of sclerite reorganisation within the order

remains uncertain, and similar reorganisations may have occurred independently in multiple lineages. Such modifications may have functional implications for ovipositor functioning. Further comparative studies across wingless insect lineages are therefore needed to clarify the tendencies of evolutionary changes of the sclerite composition of the female postabdomen.

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