Acta Arachnologica, 71 (2): 105–113, December 20, 2022

The behavioral and external morphological observations on oviposition and post-embryonic development in *Galeodes hakkariensis* Erdek 2021 (Solifugae: Galeodidae)

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Abstract — Oviposition was observed in *Galeodes hakkariensis* Erdek 2021. Part of the developmental changes post-hatch were recorded, and the cuticular surfaces of egg and first post-embryos were surveyed with a scanning electron microscope. This species has oval-shaped eggs varying from 2 mm to 4 mm in diameter. The fine structure of the external morphology of post-embryos in a solifuge is shown for the first time. The cuticular patterns and sensilla on opisthosoma and tarsal sensilla on each pedipalp and leg were described in post-embryos. The surface of each opisthosomal basiconic sensilla without the socket is covered with pores, likely functioning as chemoreceptors. Tarsal basiconic sensilla not in a socket and without pores on pedipalps and legs likely function as mechanoreceptors. The single slit sensillum on the tarsus of pedipalps functions as mechanoreceptors.

Key words — egg, *Galeodes*, oviposition, post-embryo, sensilla, Solifugae

Introduction

The developmental biology of Solifugae has been poorly known and only a few embryonic developmental stages have been entirely described. Until now, ovulation behaviour and life-cycle parameters have been studied by quite a few researchers. Hutton (1843) examined the burrowing nest and egg deposition processes of *Galeodes fatalis* (Lichtenstein 1796) (as *Galeodes vorax*). Turner (1916) recorded the observations on burrowing and oviposition behaviours of *Eremobates formicarius* (C. L. Koch 1842). Hingston (1925) also studied burrowing and egg-deposition behaviours of *Galeodes arabs* (C. L. Koch 1842). Lawrence (1947, 1949) recorded the egg-laying and deposition process on *Solpuga rufescens* (C. L. Koch 1842) (as *Solpuga hostilis*) and *Zeria caffra* (Pocock 1897) (as *Solpuga caffra*). Muma (1966a) examined the egg-laying process and behaviour of *Eremobates durangonus* and compared the egg structures with other eremobatid species. Muma (1966b) determined the lifecyle of *Eremobates durangonus* (Roewer 1934). Thaler (1982) recorded the eggs to first larvae and first larval development of *Gylippus* (*Gylippus*) *cyprioticus* Lawrence 1953 (as *Gylippus* cf. *cypriotica*). Wharton (1987) observed burrowing, mating, oviposition, and feeding behaviour of *Metasolpuga picta* (Kraepelin 1899). Punzo (1998) described the life cycle and natural history of *Eremobates marathoni* Muma 1951. Erdek & Yiğit Kayhan (2016) also described the burrowing and oviposition of *Gylippus* (*Gylippus*) *syriacus*.

Galeodes hakkariensis Erdek 2021 is a recently described galeodid. This species is found in high plateaus by the Zap River in the Hakkari province, bordering Iran and Iraq. The activity period of this species is early June–late July. In this paper, the oviposition and hatching behavior are described, and external morphologies of egg and post- embryos are described in detail including sensilla types and cuticular structures evident in these early developmental stages.

Material and methods

A female of this species was taken from Hakkari province in Southern Turkey (Turkey, Hakkari Prov., Boybeyi Village, Dikilitaş Hamlet, N 37°47’06.24”, E 44°04’48.73”, 1812 m, 7 November 2020, leg. R. Dalmaz). This female solifuge was maintained in the laboratory in a glass bell (25×40×12 cm) containing a layer of soil about 4–5cm in height. A small stone was added to provide a hiding place during the daylight resting time, and wet cotton wool was added for humidity. *Tenebrio molitor* larvae were used for feeding. The gravid female was regularly checked during daytime and nighttime. The eggs and post-embryos were prepared for scanning electron microscopy (SEM) and air-dried. These materials were gold coated in Quorum SC7620 Sputter-Coater and photographed at an accelerating voltage of 10kV in a ZEISS Sigma 300 SEM at the Science Application and Research Center in Van Yüzüncü Yıl University.

Results

Oviposition. The female G. *hakkariensis* was collected on 11 July while moving on the ground during daylight time (14:00–16:00). This galeodid was sensitive and aggressive, and its opisthosoma was swollen (Fig. 1a). Nine days after collecting, eggs became visible on the lateral and dorso-lateral surfaces of the opisthosoma (Fig. 1b–d). The gravid female stopped feeding on 24 July. In these laboratory conditions, the individual fed with *T. molitor* larvae twice a day started to wander actively on the soil surface on 28 July and took its first food on 30 July. The gravid female crumbled the chunks of big soil particles in the terrarium by biting-chewing with chelicerae. It stopped the active movement and became stagnant again on 2 August. Egg-laying began on 6 August with rhythmic contractions on the lateral side of the opisthosoma rapidly with the chelicerae in an open position, mesopeltidium and metapeltidium moving rapidly up and down in a dorsoventral direction, and opisthosomal segments contracting from posterior (anal segment) to anterior (genital segment) (Fig. 1b–c). During rhythmic contractions, the chelicerae open laterally outward on both sides. A total of 53 eggs were laid, the first two eggs one by one, the others in pairs and in multiple clumps. The apparently viable eggs were light cream-glossy white colored and the shriveled eggs were matte dark yellowish cream colored. The egg-laying took about 9 hours (from 06:28–15:51). After egg-laying, the individual collected the eggs under her body with her first pair of legs and ate one of the apparently viable eggs (Fig. 1d). Afterward, the female remained motionless on her eggs, the darkening of color was observed on the body, and she died at 12:30 on 8 August. On the same day, a few of the eggs began to hatch. In post-embryos, passive movements in the form of twitching were observed in extremities, especially pedipalps (Fig. 1e–f). On 10 August, a large number of post-embryos began to develop and segmental separation in the opisthosomal segments was apparent.

Egg and post-embryo morphology. The eggs were oval-shaped and 2–4 mm in diameter. The apparently viable and shriveled (apparently unviable) eggs, and post-embryos are in Fig. 2a. The egg on the top in Fig. 2a, which is darker than the others, is an shriveled egg and the two eggs at the bottom are the apparently viable eggs. The chorion membrane is transparent and distinctly visible (Fig. 2a–b). Ventrally, the prosoma and opisthosoma are folded. During post-embryonic development, the extremities emerge from the prosoma and the opisthosoma and begin to elongate in the anteroposterior direction. The bottom right Fig. 2a is the final state of the post-embryo before the external egg covering ruptures and there are 6 prominent protrusions in the form of dots on the dorsal aspect. Opisthosomal setae develop from these protrusions. The developed post–embryo on the right of Fig. 2a is 4 days old, the extremities are elongated and opisthosomal segmentation has begun. The 1st and 2nd, 3rd and 4th legs appear to be of equal length. The chelicerae are two-part, but there is no separation of the movable and fixed fingers, nor is there formation of the cheliceral teeth. On the dorsal aspect of the opisthosoma, there are two indistinct gray stripes of pigmentation (Fig. 2e). Opisthosomal dorsal setae appear opposite and intermittently above this pigment line. The lateral organs are foot-shaped and located near the 1st pair of legs (Fig. 2e–f). The ocular tubercle become slightly prominent.

External morphology of eggs and post-embryos. There is no specific pattern on the egg surface and there are cuticular folds, which may just be an artifact of the deydration that is inevitable when preparing the egg for SEM observation (Fig. 3a). The first part of the post-embryo to emerge from the external egg covering is the pedipalps (Fig. 3b). These extremities are disto-proximally flattened and elongated distally during development. The extremities appear in a transverse annular structure and there are granules on the surface (Fig. 3c). The exit in the external egg covering starts from the extremity tips ventrally and ends in the opisthosoma dorsally. The lateral organ is seen like a knob (Fig. 3c–d). The covering located on the dorsal part of the lateral organ is the external egg covering (Fig. 3c). There are 6 pairs of opisthosomal setae (Fig. 5a). These are without sockets and are non-flexible setae. These setae are in the form of basiconic sensilla, as each is conical in shape bulging at the base and gradually tapering towards the tip. There are cuticular prominent protruding pores on the surface of each of these setae (Fig. 3e). The 2–3 hour-post-embryo has a different cuticular pattern between the dorsal and ventral sides of the opisthosoma. It has a corrugated surface in the form of a transverse line in ventral and ornamental patterns in dorsal (Fig. 3c, f). The cheliceral development has not fully started in 4-day-old post-embryo. There is only a distinction between the upper and lower fingers of chelicerae. The cheliceral condyles and inter digital articular membrane are not formed, so there is no separation of movable and fixed fingers (Fig. 4a–c). There is a nipple-like protrusion at the tip of the dorsal outer surface of each cheliceral finger (Fig. 4c). There is no distinction of prosomal segmentation as propeltidium, mesopeltidium and metapeltidium (Fig. 4b), in addition, the articular separation of each extremity and the coxal separation of these extremities ventrally did not occur. Below the chelicerae and anteromedial part of the extremities, there is a knob-shaped oval protrusion, which is thought to be an incompletely developed rostrum. (Fig. 4b). There are no malleoli formed on the ventral surface of the 4th leg. The I–IV legs are similar and the tarsal tip of the 2nd leg as in Fig. 4d. There is only one filiform seta, which lacks a socket in the form of a basiconic sensilla. The cuticular surface of this basiconic sensillum is smooth and there is no pore. There are also incompletely formed tarsal claws as well as the beginning of an apparent arolium at the tarsal tip of the forming legs (Fig. 4d). The opisthosoma of the 4-day-old post-embryo is as in Fig. 5a. There are 6 pairs of opisthosomal setae in the form of basiconic sensilla. The cuticular surface of these setae, which are cone-shaped, bulging at the



Fig. 1. Female *Galeodes hakkariensis* Erdek 2021. (a), habitus; (b)–(c), egg–laying; (d), egg-cannibalism behavior; (e)–(f), eggs and post-embryos. Scales = 1 cm.

base, is covered with notches, and there is a pore at the tip of each notch (Figs. 5c–d). The surface of the opisthosoma is granular (Figs. 5a, c). The dorsum of the opisthosoma consists of a series of prominent tubercles surrounded by cylindrical cuticular protuberances (Fig. 5b). The pedipalps taper distally with a non-gradual indentation. The cuticle surface is smooth distally, while proximally it has a granular structure (Fig. 5e). There is also a basiconic sensillum as a filiform seta and without a socket (Fig. 5e). There is a single slit sensillum on the smooth surface of pedipalp (Figs. 5e–f).

Mold, deterioration and death. After egg-laying, cotton-like mold formation occurred on the soil surface and on post-embryos (Fig. 6a–b). There are spores and hyphae of the mold evident on the surface of the chelicerae (Figs. 6d–f). There are also bacterial formations in the form of bacilli and coccobacilli on the external egg covering (Fig. 6c, detailed view of the external egg covering surface in Fig. 3c).

Discussion

Solifuges are mysterious arachnids and it is difficult to collect them and observe their behaviors in the natural habitat. The observation of their mating, oviposition, and life cycle stages is also difficult under laboratory conditions. Some parameters such as being very fast creatures, inability

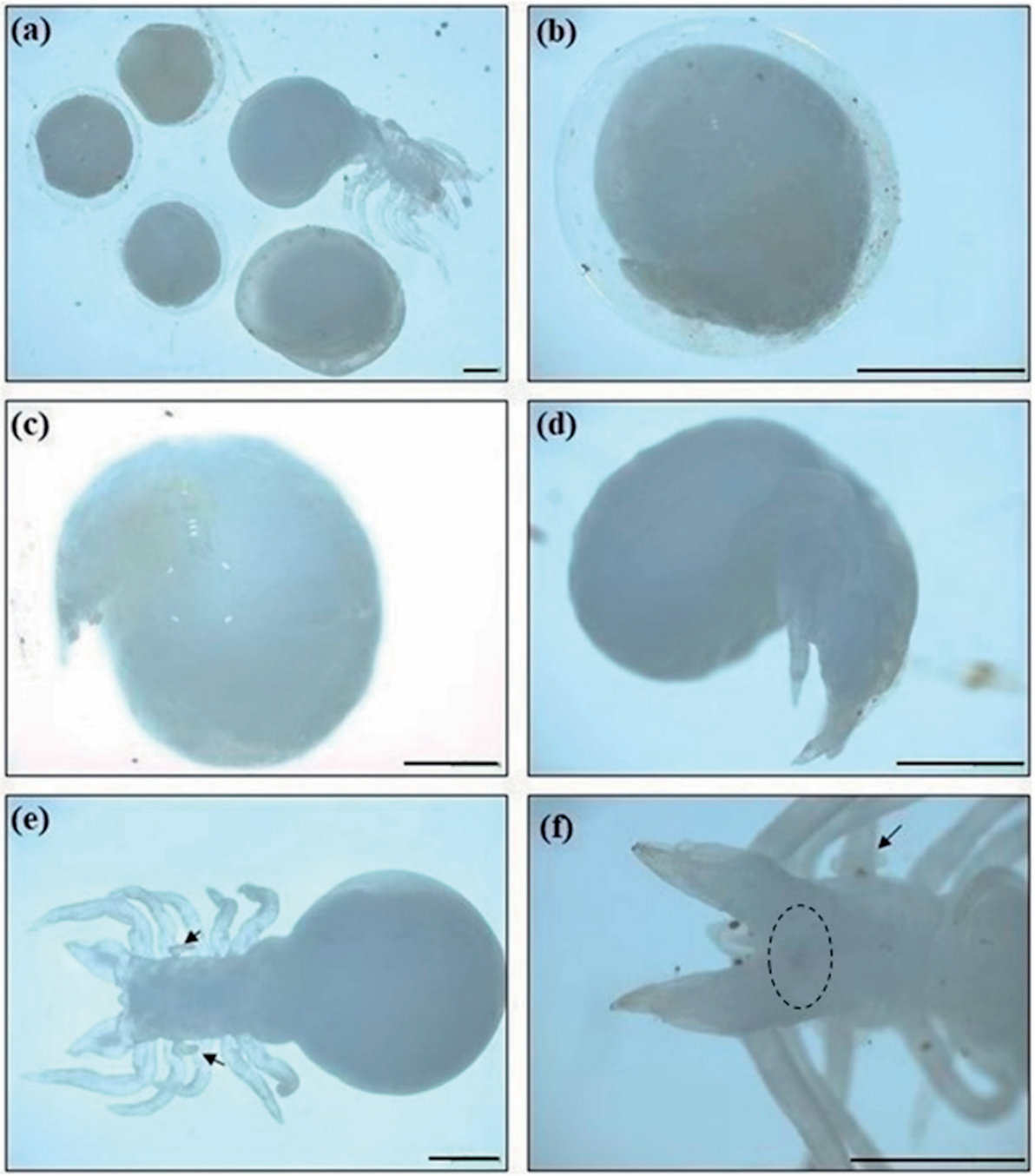


Fig. 2. (a)–(f), embryonic developmental stages of female *Galeodes hakkariensis*. Arrows show lateral organs in (e)–(f), the circle shows ocular tubercle silhouette. Scales =1 mm.

to provide the appropriate type of food, having a short life cycle, inappropriate abiotic conditions (temperature, moisture, dryness, etc.) inside the terrarium explain the difficulty of maintaining these arachnids in captivity under laboratory conditions. It is thought that the eggs and post-embryos in this study became moldy and cottony due to the inability to keep the humidity level at the appropriate level. Punzo (1998) also indicated that if the rearing and breeding conditions of solifuges are too moist, the eggs will be sensitive to attack by bacteria and fungi. The fungus on infected post-embryos are likely be ascomycetous fungus according to the appearance under the scanning electron microscope. Because of the formation of the mold, the life cycles of this solifuge could not be fully observed.

During the egg deposition, the female lay slightly on her side at the beginning of the egg-laying. Lawrence (1949) also observed this behavior in *Zeria caffra* and *S. hostilis.* But the individual female in our study changed place and position several times. In this instance, egg-laying took place in the dorsoventral position. Egg-laying of *G. hakkariensis* was completed with the deposition of 53 eggs after about 9 hours. Although the number of eggs is variable,

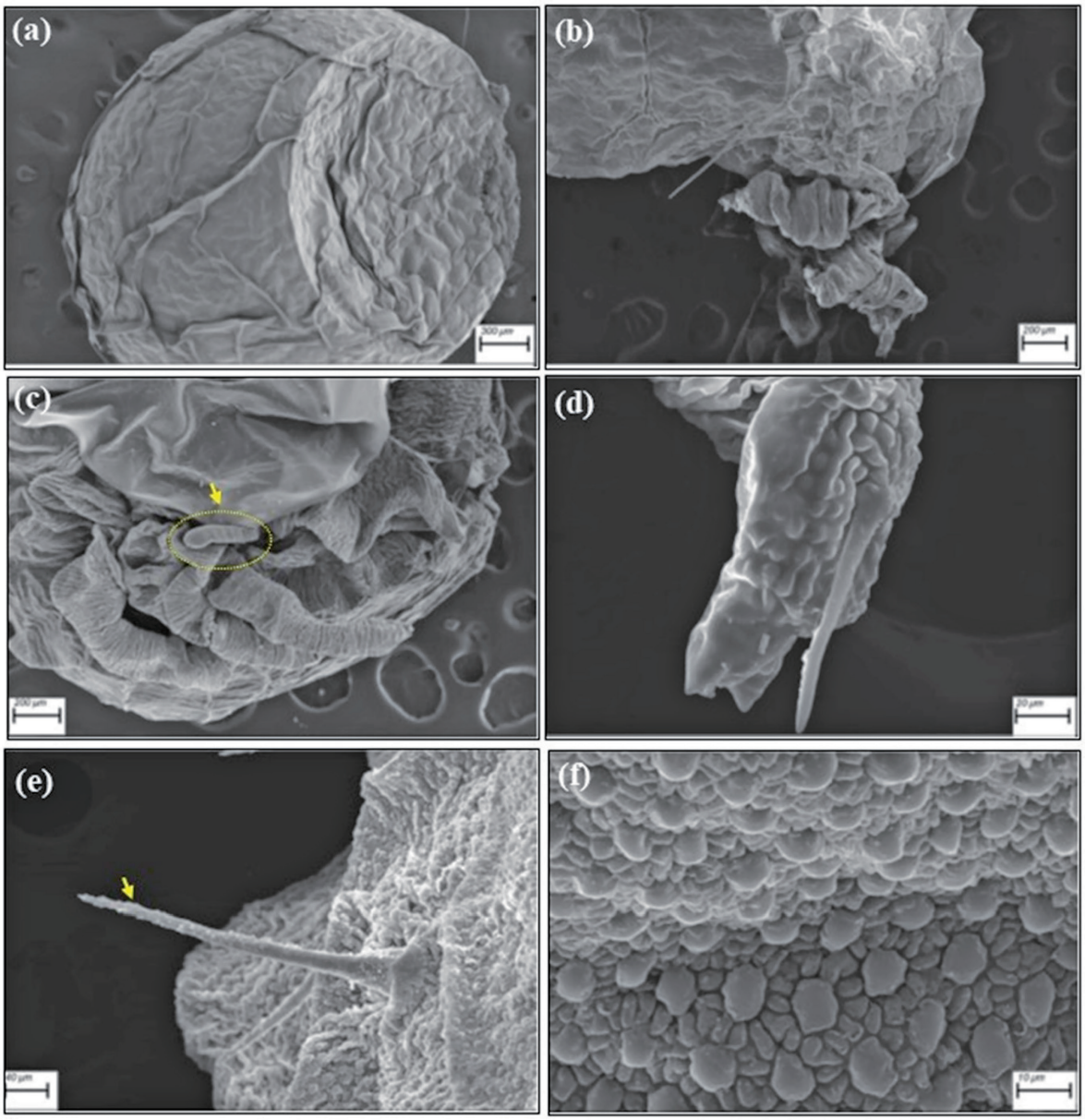


Fig. 3. Scanning electron micrographs of eggs and post-embryos. (a), the view of egg; (b), lateral side of post-embryo after the external egg covering first opened; (c), lateral side of the post-embryo after 2–3 hours, arrow and circle show lateral organ; (d), the lateral organ in detail; (e), opisthosomal dorsal seta, arrow shows setal pores; (f), cuticular patterns on the opisthosoma of post-embryo. Scales = 300 µm (a); 200 µm (b)–(c); 30 µm (d); 20 µm (e); 10 µm (f).

this period was observed to be shorter in other species: 67 eggs after 40–60 minutes in *Eremobates durangonus* (in Muma 1966a), 192 eggs after 3.5–4.5 hours in *Zeria caffra* (in Lawrence 1949), 34 eggs after 80–90 minutes in *Gylippus* (*G.*) *syriacus* (Erdek & Yiğit-Kayhan 2016), etc. These values show that the ovulation period is not directly proportional to the number of eggs. This variability in egg-laying time is most likely related to the diameter of the egg and the diameter of the genital opening, which is species-specific. The variability in the number of eggs observed may be related to the physiological condition of the individual (e.g., how well fed it was prior to egg-laying) or to other environmental factors such as humidity and temperature affecting development rather than the body size of the species. In addition to apparently viable eggs during egg-laying, a small number of shriveled eggs were also observed. Also, after egg-laying, which lasted about 9 hours, the female ate one of the apparently viable eggs. Muma (1966b) also observed egg-cannibalism for *Eremobates durangonus* and *Eremochelis bilobatus*. The female of *Gylippus* (*G.*) *syriacus* cannibalized her eggs (Erdek & Yiğit Kayhan 2016). Klann (2009) indicated the presence of a large amount of glycogen, many mitochondria, microvilli, Golgi bodies, vesicles including multilamellar bodies, and different kinds of droplets such as lipid and protein yolks produced in very young oocytes during oogenesis in subadult females. It is thought that the

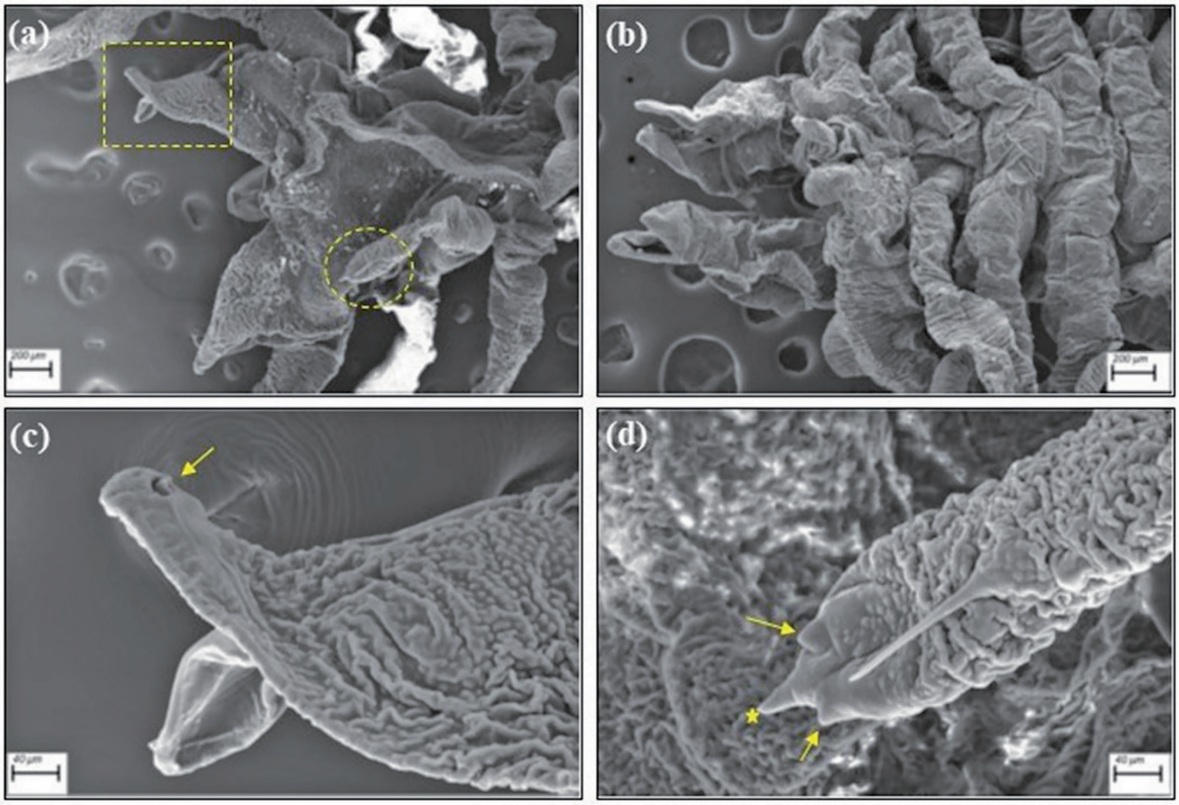


Fig. 4. Scanning electron micrographs of 4-day-old post-embryo. (a), dorsal side of prosoma, square is the structure shown in (c) and the circled structure is shown magnified in (d); (b), ventral side of the prosoma; (c), dorsal surface of the fixed cheliceral finger, arrow shows a nipple-like protrusion; (d), the tarsal tip part of embryonic 2nd legs, arrows show tarsal claw base, asterisk shows undeveloped arolium. Scales = 200 µm (a)–(b); 40 µm (c)–(d).

female ate one of her eggs after laying to regenerate the energy she lost during ovulation. Erdek & Yiğit Kayhan (2016) also suggested that female solifuges eat their own eggs in order to prevent loss of the nutrients and to restart the ovulation cycle. The egg chorion of *G. hakkariensis* has no specific cuticular ornamentation. Muma (1966a) and Erdek & Yiğit Kayhan (2016) defined different cuticular ornamentation of egg-chorion. Muma (1966a) observed widely spaced-truncate papillae on the egg-chorion of *Eremobates durangonus* and *Eremochelis bilobatus*, weak, faint to invisible nodular papillae on egg-chorion of *Eremobates nodularis*, moderately-spaced rounded papillae on egg-chorion of *Eremobates palpisetulosus*, distinct series of fine nodular papillae egg-chorion of *Eremorhax magnus*. In light of this information, Erdek & Yiğit Kayhan (2016) claimed that the morphological characteristics of the eggs, pre-depositional, and incubation periods reveal some differences and similarities of ootaxonomic significance for different Solifugae families.

The lateral organ is a foot-shaped protuberance at the sides of body located near the 1st pair of legs with its tip folded in the shape of a toe at the distal end. Roewer (1934) remarked that the shape and size of the lateral organ are different in *Galeodes*. Lawrence (1947) described the lateral organ of *Solpuga hostilis* as an aggregate of chitinous granules surrounding an oval depression, Junqua (1966) described it as slipper-shaped in *Othoes saharae*, and Thaler (1982) observed the lateral organ as a small cuticular protrusion in *Gylippus cyprioticus*. Punzo (1998) claimed that lateral organ exists in the first nymphal instar but in some others disappears before the first post-embryo stage. Although the lateral organ function is not exactly known, Heymons (1904) suggested that it functions as an accessory respiratory organ until the formation of the tracheal system is completed and Lawrence (1947) asserted that the lateral organ may be used for breaking the egg chorion. There is no evidence of a respiratory function, because spiracular opening- like structures couldn't be observed.

There is a nipple-like protrusion at the tip of the dorsal fixed cheliceral finger. Muma (1966a) also observed this structure on *Eremobates durangonus* and described it as a spine-like egg burster used in rupturing the egg chorion. In this study, in addition to this hypothesis, we suggest that it may act as the first laceration point in the chelicerae during molting. The type of basiconic sensilla (*Sensilla basiconica*) is non-socketed, with pores at the terminal end and surface on the dorsal side of the opisthosoma, and as chemoreceptors or in hygroreception and thermoreception used for detecting climatic conditions. Thaler (1982) observed the sensilla also on the dorsal side of the prosoma on *Gylippus cyprioticus*, but there are no prosomal sensilla on the post-embryo of *Galeodes hakkariensis*. The other type of basiconic sensil-

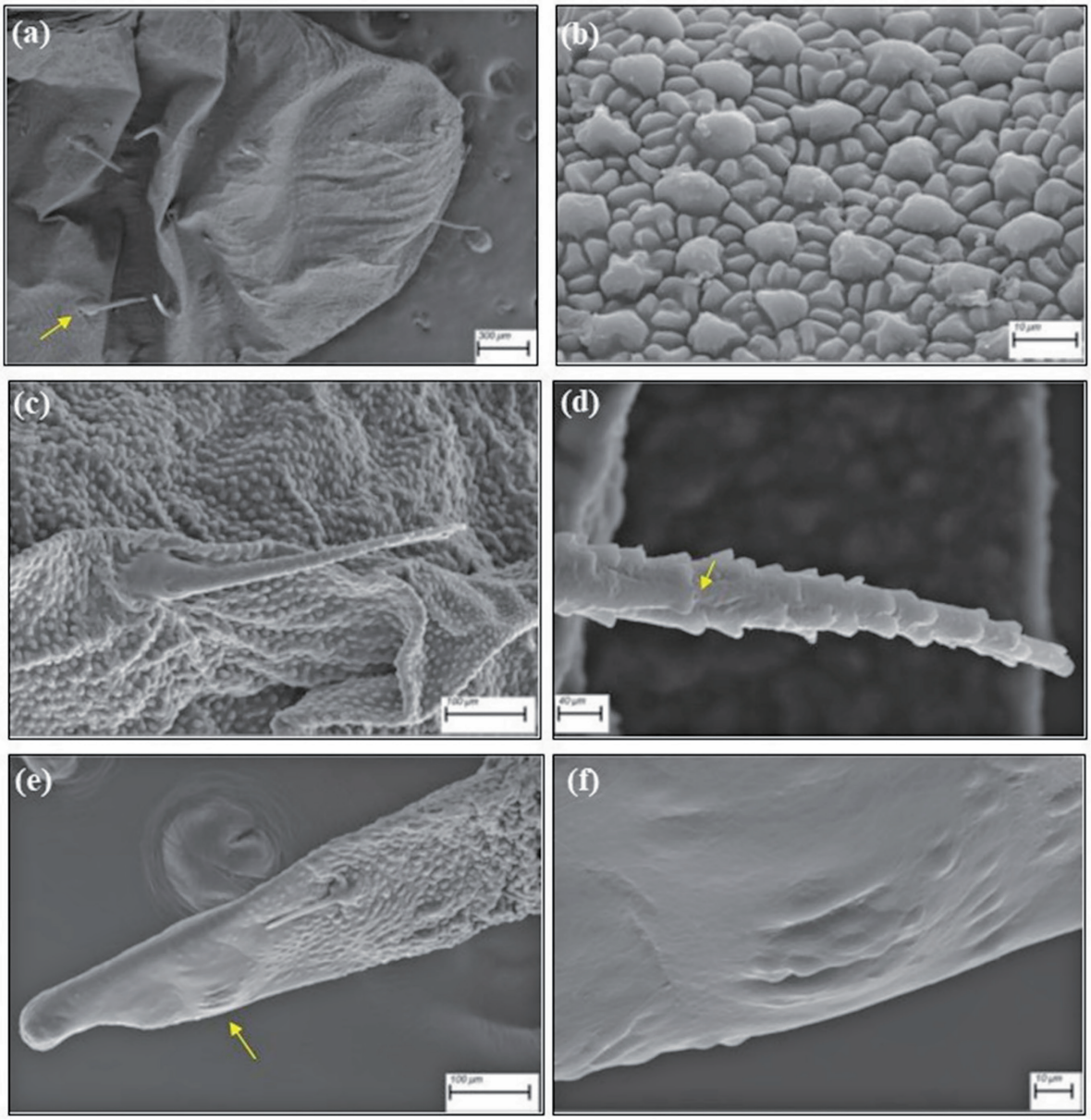


Fig. 5. Scanning electron micrographs of 4-day-old post-embryo. (a). dorsal side of the opisthosoma, arrow shows the dorsal seta on opisthosoma; (b), the cuticular pattern of the opisthosoma; (c), detail of opisthosomal seta; (d), the surface of opisthosomal seta in detail, arrow shows setal pore; (e), tarsal tip part of embryonic pedipalp, arrow shows single slit sensillum; (f), single slit sensillum in detail. Scales = 300 µm (a); 100 µm (c), (e); 40 µm (d); 10 µm (b), (f).

la, located on pedipalp tarsus, is also non-socketed, has an aporous surface, and may function as a mechanoreceptor. There is no observed active movement of the post-embryos. Muma (1966b) described the movement of post-embryos as spasmodic and clumsy associated with long periods of quiescence. The observations within the scope of this study suggest that this first movement are the involuntary twitches that allow exit of the post-embryo emerging from the egg.

The single slit sensillum is apparent on the tarsus of the embryonic pedipalp. Barth & Stagl (1976) examined the slit sense organs on the legs of different arachnid orders; Amblypygi, Araneae, Opiliones, Scorpiones, and Uropygi. Although the isolated slit sensillum is defined as the slit sensillum smaller than 30 µm, the isolated single slit sensillum on the tarsus of the embryonic pedipalp is 34.14 µm. The slit sensilla are the most numerous on the legs (McIver 1975). Bird & Wharton (2015) demonstrated the telotarsus of the first leg of *Melanoblossia ansie* and Erdek & Gharakhloo (2019) demonstrated the slit sensillum on the malleolar stalk of *Rhagodes eylandti*. It was also observed on the metatarsi of pedipalps of gylippids and karschiids (author, pers. obs.). Barth (1985) and Foelix (2011) said that the slit sensilla are specific stress (strain) receptors, providing awareness of mechanical events occurring within cuticles in arachnids.

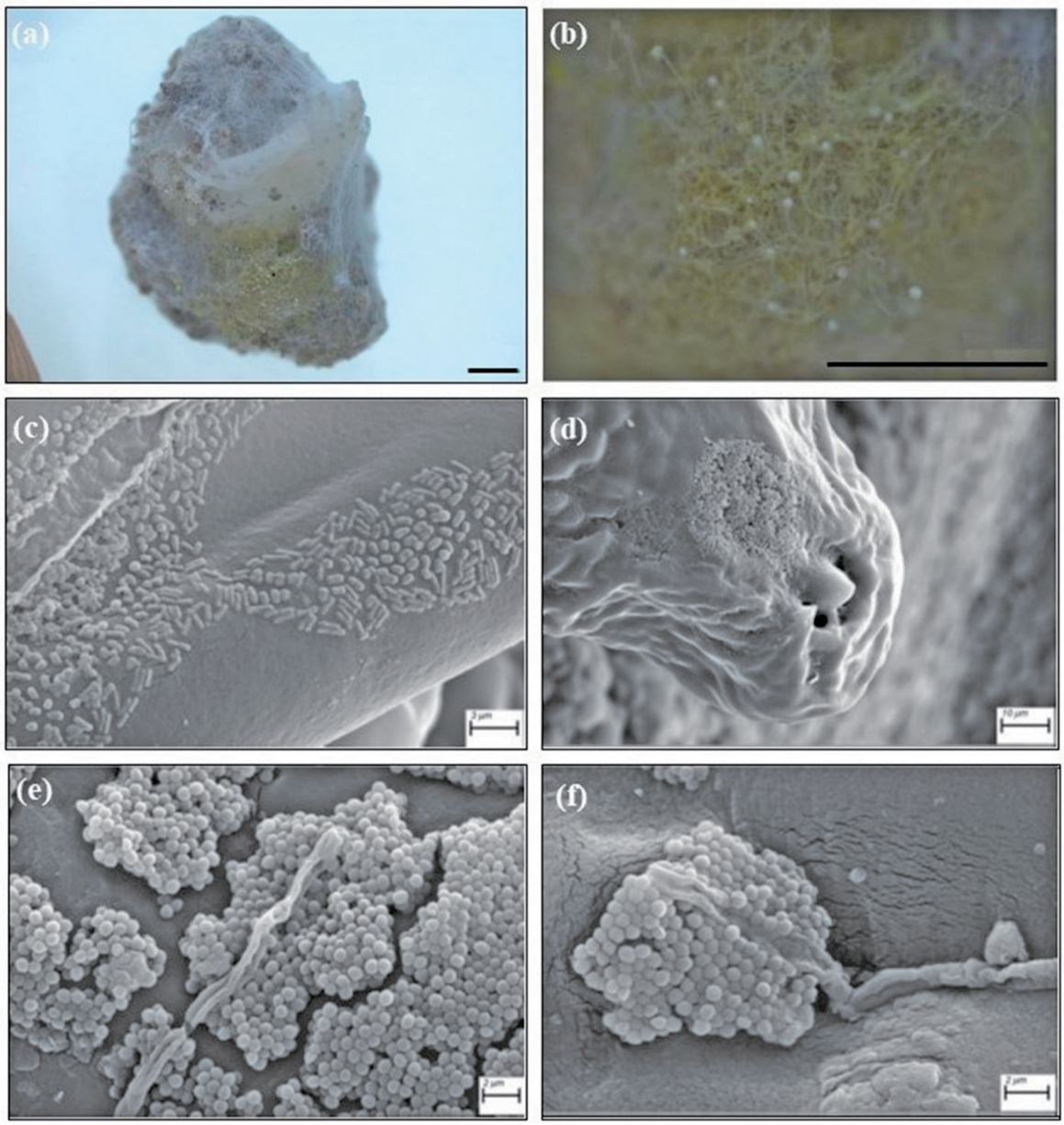


Fig. 6. Molds/fungi infecting the embryos. (a), the general view of embryo infected with microorganisms; (b), close-up the surface of the infected embryo; (c), bacilli and coccobacilli form on the external egg covering; (d), molds on the tip of the chelicerae; (e)–(f), spores and hyphae of the fungus, close up the surface of chelicera. Scales = 1 mm (a)–(b); 10 µm (d); 3 µm (c); 2 µm (e)–(f).

Funding

This study was supported by the Scientific Research Projects Coordination Unit of Hakkari University, Turkey (Project No: FM19BAP3).

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Received June 8, 2022 / Accepted August 30, 2022