STUDIA UNIVERSITATIS BABEŞ-BOLYAI BIOLOGIA, 67, 1, 2022 (p. 49-62)
doi:10.24193/subbbiol.2022.1.03

Cuticle structure of Carpathian endemic species: *Trachelipus trilobatus* (Crustacea, Isopoda, Oniscidea) described with the scanning electron microscope

Diana Cupșa[1], Traian-Octavian Costea[2], Alfred-Ștefan Cicort-Lucaciu[1],
Severus-Daniel Covaciu-Marcov[1] and Sára Ferenți[2]✉

[1]University of Oradea, Faculty of Informatics and Sciences, Department of Biology, Oradea, Romania; [2]University of Oradea, Nanoscience Research Platform – SMARTMAT, Oradea, Romania;
✉***Corresponding author, E-mail: ferenti.sara@gmail.com***

Article history: Received: 15 February 2022; Revised: 24 April 2022;
Accepted: 23 May 2022; Available online: 30 June 2022.

Abstract. The cuticle is the interface between an animal and its environment; thus, it has a special importance. In Arthropods, the cuticle is not uniform, having numerous formations, which is also the case of epigeic terrestrial isopods. Our study presents data on cuticle surface morphology, obtained with a scanning electron microscope, of an endemic terrestrial isopod species, *Trachelipus trilobatus*. Here we present SEM images of some external morphological features of this species, which were previously described only at the light microscope. Although *T. trilobatus* was frequently encountered in caves, the aspect of its cuticle is characteristic for an epigeic isopod, presenting numerous micro-scales, spines, and tricorn sensilla, which are considered hygroreceptors. This fact proves that originally *T. trilobatus* is an epigeic species, which secondarily adapted to karst areas with caves. Nevertheless, it regularly leaves the caves and the limestone cracks and emerges on the soil surface. Therefore, *T. trilobatus* is able to receive information about environmental humidity, especially on the soil surface, which, when unfavorable, causes the species retreat into caves or cracks. Climatic fluctuations from the glacial periods could direct *T. trilobatus* to this environment and way of life, modifying its morphology, but not its cuticle.

Keywords: SEM, cuticle surface, endemic species, ecology, sensory structures.

Introduction

Many terrestrial isopod species in Romania are endemic; their percentage is much higher than in other regions in Europe, except for the Mediterranean area (Sfenthourakis and Hornung, 2018). Thus, according to a recent review, in the country, 96 terrestrial isopod species are present, and 42 of them are endemic (Giurginca, 2022). In the case of terrestrial isopods in Romania, the genus *Trachelipus* contains numerous endemic species, some even endemic to the country (Tomescu *et al.*, 2015). Among them, large sized species *T. trilobatus*, *T. ater,* and *T. vareae* have limited distribution to only some regions in the Carpathians (Tomescu *et al.*, 2015), and they are considered to have a Mediterranean aspect (Radu, 1958). The larger and the most outstanding is *T. trilobatus*, the species with the smallest distribution range, as it is present only in the region of the Herculane Spa, in south-western Romania (Tomescu *et al.*, 2015). Even in the last years, *T. trilobatus* has been mentioned in the Herculane Spa area (Pop *et al.*, 2019), although upstream from its previous records (Ferenți *et al.*, 2020). Its small distribution range should facilitate the knowledge of the species, but this is not a fact, as *T. trilobatus* is an elusive species, related to restrictive habitats, either gorges and steep limestone walls from forested areas, or caves (e.g., Tabacaru and Giurginca, 2013; Tomescu *et al.*, 2015; Pop *et al.*, 2019; Ferenți *et al.*, 2020). Thus, neither its' distribution nor its ecology, is fully understood. Recent morphological data are also scarce and presented with classic light microscopy methods (Tomescu *et al.*, 2015), although scanning electron microscope is considered an appropriate method to investigate the cuticle surface of terrestrial isopods (Hornung, 2011). Considering that SEM was often used to describe the cuticle of terrestrial isopods (Holdich and Lincoln, 1974; Schmalfuss, 1978, 2011; Ziegler and Altner, 1995; Giurginca *et al.*, 2016; Vittori and Gantar, 2020), and due to the zoogeographic and conservation importance of *T. trilobatus* (Tomescu *et al.,* 2015; Ferenți *et al.,* 2020), we proposed to study the cuticle morphology of this species with SEM. We hypothesized that SEM would offer useful information about *T. trilobatus* morphology, which could help in understanding its ecology, and its relationship with the epigeic or cavernicolous environment. Our objective was to describe in detail, for the first time, the morphological characters, and the cuticle of this species with SEM.

Materials and methods

The study with SEM was performed in the summer of the year 2021. We analyzed two *T. trilobatus* individuals from Herculane Spa, which were utilized in the previous study (Tomescu *et al.*, 2015). The studied individuals were conserved in test tubes with ethylic alcohol. The methods used in the SEM study were the same used for terrestrial isopods by other authors (Holdich and Lincoln, 1974; Schmalfuss, 1978, 1998; Meyer-Rochow, 1980; Ziegler and Altner, 1995; Csonka *et al*., 2018). Thus, the isopods were dehydrated, fixed, and then covered with a 2 nm layer of gold using the Quorum Q T150 ES Magnetron Sputtering. The Electron Microscope used is a Leo 438 VP SEM, with an acceleration voltage of 20 kV at various magnifications according to the size of the structure studied. We investigated both the cuticle external morphology, but also anatomic elements with taxonomic characters, which were previously used for determining the species (Tomescu *et al*., 2015). Thus, we tried to obtain clear images of the appendages, head, eyes, etc. Also, we investigated the structure of the cuticle and observed its structures, compared them with the data from the literature (Holdich and Lincoln, 1974; Schmalfuss, 1978; Ziegler and Altner, 1995; Giurginca *et al*., 2016; Csonka *et al*., 2018). Totally, we analyzed 234 SEM images of different body segments and cuticles of the two studied *T. trilobatus* individuals.

Results

The head, like the entire dorsal part of the isopod, is covered with numerous micro-scales and tricorn sensilla (Fig. 1). The eyes consist of 24 ommatidia, between which tricorn sensilla can be present, especially at the marginal ones (Fig. 1). The cephalic lobes are long. The length of the lateral lobes is almost half of the total distance between the lobes' tip and the posterior edge of the head. The frontal lobes' length exceeds half of the lateral lobes' length. The frontal lobe ends with a short rostrum. Even with these long cephalic lobes, the head width is larger than its length, and clearly exceeded anteriorly by the epimers of the first thoracic segment (Fig. 1).

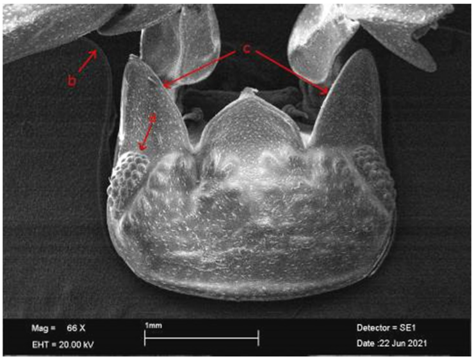

Figure 1. *T. trilobatus* head a. eyes, b. anterior margin of the first epimer, c. lateral lobes

The first antennae are situated in the space between the lateral lobes and the frontal lobe, formed by three segments, of which the last one has numerous sensilla (Fig. 2 a). The second antennae segments are covered with small micro-scales and tricorn sensilla, and the antennae flagellum presents spines (Fig. 2 b). The flagellum is shorter than the segment before and continues with the terminal organ, which has the aspect of a short extension, with slightly widened tip. The terminal organ has a smooth tip (it is the only component of the second antennae with smooth cuticle) (Fig. 2 c, d).

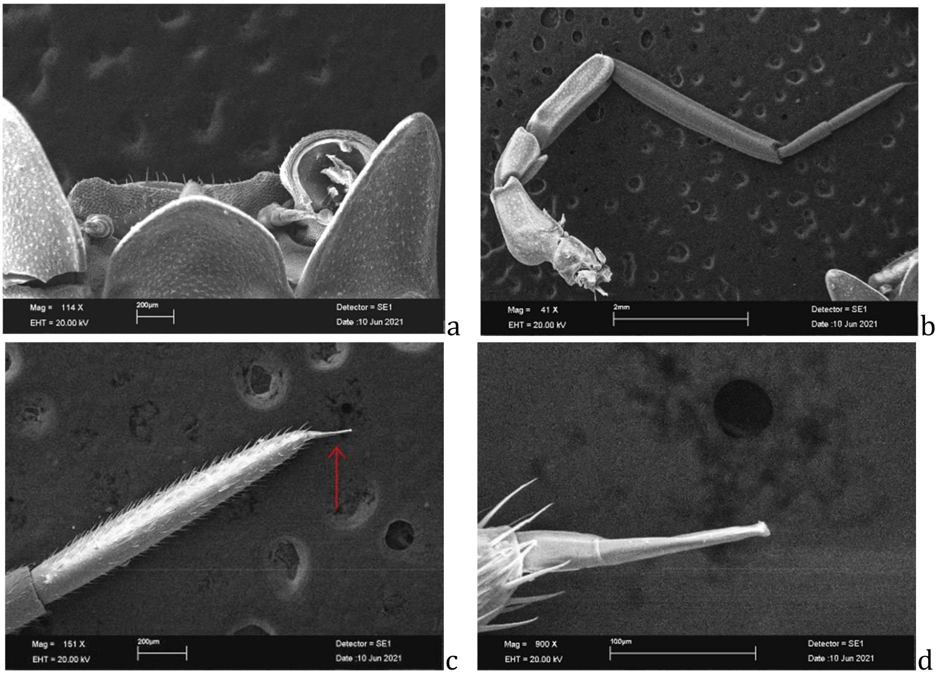

Figure 2. *T. trilobatus* a. first antennae, b. second antennae, c. second antennae tip with the terminal organ (shown by the arrow), d – terminal organ of the second antenna

On the dorsal side of the pereon *T. trilobatus* presents numerous micro-scales, which form a continuous layer (Fig. 3 a). Beside scales, numerous uniformly distributed tricorn sensilla are present on the dorsal surface of the animal (Fig. 3 a). The pleon is covered with tricorn sensilla, just as the rest of the dorsal side of the animal. The tip of some pleonal epimers can present relatively large-sized terminal setae (Fig. 3 b).

On the anterior part of the thoracic epimers, there are glandular pore fields with a regular disposition present at the edges of the epimers (Fig. 3 c).

The glandular pore fields are surrounded by micro-scales and tricorn sensilla. In many cases, the product of the glandular pore fields is also visible. Fields with numerous, supposedly glandular openings are also present on the tergal face of the pleon (Fig. 3 d).

Also on the thoracic segments the noduli laterals are present in their posterior and external part. They have the aspect of long, filiform extensions, connected with the deeper layers of the cuticle (Fig. 3 e). The noduli laterals are present on the thoracic segments 2-7 and are oriented in the caudal direction.

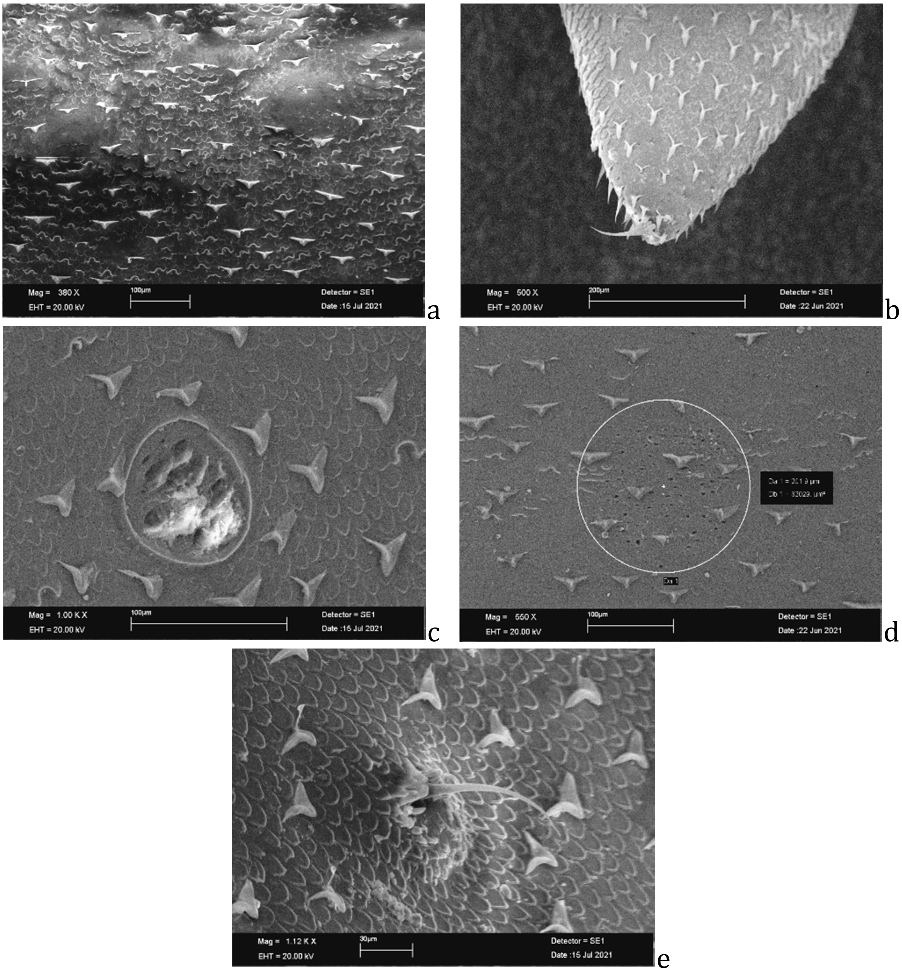

Figure 3. *T. trilobatus* a. the surface of the pereonal segments, b. the edge of a pleonal segment with terminal setae, c. glandular field on the pereonal epimers, d. surface with pores on the mediodorsal part of the pleonal segments, e. nodulus lateralis

Pereopods. In their turn, the legs are covered with micro-scales. The first legs present numerous spines on their distal segments, but also numerous micro-scales which are very evident and compact (Fig. 5 a). The surface of the legs is covered with tricorn sensilla. Unlike the first leg, the seventh leg pair does not present so many spikes on their distal segments, but the micro-scales are equally numerous (Fig. 5 b). The basis does not present numerous cuticular structures, micro-scales are present on the dorsal part, where they form a continuous layer, partially covering one another, and a few tricorn sensilla and thin setae on the rest of the segment. The ischium presents on its ventral part a field with numerous triangular scales, and four very well-developed setae (Fig. 5 c). On the merus, carpus, and propodus the setae are mostly situated dorsally, while the tricorn sensilla are more evenly distributed (Fig. 5 d, e, f, g). The dactyl has some simple elongated scales on its external part, and a few well-developed setae (Fig. 5 h).

Cuticular structures are also present on the pleopods, mostly on the margin as simple setae, the first endopod has mostly a smooth surface, and the first male exopodite presents some tricorn sensilla (Fig. 6 a, b, c).

On the telson the distribution of tricorn sensilla is similar to the one observed on the dorsal part of the body, uropods end with a filiform structure (Fig. 6 d).

Discussion

Differences in the cuticular structures could be explained by the differences in ecology and behavior of different terrestrial isopod species (Schmalfuss, 1978). Thus, description of cuticle structures could help in understanding the ecology of *T. trilobatus*, an endemic species with a very small distribution range (e.g., Tomescu *et al*., 2015; Ferenți *et al*., 2020). The structures present on the surface of the antenna of *T. trilobatus* are similar to the ones that are present on the antenna of other terrestrial isopod species (e.g., Khisametdinova and Schmalfuss, 2012). This resemblance is even higher in comparison with other species of *Trachelipus* genus, including the terminal organ at the tip of the second antenna (Schmalfuss and Khisametdinova, 2015). In the case of terrestrial isopods, the second antenna is considered the most important sensory organ (Schmalfuss, 1998), thus it is expectable to have a similar structure within the same genus.

Micro-scales are common elements in the cuticle of terrestrial isopods (Holdich and Lincoln, 1974; Schmalfuss, 1978; Price and Holdich, 1980; Wood *et al*., 2017; Štrus *et al*., 2019), thus their abundance in this species is not surprising. Tricorn sensilla are numerous and uniformly distributed on the dorsal

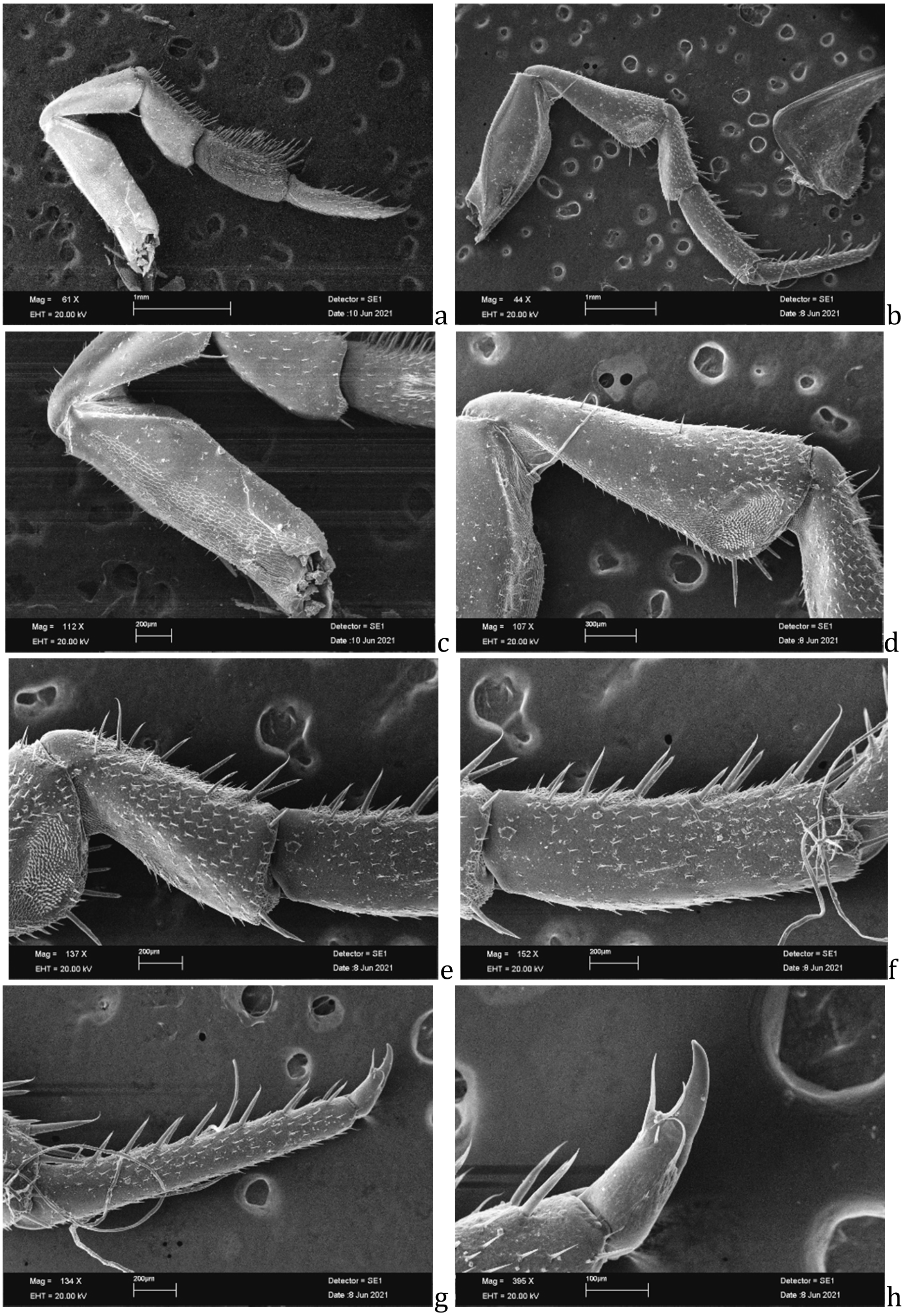

Figure 5. *T. trilobatus* a. first pereiopod, b. 7th pereiopod, and its segments: c. basis, d. ischium, e. merus, f. carpus, g. propodus, h. dactyl

side of *T. trilobatus*. These structures are present in terrestrial isopods (e.g., Holdich and Lincoln, 1974; Price and Holdich, 1980; Hatanaka, 1989; Csonka *et al*., 2018; Štrus *et al*., 2019; Seidl *et al*., 2021), but they lack in aquatic isopods (e.g., Schmalfuss, 1978; Powell and Halcrow, 1982). They were assigned the role of hygroreceptors (Price and Holdich, 1980), although there are uncertainties about their exact function (Hatanaka, 1989; Ziegler and Altner, 1995). The high number of these cuticular formations indicated that *T. trilobatus*, at least in one phase during its past, evolved in environments in which the level of humidity changed rapidly.

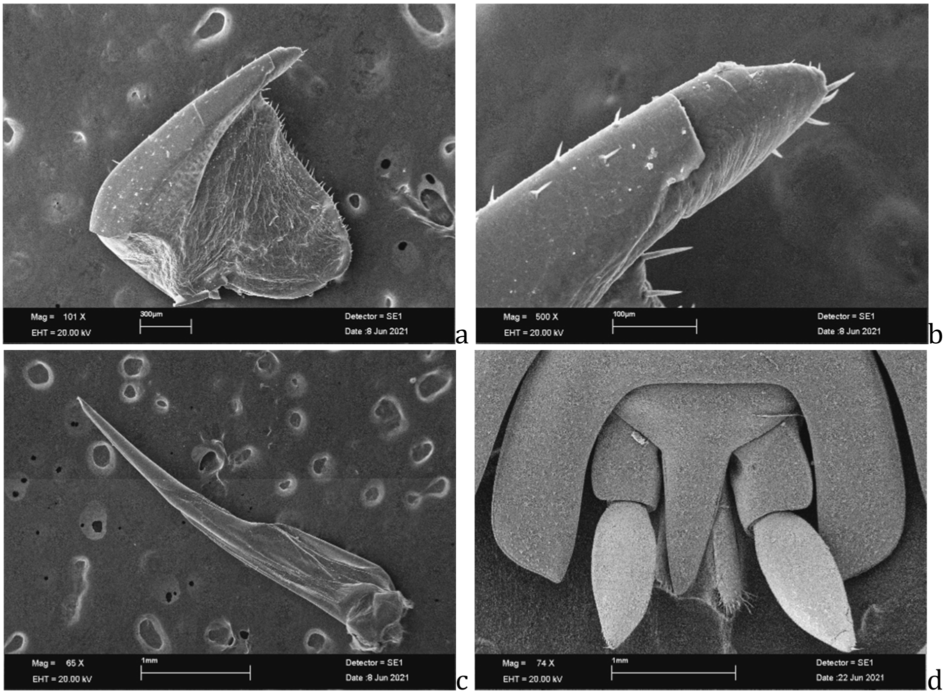

Figure 6. *T. trilobatus* a. first male exopod and b. the exopod's tip, c. first male endopod, d. telson and uropods

Thus, for the species, it was very important to react quickly to those changes in order to avoid dehydration. It seems that in the case of isopods the water loss occurs passively, and the larger size reduces this loss (Dias *et al*., 2012), and *T. trilobatus* is a larger species (Radu, 1985; Tomescu *et al*., 2015). This fact probably indicates that initially, *T. trilobatus* was an epigeic animal, because in the case of epigeic terrestrial isopods this type of sensilla are numerous (Holdich and Lincoln, 1974; Price and Holdich, 1980; Csonka *et al*., 2018; Štrus *et al.*, 2019; Seidl *et al.*, 2021). Thus, although *T. trilobatus* was frequently identified in caves (Tabacaru and Giurginca, 2013; Tomescu *et al.*, 2015), and was even considered by some authors as a troglobitic species (Boitan and Negrea, 2001), it was probably initially epigeic.

Probably even nowadays *T. trilobatus* moves between the numerous limestone cracks and caves from Herculane Spa and the soil surface, where it can be detected only sometimes and in certain habitat types (Tabacaru and Giurginca, 2013; Tomescu *et al.*, 2015; Pop *et al.*, 2019; Ferenți *et al.*, 2020). It is known that many terrestrial isopod species migrate due to fluctuations in environmental factors (Warburg *et al.*, 1984). Therefore, this species' annual cycle should be studied in its surface habitats. Also, from the biogeographic point of view, remains to be seen what determined the species to retreat in the limestone areas in which it has contact with the underground environment. Probably in the glacial periods, once the weather cooled, *T. trilobatus* was "lucky enough" and found the possibility to avoid the effects of climate cooling. Probably, *T. trilobatus* exits and enters the caves and cracks depending on the surface hydric regime. Thus, in the dry and cold periods, the species descends in caves or cracks because it has numerous tricorn sensilla which detect the decrease of humidity. This assumption is sustained by the complete absence of tricorn sensilla in the case of *Mesoniscus graniger* (Giurginca *et al.*, 2016), which is a species usually present in caves and rarely endogeic (e.g., Tabacaru and Giurginca, 2013; Giurginca, 2000-2001, 2009; Ferenți and Covaciu-Marcov, 2018; Pop *et al.*, 2021). Thus, in those extremely and constantly humid conditions, it does not need tricorn sensilla (Giurginca e*t al.*, 2016). The presence of numerous tricorns in *T. trilobatus* indicates that this is an epigeic species. The climate conditions had a great impact on the species. This impact was particularized by the peculiarities of the Herculane Spa region, which because of the karst (e.g., Povară and Conovici, 2013; Ponta *et al.*, 2013; Povară *et al.*, 2015) offered access and shelter in caves and cracks to this species.

At the same time, it seems that in the case of the genus *Trachelipus*, there is a high cuticle uniformity, as in the congeneric species *T. rathkii*, the cuticle morphology is very similar, with numerous micro-scales and tricorn sensilla (Csonka *et al.*, 2018). The uniformity of the cuticle in the case of the genus *Trachelipus* indicates a high morphological conservatism at this level, despite the obvious morphological differences between the two species (Tomescu *et al.*, 2015). At the same time, the two species are present in very different habitats, as *T. rathkii* is considered a eurytopic species (Tomescu *et al.*, 2015). However, also in this case the humidity is the connecting factor, hence the function of tricorn sensilla as hygroreceptors (Price and Holdich, 1980). Thus, in different environments, with different humidity, the existence of a high number of hygroreceptors is very important, and *T. rathkii* was identified starting in the vicinity of thermal waters (Ferenți *et al*., 2013), going in urban areas (e.g., Vilisics and Hornung, 2009; Giurginca *et al*., 2017) and reaching even to Siberia (Khisametdinova *et al*., 2016) and Finland (Vilisics and Terhivuo, 2009). Unlike this, *T. trilobatus* is related to restrictive habitats (Tomescu *et al*., 2015; Pop *et al*., 2019; Ferenți *et al*., 2020) but nevertheless, it has equally numerous tricorn sensilla.

The surface structures and the cuticle formations of terrestrial isopods are considered to have an anti-adhesive function (e.g., Schmalfuss, 1977, 1978; Powell and Halcrow, 1982; Wood *et al*., 2017). This function is maintained also in the case of a cave species, like *Mesoniscus graniger* (Giurginca *et al*., 2016). Probably those structures have the same function also in the case of *T. trilobatus*, moreover because this species shelters under stones in wet areas, where soil particles could easily adhere to the animals' surface. The large surface and the wide aspect of this isopod (Radu, 1985; Tomescu *et al*., 2015) offer a larger contact surface for different soil particles, thus *T. trilobatus* needs numerous anti-adhesive structures.

Noduli laterals, considered sensilla (Schmidt, 2002, 2008) are situated in the lateral edge of the thoracic segments 2-7, and probably had a tactile function. In the case of other species, such sensilla were considered to be gauge sensors (Jans and Ross, 1963; Holdich and Lincoln, 1974). Thus, they can be extremely useful for a species that shelters in limestone cracks, caves, or under stones. At most, the location of this sensilla is curious, as they are situated on the posterior part of the segments, and lack from the first thoracic segment. It seems that *T. trilobatus* is an exception in its genus, having the noduli laterals situated posterior to the glandular fields, a fact considered related to the life in caves and very wet habitats (Radu and Tomescu, 1970). Probably in that position, they are more useful, and the pressure exercised upon them informs the animal to stop advancing in limestone cracks, if they are too tight. At the same time, in the cephalic region, there are receptors at the level of the terminal organ of the antenna. This is probably an adaptation to a way of life in which the animal shelters in very narrow spaces.

The SEM analysis revealed morphological aspects which now are much clearer than in the previous studies realized with classic light microscopy (Tomescu *et al*., 2015). It is the case of the genital parts, which now could be observed distinctly, or the case of the appendages, in which the dactylus is extremely similar to the one recently described in another terrestrial isopod species (Vittori, 2021). This highlights the utility of SEM in helping to understand the adaptations and the way of life of *T. trilobatus*, an endemic species with a very small distribution range (Tomescu *et al*., 2015; Ferenți *et al*., 2020). Thus, studies on species from different environments are necessary, and also studies on other endemic species, as most previous studies aimed a common species such as *Porcellio scaber* (Holdich and Lincoln, 1974; Ziegler and Altner, 1995; Csonka *et al*., 2018; Vittori, 2021).

References

Boitan, V., & Negrea, Ș. (2001). Contribution to the knowledge of the terrestrial cavernicolous fauna from the middle Cerna valley (Banat, Romania). *Trav. Mus. Natl. Hist. Nat. Grigore Antipa*, *43,* 11-22.

Csonka, D., Halasy, K., Buczkó, K., & Hornung, E. (2018). Morphological traits - desiccation resistance - habitat characteristics: a possible key for distribution in woodlice (Isopoda, Oniscidea). *ZooKeys, 801,* 481-499.

Dias, A.T.C., Krab, E.J., Mariën, J., Zimmer, M., Cornelissen, J.H.C., Ellers, J., Wardle, D.A., & Berg, M.P. (2012). Traits underpinning desiccation resistance explain distribution patterns of terrestrial isopods. *Oecologia, 172,* 3, 667-677.

Ferenți, S., & Covaciu-Marcov, S.-D. (2018). Beyond the rule: a mountainous cave species, *Mesoniscus graniger* (Isopoda, Oniscidea) on a plain of south-western Romania. *Oltenia. Studii și Comunicări. Științele Naturii, 34,* 1, 89-92.

Ferenți, S., Cupșa, D., Cicort-Lucaciu, A.-Ș., & Covaciu-Marcov, S.-D. (2013). Winter activity of terrestrial isopods from thermal habitats in western Romania. *Arch. Biol. Sci., 65,* 2, 795-800.

Ferenți, S., Cadar, A.-M., & Maier, A.-R.-M. (2020). New distribution records of an endemic terrestrial isopod species (*Trachelipus trilobatus*) in the Romanian Southern Carpathians. *Ecologia Balkanica, 12,* 2, 207-211.

Giurginca, A. (2000-2001). The spreading of the genus *Mesoniscus* in the Romanian Carpathians. *Trav. Inst. Speol. Émile Racovitza, 39-40,* 11-22.

Giurginca, A. (2009). Aspects concerning the genus *Mesoniscus*: morphology, spreading, historical biogeography. Ed. *Politehnica Press* Bucharest, pp. 128.

Giurginca, A. (2022). Oniscidea of Romania. Ed. *Transversal Press* Târgoviște, pp. 240.

Giurginca, A., Šustr, V., & Tajovský, K. (2016). Morphological structures on the integument of *Mesoniscus graniger*. *Trav. Inst. Speol. Émile Racovitza, 55,* 129-133.

Giurginca, A., Baba, Ș.-C., & Munteanu, C.-M. (2017). New data on the Oniscidea, Diplopoda and Chilopoda from urban parks of Bucharest. *North-West. J. Zool., 13,* 2, 234-243.

Hatanaka, T. (1989). Response of dorsal tricorn-type sensilla on *Ligia exotica*. *Comp. Biochem. Physiol., 92A,* 4, 513-319.

Holdich, D.M., & Lincoln, R.G. (1974). An investigation of the surface of the cuticle and associated sensory structures of the terrestrial isopod, *Porcellio scaber*. *J. Zool., 172,* 469-482.

Hornung, E. (2011). Evolutionary adaptation of oniscidean isopods to terrestrial life: Structure, physiology and behavior. *Terr. Arthropod Rev., 4,* 95-130.

Jans, D.E., & Ross, K.F.A. (1963). A histological study of the peripheral receptors in the thorax of land isopods, with special reference to the location of possible hygroreceptors. *Q. J. Microsc., 104,* 3, 337-350.

Khisametdinova, D., & Schmalfuss, H. (2012). Three new species of *Porcellium* (Isopoda, Oniscidea) from the Caucasus region. *Stuttg. Beitr. Naturkd. A., 5,* 103-113.

Khisametdinova, D., Nefediev, P.S., & Tuf, I.H. (2016). New records of woodlice in the south of western Siberia, Russia (Isopoda: Oniscidea). *Zool. Bespozvon., 13,* 1, 51-55.

Meyer-Rochow, V.B. (1980). Cuticular surface structures in *Glyptonotus antarcticus* - a marine isopod from the Ross Sea (Antarctica). *Zoomorphologie, 94,* 209-216.

Ponta, G., Povară, I., Isverceanu, E.G., Onac, B.P., Marin, C., & Tudorache, A. (2013). Geology and dynamics of underground waters in Cerna Valley/Băile Herculane (Romania). *Carbonates Evaporites, 28,* 31-39.

Pop, D.-R., Dordea, D.-N., Cicort-Lucaciu, A.-Ș., Covaciu-Marcov, S.-D., & Ferenți, S. (2019). A hot-spot of native terrestrial isopods in an urban area in the Carpathians, Herculane Spa: an emerging of the past into the present. *Spixiana, 42,* 2, 219-228.

Pop, D.-R., Ferenți, S., Maier, A.-R.-M., Cadar, A.-M., Covaciu-Marcov, S.-D., & Cupșa, D. (2021). A journey on the railway to nowhere: terrestrial isopod assemblages on an abandoned railway in western Romania (Crustacea, Isopoda). *Spixiana, 44,* 2, 135-143.

Povară, I., & Conovici, M. (2013). Tectono-karst depressions in the central-western area of the Mehedinți Mountains (SW Romania). *Trav. Inst. Speol. Émile Racovitza, 52,* 37-49.

Povară, I., Conovici, M., Munteanu, C.-M., Marin, C., & Ioniță, E.D. (2015). Karst system within the Southern Carpathians structure (Romania). *Carpathian J. Earth Environ. Sci., 10,* 2, 5-17.

Powell, C.V.L., & Halcrow, K. (1982). The surface microstructure of marine and terrestrial isopoda (Crustacea, Peracarida). *Zoomorphology, 101,* 151-164.

Price, J.B., & Holdich, D.M. (1980). The formation of the epicuticle and associated structures in *Oniscus asellus* (Crustacea, Isopoda). *Zoomorphologie, 94,* 321-332.

Radu, V.G. (1958). Genul Tracheoniscus în Fauna R.P.R. *Comunicările Academiei Republicii Populare Române, 8,* 1, 53-59. [in Romanian].

Radu, V.G. (1985). Fauna R. S. R. Crustacea. vol. IV, Fascicola 14 Ordinul Isopoda, Subordinul Oniscoidea, Crinochaeta. Editura *Academiei R. S. R.* Bucharest, pp. 158. [in Romanian].

Radu, V.G., & Tomescu, N. (1970). Analiza comparativă a dispoziției nodulilor laterali și a câmpurilor glandulare epimerale la speciile genului *Tracheoniscus* din România. *Studia Univ. Babeș-Bolyai, Biologia, 1,* 83-91. [in Romanian].

Schmalfuss, H. (1977). Morphologie und funktion der targalen längsrippen bei landisopoden (Oniscoidea, Isopoda, Crustacea). *Zoomorphologie, 86,* 155-167.

Schmalfuss, H. (1978). Morphology and function of cuticular micro-scales and corresponding structures in terrestrial isopods (Crust., Isop., Oniscoidea). *Zoomorphologie, 91,* 263-274.

Schmalfuss, H. (1998). Evolutionary strategies of the antennae in terrestrial isopods. *J. Crustac. Biol., 18,* 1, 10-24.

Schmalfuss, H. (2011). The terrestrial isopods (Isopoda: Oniscidea) of Greece, 27th contribution. The genus *Armadillidium* (Armadillidiidae) on the Ionian Islands. *Stuttg. Beitr. Naturkd. A., 4,* 1-42.

Schmalfuss, H., & Khisametdinova, D. (2015). *Trachelipus* species (Isopoda: Oniscidea) of the eastern Black Sea coast. *Stuttg. Beitr. Naturkd. A., 8,* 9-20.

Schmidt, C. (2002). Contribution to the phylogenetic system of the Crinocheta (Crustacea, Isopoda). Part 1. (Olibrinidae to Scyphacidae s. str.). *Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologische Reihe, 78,* 2, 275-352.

Schmidt, C. (2008). Phylogeny of the terrestrial isopods (Oniscidea): a review. *Arthropod Syst. Phylogeny, 66,* 2, 191-226.

Seidl, B., Reisecker, C., Neues, F., Campanaro, A., Epple, M., Hild, S., & Ziegler, A. (2021). The dorsal tergite cuticle of *Helleria brevicornis*: ultrastructure, mineral distribution, calcite microstructure and texture. *J. Struct. Biol. X, 5:* 100051. https://doi.org/10.1016/j.yjsbx.2021.100051.

Sfenthourakis, S., & Hornung, E. (2018). Isopod distribution and climate change. *ZooKeys, 801,* 25-61.

Štrus, J., Tušek-Žnidarič, M., Repnik, U., Blejec, A., & Summers, A. (2019). Microscopy of crustacean cuticle: formation of a flexible extracellular matrix in moulting sea slaters *Ligia pallasii*. *J. Mar. Biolog. Assoc., 99,* 857-865.

Tabacaru, I., & Giurginca, A. (2013). Cavernicolous Oniscidea of Romania. *Trav. Inst. Speol. Émile Racovitza, 52,* 3-26.

Tomescu, N., Teodor, L.A., Ferenți, S., & Covaciu-Marcov, S.-D. (2015). *Trachelipus* species (Crustacea, Isopoda, Oniscidea) in Romanian fauna: morphology, ecology, and geographic distribution. *North-West. J. Zool., 11,* Supplement 1, S1-S106.

Vilisics, F., & Hornung, E. (2009). Urban areas as hot-spots for introduced and shelters for native isopod species. *Urban Ecosyst., 12,* 333-345.

Vilisics, F., & Terhivuo, J. (2009). Inspection on materials contributing to the knowledge of terrestrial isopoda (Crustacea, Oniscidea) in Finland. *Memo. Soc. Fauna Flora Fenn., 85,* 9-15.

Vittori, M. (2021). Structure of a hinge joint with textured sliding surfaces in terrestrial isopods (Crustacea: Isopoda: Oniscidea). *Zoological Lett., 7,* 7. https://doi.org/10.1186/s40851-021-00177-9.

Vittori, M., & Gantar, I. (2020). The origin of microscopic spheres on the exoskeleton of the woodlouse *Porcellionides pruinosus* (Crustacea: Isopoda) and their effect on its hydrophobicity. *Arthropod Struct. Dev., 58,* 100968. https://doi.org/10.1016/j.asd.2020.100968.

Warburg, M.R., Lisenmair, K.E., & Bercovitz, K. (1984). The effect of climate in the distribution and abundance of isopods. *Symposia of the Zoological Society of London, 53,* 339-367.

Wood, C.T., Kostanjšek, R., Araujo, P.B., & Štrus, J. (2017). Morphology, microhabitat selection and life history traits of two sympatric woodlice (Crustacea: Isopoda: Oniscidea): a comparatice analysis. *Zool. Anz., 268,* 1-10.

Ziegler, A., & Altner, H. (1995). Are the most numerous sensilla of terrestrial isopods hydroreceptors? Ultrastructure of the dorsal tricorn sensilla of *Porcellio scaber*? *Cell Tissue Res., 282,* 135-145.