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# When opposites attract: a syninclusion of extinct mites and a bradytelic bristly millipede in Baltic amber

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**Abstract**

Amber resin is known for its exceptional preservations thanks to quick encapsulation of animals and plant material. Fast encapsulation not only helps preserve detailed organisms, but it also offers a glimpse into "frozen behaviors" from up to hundreds of million years, which provide information into the configuration of past ecosystems. We here investigated a syninclusion preserved in Baltic amber (~40 mya) consisting of a fossilized bristly millipede and two mite specimens, located in close proximity to the millipede's ventral side. The two mites are representatives of *Glaesacarus rhombeus*, a frequently reported species of mite in Eocene amber whose lineage is considered to be now extinct. The bristly millipede is a female adult identified as a representative of *Polyxenus*. The specimen exhibits remarkable morphological similarities to the extant species *Polyxenus lagurus*, indicating the possibility of *P. lagurus* thriving since the Eocene. The striking persistence of morphological traits over millions of years suggests a stable ecological niche and effective adaptive strategies in *Polyxenus*. This unexpected association sheds new light on the ecosystem of Eocene forests and the potential effectiveness of defensive mechanisms, already present at that time, since one of the two mites is touching and seemingly surrounded by the posterior defensive setae of the millipede. Together, these findings enhance our understanding of the life of fossil Polyxenida and the evolutionary stability of *Polyxenus*, highlighting their long-term evolutionary resilience and success.

**Keywords** Polyxenidae, Acari, *Glaesacarus rhombeus*, Eocene, Symbiosis, Frozen behavior

## Introduction

Fossiliferous resin, commonly known as amber resin, is a unique material that offers the opportunity to observe organisms from deep time (Penney, 2010; Veltz et al., 2013) as well as the traces of resin-producing-trees (Klages et al., 2024; Langenheim, 1969). Although amber resins have been found all over the world, certain periods are better represented than others (Seyfullah et al., 2018; e.g., mass resin interval, Delclòs et al., 2023). In human societies, fossil resins have a strong cultural component: traded as jewellery, material of faith (e.g. tears of the god Apollo), paintings or medicine. Over time, studies started to investigate the fossil inclusions, with an increase of studies in the nineteenth century. The historical book of Berendt (1854) was, and still is, the reference on fossils preserved in Baltic amber (Eocene Epoch, ~40 mya).

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Nowadays the oldest fossil resin has been dated to be from ~ 320 mya (Bray & Anderson, 2009), but the oldest amber with recorded inclusions is found in Italy, the age of which has been estimated to be ~ 230 million years ago (Schmidt et al., 2012).

Usually, preserved specimens in amber are in remarkable condition with a high amount of observable details, allowing studies on new species of animals (Haug et al., 2024), plants (Feldberg et al., 2021; Moreau et al., 2017), and fungi (Halbwachs, 2019). Amber also provides a window into past ecology of organisms, revealing the life of euarthropodans and even deep-time interactions (Arillo, 2007; Kiesmüller et al., 2022; Tihelka et al., 2021). The latter example is known as "frozen behavior". Frozen behavior is considered to be an exceptional type of preservation that improves our understanding of past ecosystems and communities (Arillo, 2007).

Despite the commonness of amber and fossil inclusions, a certain bias is underlying regarding fossilized euarthropodans. The likelihood of becoming entrapped in tree resin, which later becomes amber, is influenced by the lifestyle of organisms. Indeed, the lifestyle of encapsulated euarthropodans is often associated with a specific habitat: tree bark surface (Solórzano-Kraemer et al., 2015, 2018). The millipede group Polyxenida, known as "bristly millipedes" or "bark-dwelling millipedes", certainly fits in that aspect.

Polyxenids are small-sized millipedes of up to 6 mm in length. They are ubiquitous in the world and are often found in and on tree bark (Manton, 1957). They differ from all other millipedes by not using chemical defence, but by relying on modified sets of setae usually referred to "trichomes". These setae can detach when it is attacked, and due to the serrated structure of the setae, predators can get entangled when trying to clean them off (Eisner et al., 1996).

Fossils of bristly millipedes have been reported from all over the world (Dominican amber, Santiago-Blay & Poinar, 1992; Penney & Green, 2011; Chiapas amber, Álvarez-Rodríguez et al., 2024; Baltic amber, Haug et al., 2018; Canadian amber, Le Cadre et al. in review; Myanmar amber, Rasnitsyn & Golovatch, 2004; Wesener & Moritz, 2018; Lebanese amber, Nguyen Duy-Jacquemin & Azar, 2004). In Baltic amber, bristly millipedes are relatively common, with most reports dating back to the mid-nineteenth century with five described extinct species (Koch & Berendt, 1854). Even though they are common in amber, little is known concerning their past life, but it is expected that they lived the same way as extant representatives.

We hereby report a new fossil specimen of *Polyxenus* from Baltic amber and compare it to collected specimens of the extant species *Polyxenus lagurus* Linnaeus, 1758, from which it is surprisingly indistinguishable. We discuss the possible implication and interpretation of such discovery in the light of bradytely. Additionally, on the ventral side of the terminal end of the bristly millipede, the specimen is surrounded by two representatives of the astigmatan mite ingroup Glaesacaridae. We discuss the origin of their common encapsulation in resin and the possibility of an interaction between these specimens.

## Material and methods

### Fossil material

The amber piece investigated is from the Senckenberg Forschungsinstitut und Naturmuseum (SMF), Frankfurt-am-Main (Germany) managed by Monica Solórzano-Kraemer and is lodged under the number SMF Be 1855. Within the amber is a complete adult female representative of Polyxenidae (SMF Be 1855a), and two mites (SMF Be 1855b/c) in close proximity to its terminal end.

### Documentation of fossil specimens

The amber was investigated with a digital microscope and additional, lateral and inaccessible characters were obtained by scanning the amber using synchrotron-radiation based x-ray computed micro-tomography (SRµCT) at DESY (Hamburg, Germany).

In order to reduce the impact of light deformation due to amber curves we used a drop of glycerol, followed by a cover-glass. Images were obtained using a Keyence VHX-6000 digital microscope, and different light-settings were used (ring, cross-polarized coaxial with/without transmitted light) at different magnification (200x–300x). Sharp images are obtained using the built-in stacking software and HDR function.

Stereoscopic images were also obtained using the tilting possibility of the microscope (− 5° to 5°). Both stereoscopic image construction and post-processing of the images has been done using the software Photoshop CS2 version 9.0 (9.0 × 211).

The SRµCT scan has been done at the Imaging Beamline P05 (Greving et al., 2014; Wilde et al., 2016), at the storage ring PETRA III (Deutsches Elektronen Synchrotron, DESY, Hamburg, Germany), operated by the Helmholtz-Zentrum Hereon. We used a photon energy of 20 keV, a sample to the detector distance of 50 mm, and an exposure time of 250 µs. A number of 3501 equally spaced projections between 0 and π have been recorded using a custom developed CMOS camera system with an effective pixel size of 0.64 µm (Lytaev et al., 2014). Tomographic reconstruction has been done by applying a transport of intensity phase retrieval approach and using the filtered back projection algorithm (FBP) implemented in a custom reconstruction pipeline (Moosmann et al., 2014) using Matlab (Math-Works) and the Astra Toolbox (Palenstijn et al., 2011; van Aarle et al., 2015, 2016).

For the processing raw projections were binned two times for further processing resulting in an effective pixel size of the reconstructed volume of 1.28 µm. For more details on the methodology see Baranov et al. (2021).

### Scanning-electron documentation of extant *Polyxenus lagurus*

We collected five specimens of *Polyxenus lagurus* on 05.11.2024 in the vegetation area close to the Zoologische Staatssammlung Munich (ZSM; 48° 09′ 50.7″ N 11° 29′ 03.4″ E). All collected specimens were stored in ~70% EtOH for further documentation. In total, we collected one adult and two subadult females, as well as two juveniles; only the adult and subadults were documented in this study.

We dehydrated the specimens in a graded acetone series (70%, 80%, 90%, 10 min. each, plus 3×100%, 20 min. each) and critical point dried them in a Polaron E3000. We then mounted the dried specimens on SEM stubs with self-adhesive carbon stickers and coated them with gold on a Polaron Sputter Coater. SEM pictures (2048×1536 px; 72 dpi; color depth 8 bit) were made with a LEO 1430VP at 20 kV.

### Terminology

The female *Polyxenus* was described following the terminology of Short et al. (2020).

For the description of mites, terminology of anatomical features and setae follow O'Connor (2009a) and Sidorchuk and Klimov (2011).

## Results

### Identity of the fossil bristly millipede

**Order Polyxenida Lucas, 1840**

**Family Polyxenidae Lucas, 1840**

**Subfamily Polyxeninae Lucas, 1840**

Remarks:

The specimen is a typical representative of Polyxeninae, in that the terminal end of the specimen has ornamental fan-like sets of dorsal setae. Additionally, the shape of the hooked setae is characteristic of Polyxeninae (comb-shaped), and the caudal bundles are relatively widely medially separated into two sets (Fig. 1B).

**Genus *Polyxenus* Latzel, 1884**

General features: *Polyxenus* can be distinguished from *Propolyxenus* by the number of transverse rows of setae on the tergites, two rows for *Polyxenus* and three rows for *Propolyxenus*, respectively (Short & Huynh, 2011). The bristly millipede here in amber SMF Be 1855 only possesses two rows of setae, indicating that it is a representative of *Polyxenus* Latzel, 1884.

***Polyxenus* aff. *lagurus* Linnaeus, 1758**

(Figures. 1A–C, 2).

*Material examined*: Adult female (SMF Be 1855a), in Baltic amber. The amber is stored in the SMF amber collection.

Description:

*General features*: Five ommatidia on each side of the head, close to the ommatidia are three trichobothria, arranged in a triangle. The closest trichobothrium to the posterior vertex is immediately adjacent to the last seta and smaller than the other two. Posterior vertex with two groups of setae, each group with 18 setae in two rows; the six most distal ones of the anterior row closely arranged. Lateral protuberances each with three setae. Approximately 25±2 ornamental setae arranged into a fan at the terminal end. Tergites with two rows of setae posteriorly connecting with rosettes of setae laterally, however that is not the case for the terminal tergite, bearing the caudal bundles.

*Measurements:* Body length of ~2.6 mm without the caudal bundles, with caudal bundles ~3.5 mm. Head measuring 310 µm, collum measuring 140 µm. Tergite width measurements from the most anterior to posterior, 300 µm, 250 µm, 260 µm, 300 µm, 300 µm, 340 µm, 325 µm, 310 µm and 155 µm. The length of the legs are as follows: 475 µm, 545 µm, 585 µm, 575 µm, 580 µm, 580 µm, 585 µm, 620 µm, 585 µm, 610 µm, 615 µm, 650 µm and 600 µm.

*Head* (Fig. 2A, E, F): Five ommatidia are located on each side of the head, with three positioned laterally. On the head are inserted two well separated tufts of 18 setae each on the posterior vertex, each group are made of an anterior row of 12 setae and posterior row of six setae. The six anterior distal setae are inserted closely to one another. A single pair of setae are present medially, posterior to the posterior vertex. Three trichobothria are located on each side of the head (not visible on the right side, as the specimen is badly preserved), and are arranged into a triangle with the small trichobothrium closely inserted to the most distal setae of the posterior vertex. The two remaining trichobothria are inserted on large cylindrical funiculi, slightly elevated from other setae insertions (Fig. 2A). The lack of details due to the preservation of both

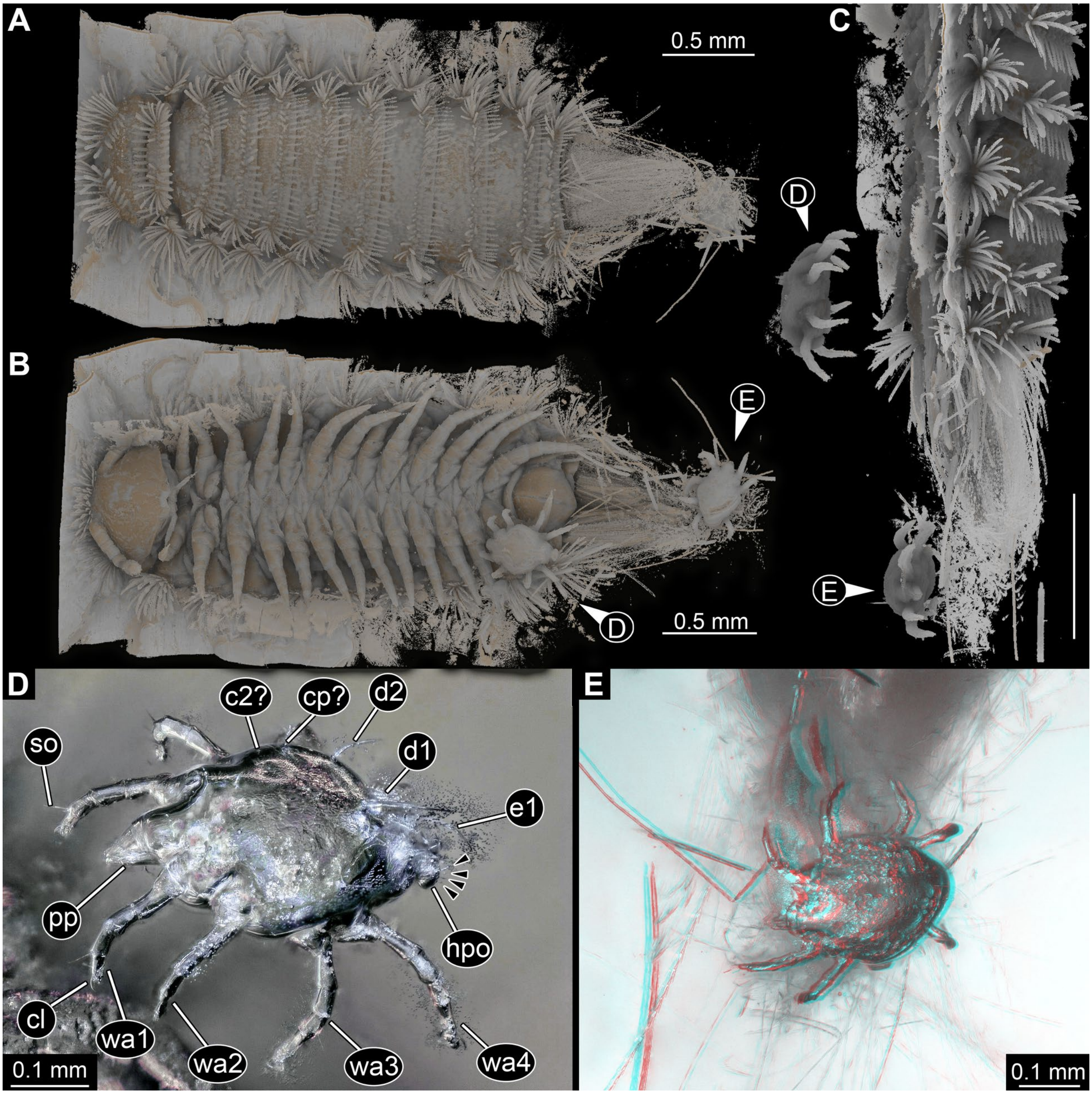

**Fig. 1** Syninclusion of two glaesacarid mites with *Polyxenus* aff. *lagurus* in the Baltic amber SMF Be 1855. **A**, **B** Dorsal and ventral views of *Polyxenus* aff. *lagurus*, rendered from the SRμ-CT scan. **C** Close lateral view of the two glaesacarid mites, next to the bristly millipede, from the rendered SRμ-CT scan. **D** Lateral view of the glaesacarid mite (SMF Be 1855b); arrows pointing to setae on hysterosomal pad-like organ. **E** 3D Stereoscopic image of the glaesacarid mite (SMF Be 1855c). Scale C = 0.5 mm. Abbreviations: c2?: possible seta *c2*; cl: tarsal claws; cp?: possible seta *cp*; d1: seta *d1*; d2: seta *d2*; e1: seta *e1*; hpo: hysterosomal pad-like organ; pp: pedipalps; so: tibial solenidion (φ); wa: walking appendage 1–4

the labrum and clypeo-labrum limit the visibility of setae and papillae. Gnathochilarium with lateral palps 160 μm long, with at least 13 sensilla. The proportions of the antennae are as follows, from proximal to distal elements: 92 μm, 45 μm, 35 μm, 60 μm, 56 μm, 78 μm, 52 μm and 16 μm (Fig. 1G). The preservation does not allow for the observation of the fine antennal sensilla. A possible single sensillum is visible on the last antennal element, but not depicted here due to uncertainty.

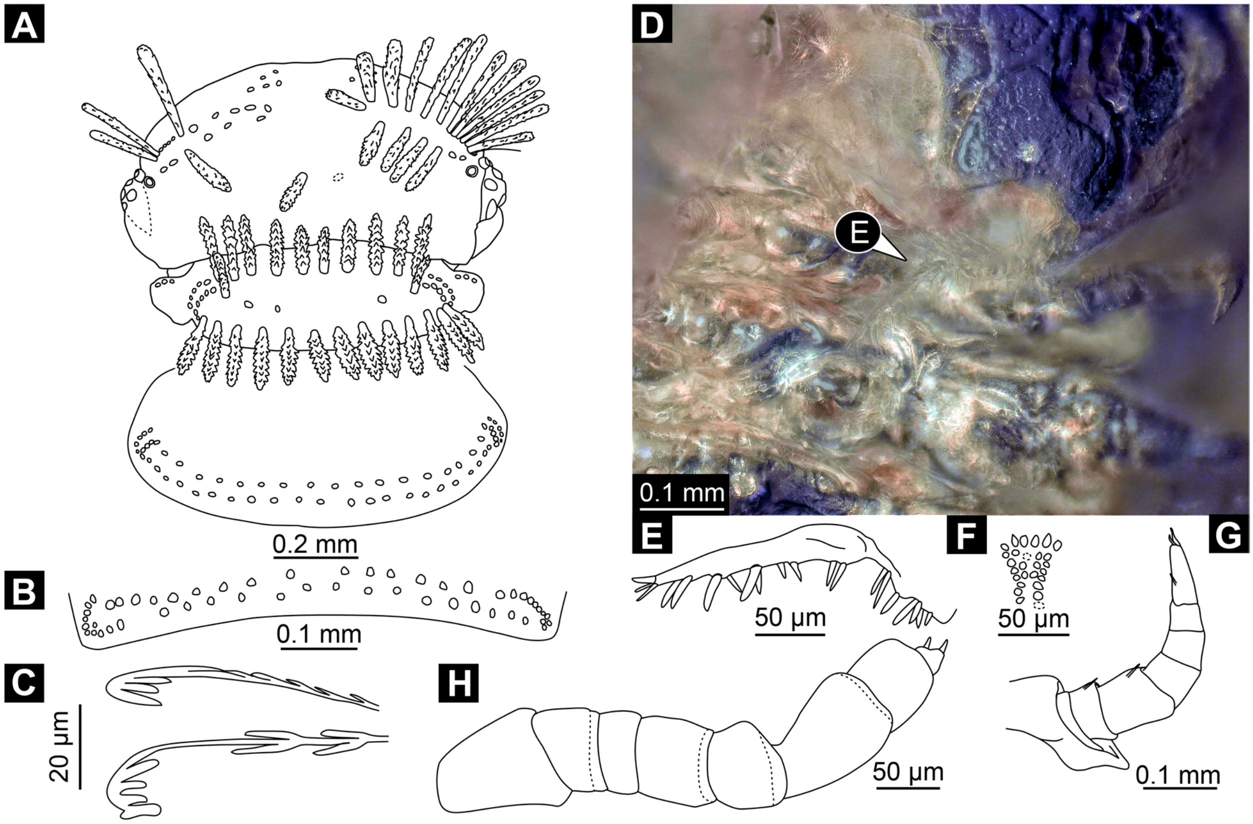

**Fig. 2** Adult female of *Polyxenus* aff. *lagurus* in the Baltic amber SMF Be 1855. **A** Dorsal view of the head, collum and first tergite. **B** Dorsal view of the 10th tergite. **C** Two defensive hooked setae from the caudal bundles. **D** Ventral side of the first trunk segments of the specimen. **E** Right gnathochilarium. **F** Pattern of the ornamental setae. **H** Right antenna. **G** Right leg of the 13th pair showing leg setae and spine on Tarsus 2

*Trunk* (Figs. 1A, B; 2A, B)*:* The collum has two rows of inserted setae (anterior/posterior), and an additional two rows of setae are inserted laterally (i.e., rosette, Fig. 1A); in total 49 setae are inserted on the collum. The lateral protuberances on either side of the collum with three setae each. The insertions of the setae and spine on the legs are as shown in Fig. 1H**.** Due to the poor preservation and slight decay of the cuticle, round protrusions are found along the legs of this specimen (see Suppl. Figure 1).

*Terminal end* (Figs. 1A, B; 2C, D)*:* A relatively small number of ornamental setae are forming the fan; between 25–27 setae (Fig. 2F) are present dorso-medial to the widely separated caudal bundles.

Remarks:

Several extinct species of *Polyxenus* have been already diagnosed by Koch and Berendt (1854) from fossil material, namely *P. ovalis*, *P. conformis*, *P. caudatus*, *P. colurus* Menge, 1854 and *P. lophurus* Menge, 1854. From these, *Polyxenus* aff. *lagurus* when compared to the diagnosis of *P. conformis* is similar in body length, but the proper measure is questionable as Koch and Berendt (1854) used the "Line". The "Line" is an old unit of measurement based on a certain proportion of an inch; however, it varies considerably between countries. If we refer to the Anglo-Saxon value *P. conformis* measures ~3.1 mm in length. The length including the caudal bundles is not available, as in the original diagnosis their specimen was lacking complete bundles (*cf.* p. 11 Koch & Berendt, 1854). Proper comparison is also very limited with these historical species as the descriptions lack important characteristics such as the number of ommatidia, the setae arrangement, shape of the terminal hooked setae, just to cite a few important diagnostic features (see "Discussion").

### ***Polyxenus lagurus*** **Linnaeus, 1758**

*Material examined:* One female adult and two female subadults, collected in Munich (48° 09′ 50.7″ N; 11° 29′ 03.4″ E).

*General features*: Five ommatidia are located on the head, including one positioned laterally (Fig. 3B/C).

Two groups of setae are visible on the posterior vertex, each with 25 ± 2 setae (female adult), arranged in two rows with the six most distal setae of the anterior rows closely arranged into a fan-like structure (Fig. 3C). A single pair of setae are medially posterior to the posterior vertex. Three trichobothria are arranged into a triangle (Fig. 3B/C), the closest trichobothria to the posterior vertex is immediately adjacent to the last seta and is smaller than the other two trichobothria. On the 6th antennal article, six sensilla are located; on the 7th antenna article only five sensilla are visible. Thirty-two ± 4 setae are inserted on each side of the collum (female ad.; total 67), and four setae are inserted on the lateral protuberances (Fig. 3B). Tergites have two transverse rows of setae, with rosettes of setae laterally. Approximately 22 ± 2 ornamental setae are arranged into a fan dorsal to the caudal bundles.

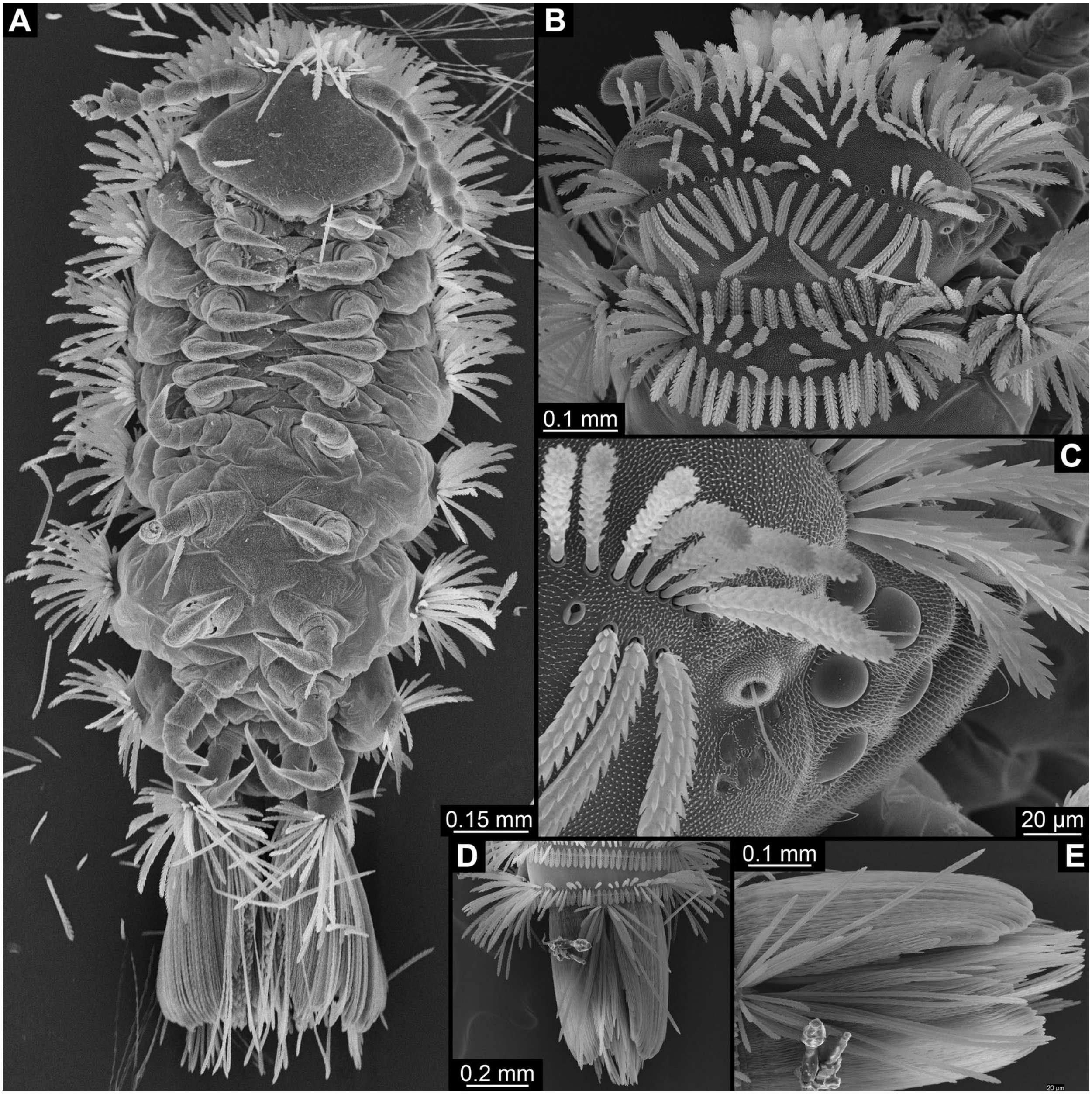

**Fig. 3** SEM pictures of two female *Polyxenus lagurus,* a subadult (f1) and an adult (f2). **A** Female subadult (f1) ventral view. **B** Anterior body part of the female adult (f2), dorsal view. **C** Trichobothria and ommatidia of the female adult (f2). **D** 11th tergite and the caudal bundles of the female adult (f2), dorsal view. **E** Ornamental setae pattern (f2), dorsal view

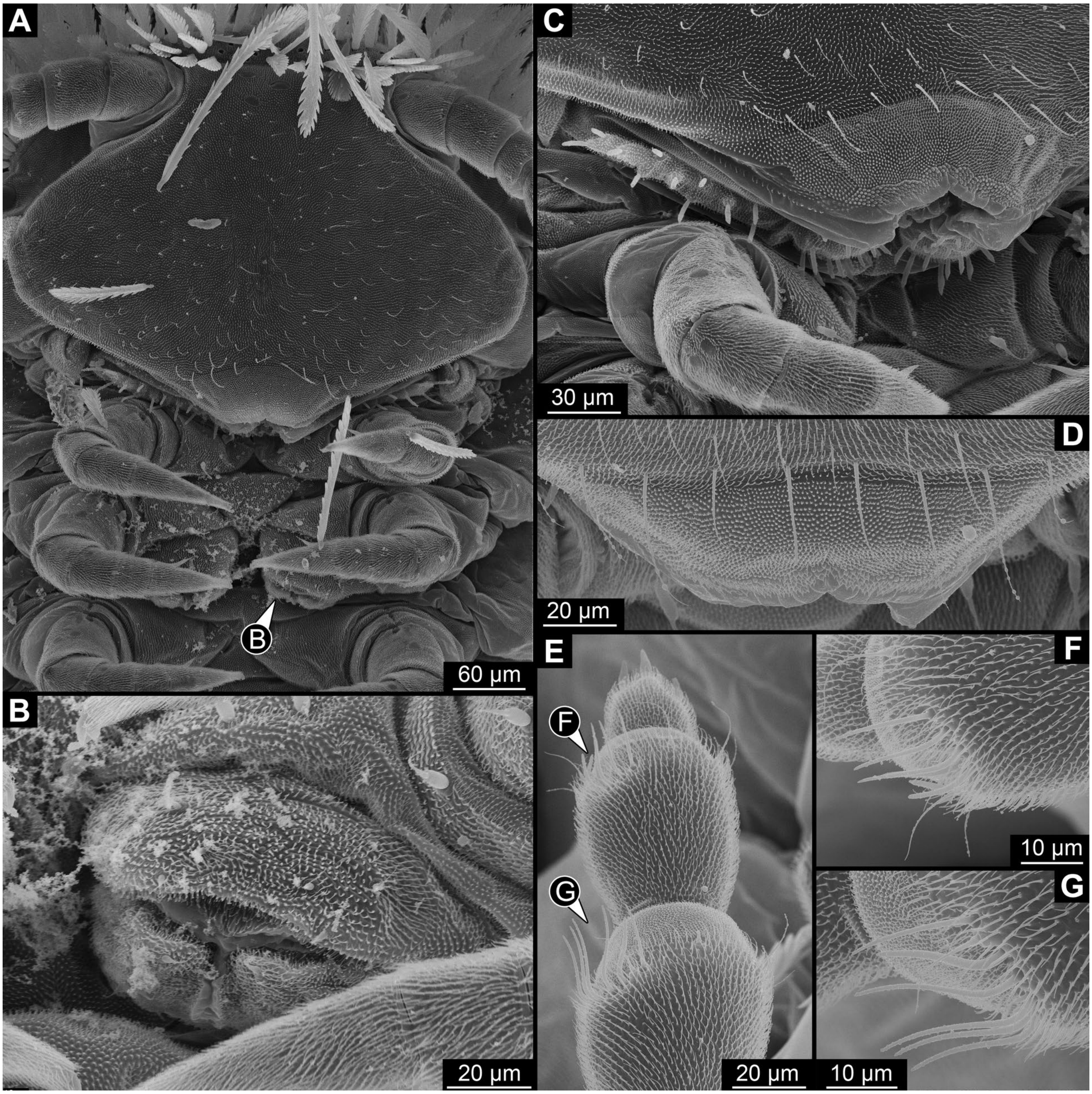

**Fig. 4** SEM pictures of two female subadults (f1 and f3). **A**–**C** f1. **A** Ventral view of the head capsule. **B** Vulva. **C** Gnathochilarium and labrum. **D**–**G** f3. **D** Labrum and papillae. **E** Left antenna. **F** Sensilla of the 7th antennal article. **G** Sensilla of the 6th antennal article

## Description of the mites

Two mites preserved in close proximity to the bristly millipede. One of the mites, SMF Be 1855b, is located close to the ventroposterior region of the millipede (Fig. 1D), with an apparent terminal hysterosomal pad-like organ. The second mite, SMF Be 1855c, is entangled in the ornamental setae ventrally (Fig. 1E). Both mites have a conspicuous narrowing in front of legs 1, a protruding gnathosoma, body diamond-shaped and four pairs of legs.

### *Mite SMF Be 1855b*

The mite is preserved in laterodorsal position. Pedipalps are visible (Fig. 1D); chelicerae are not accessible due to pedipalps in front of them. The cuticle is generally smooth, but some striations are present, possibly due to preservation. Setae on prosoma are short; visible setae: *ro*, *le*, possibly *ex* on cuticular protrusion; *elc* is absent or not visible. The setae on hysterosoma are long; visible setae: possibly *in*, the pore of *cp* and *c2* visible but not the setae; *d2*, *d1*, *e1* on cuticular protrusion; *c1* is not visible or absent. The posterior end of the idiosoma (trunk region in mites) bears a globular terminal hysterosomal pad-like organ (Fig. 1D); with at least five short setae on hysterosomal pad-like organ (four visible on Fig. 1D). Four walking appendages (legs) with a visible solenidion on tibia (designated as "ϕ") of four legs (Fig. 1D) and a robust, curved tarsal claw (Fig. 1D).

#### *Mite SMF Be 1855c*

The mite is preserved in dorsal position. Pedipalps are visible. Due to its position, most setae are not accessible: a single long hysterosomal seta is visible; solenidion is visible on genu and tibia (designated as "ς" and "ϕ", respectively) of leg 2; two additional setae are visible on ventral side of distal elements of leg 2 (possibly tibia and/or tarsus).

## Discussion

### Identity of the bristly millipede

Taxonomy and identification of fossils are often difficult and hampered by the lack of diagnostic characters or problems accessing them. Despite these limitations, bristly millipedes seem to have remained the same for more than 100 million years (Nguyen Duy-Jacquemin & Azar, 2004), and identification to extant low taxonomic levels (i.e., subfamily or genus) is relatively easy compared to other groups of Diplopoda (e.g., Polydesmida, Wesener & Moritz, 2018; Su et al., 2019, 2020). The following diagnostic characters observed in the reported specimen in the amber piece SMF Be 1855 confirm its classification within the extant genus *Polyxenus*: presence of ocelli (five ommatidia), arrangement of setae on posterior vertex, two rows of setae on tergites, arrangement of the ornamental setae, shape of the hooked setae of the terminal bundles, presence of a spine on tarsus 2.

Although several fossil species of *Polyxenus* have been previously described by Koch and Berendt (1854), comparing the herein described fossil species to them is not an easy task. Koch and Berendt (1854) material certainly need proper rediagnosis; for example, the *Polyxenus ovalis* drawing (table I fig. 3 p. 125, Koch & Berendt, 1854) is a description of a moult remains instead of a "living" animal (pers. obs. by JLC). Yet, the paratype included in the collection is a fully preserved specimen (pers. obs. by JLC). Similarly, in their original description and drawings of *Polyxenus conformis,* the specimen lacks ornamental setae and has an additional lateral bundle (see table XVI fig. 133 p. 322 Koch & Berendt, 1854). Furthermore, a more recent newly described species, *Polyxenus miocenica* (Srivasta et al., 2006) is very likely to be a wrongly diagnosed millipede as its description has nothing similar to the classic body plan of *Polyxenus* Latzezl, 1884. In *P. miocenica*, 22 segments have been reported, two pairs of legs in each segment, long legs (3.7 cm); instead, in *Polyxenus* there are 11 segments (including the head), one pair of legs on the first three leg-bearing segments and the remaining ones bearing two pairs of legs (in total 13 pairs in the adults), and the legs are rather short (< 1 mm in length). *Polyxenus miocenica* is likely to be a wrongly inferred Polydesmida (based on their description and reference to *Polydesmus* in their discussion), lacking diagnostic characters to assign it to the group *Polyxenus* and should be placed as Diplopoda *incertae sedis* (see Short & Le Cadre, 2025).

Surprisingly, no investigated characters of the here described *Polyxenus* specimen show any major differences from the extant species *Polyxenus lagurus* (Figs. 3, 4). If we consider species only from the morphospecies concept, this would be the earliest representative of *P. lagurus*, suggesting an occurrence already during the Eocene, surviving and thriving in Europe until the present day. This specimen is not a single find; few discrepancies are found with the previously described species *P. ovalis* and *P. conformis* (Koch & Berendt, 1854) which share high similarities with *Polyxenus* aff. *lagurus* and *P. lagurus* (pers. obs. by JLC). In the past a subspecies was created (i.e., *P. lagurus var. caucasicus*, Lignau, 1924), but was later invalidated by Short et al. (2020) after reinvestigation.

However, here we cannot surely state that the investigated fossil SMF Be 1855a is indeed a representative of *P. lagurus* as only DNA sequencing can be used to diagnose a new species (see also discussion in Haug & Haug, 2017 regarding species concepts in deep-time; Short et al., 2020). Nonetheless, observed data suggest that early representatives indistinguishable from extant *P. lagurus* were already roaming Europe during the Eocene.

The concept of morphological stasis has been reported in representatives of micro-organisms for a long period of time (e.g. Girard & Adl, 2011; Martín-González et al., 2008). Morphological stasis is also known in some groups of Euarthropoda (e.g., beetles, Cai et al., 2019; Diptera, Baranov et al., 2019; millipedes, Su et al., 2022). Such phenomenon of long-term survival and "evolutionary stasis" is known as "Bradytely" (Eldredge, 1984; Simpson, 1953; Stanley, 1984). This long-term persistency is likely due to the persistence and stability of habitats (Baranov et al., 2019; Cai et al., 2019), allowing groups to be "champions at warding off extinction" (Stanley, 1989). Fossils of close relatives or even extant species in deep-time are a remarkable finding but not new. Here, *P.* aff. *lagurus* is yet again another example of how successful bristly millipedes are and shows evidence of "bradytely" in *P. lagurus* since at least the Eocene.

In particular, the species *P. lagurus* is interesting due to its particular reproduction strategies, relying on thelytokous parthenogenesis (i.e., females producing female offsprings without the need of males) in a number of populations over the world (Schömann, 1956). In Europe the two different populations, i.e. sexual and parthenogenetic, are occurring but are geographically distant (see fig. 3.19 p.127 Udvardy, 1969; Enghoff, 1976). However, it is unclear whether parthenogenesis was already the mode of reproduction of *P.* aff. *lagurus* during the Eocene. The area where Baltic amber is from (i.e., Fennoscandia), is often linked with a high percentage of thelytoky in extant *P. lagurus* (Udvardy, 1969). This finding of a single fossil female of *P.* aff. *lagurus* does not allow us to determine its mode of reproduction, only an exhaustive and proper sampling of fossils followed by the investigation of the sex-ratio could start revealing a signal. If already at that time parthenogenesis was occurring and limiting the rate of *P. lagurus* diversification, it would certainly explain why few morphological changes have accumulated over such a long period of time, in addition to the habitat stability.

### Identity of the mites

The four pairs of legs in both mites indicate that their life stage is post-larval. The general body shape, diamond-like with a protrusion of the body anterior to the first pair of legs, as well as the setae disposition particularly visible on mite SMF Be 1855b, is compatible with characteristics of *Glaesacarus rhombeus* (Koch & Berendt, 1854), a mite species that belongs to the group Glaesacaridae (Sidorchuk & Klimov, 2011). Additionally, mite SMF Be 1855b bears a terminal hysterosomal pad-like organ which indicates that it is a female *G. rhombeus* (Sidorchuk & Klimov, 2011).

Representatives of the extinct genus *Glaesacarus* have been extensively studied from Baltic amber, making up around 15% of Baltic amber inclusions (Grünemaier, 2017). Likewise, *G. rhombeus* is also typically found in Rovno amber (Perkovsky et al., 2007), with an estimate of 27% of all mites in Rovno amber belonging to this lineage (Legalov et al., 2021). This mite species is not found elsewhere in fossil deposits and is considered extinct, with no modern representatives of Glaesacaridae nor close relatives in extant fauna. Glaesacaridae is within the group of astigmatan mites, whose diet and lifestyle are diverse, including detritivorous, predatory, parasitic and commensalistic, depending also on their life stage (O'Connor, 2009b). Despite the ubiquity of *G. rhombeus* in Eocene amber, their ecology remains a mystery. Given their high abundance in amber pieces and their usual occurrence next to wingless psocopteran specimens and frass, this lineage has been linked with wood burrows and life on tree bark (Larsson, 1978). It has been suggested that their lifestyle is in some way closely associated with the flow of tree resin (Grünemaier, 2017; Kolesnikov et al., 2025).

### Interaction in amber

A syninclusion refers to two or more specimens preserved together within the same piece of resin. As opposed to a para-syninclusion (sensu Solórzano-Kraemer et al., 2023), in which two or more specimens are found together in a piece of amber due to successive tree resin flows trapping originally distant organisms. The fact that the only two *Glaesacarus* mites found in SMF Be 1855 amber piece are in close proximity to the bristly millipede, with one of them even touching (i.e., "sitting on") the millipede setae (mite SMF Be 1855c), points to the possibility of a real syninclusion (or eusyninclusion, sensu Solórzano-Kraemer et al., 2023). The alternative of a flow of resin pushing the mite close to the bristly millipede and detaching some of the setae seems unlikely, since it would have pushed the setae further away from the body of the bristly millipede, as observed in other pieces of amber (e.g., fig. 6A in Su et al., 2019).

Hence, in order to be entrapped together, the specimens would have to be in close proximity while still alive, which could be the result of either interacting with each other or having been using the same microhabitat without a direct interaction taking place. Nevertheless, interpreting possible interactions is challenging, since the suffocation of the individuals when entrapped in the resin may distort the behavior in which they were participating, in their attempt to escape the sticky material (see Arillo, 2007). The possible interpretations for the syninclusion reported here are the following:

1. *Polyxenus* post-mortem interaction: The abundance of *Glaesacarus rhombeus* in Eocene amber has drawn researchers to the conclusion that there seems to be a particular link between this species and tree resin. According to Grünemaier (2017), *G. rhombeus* mites could be detritivorous and be taking advantage of the fact that other euarthropodans had become stuck in the tree resin and moved on the resin surface to feed on either the entrapped euarthropodan, as a scavenger, or fungi growing on the surface of its decaying body, later becoming entrapped themselves into another flow of new fresh resin. In the amber reported here, neither direct interactions between the mouthparts of the mites and the millipedes, nor different flows of resins have been found. Still, a possible scenario is that detritivorous *G. rhombeus* was feeding on the decaying body or fungi growing on a recently dead *Polyxenus* when a resin flow entrapped them all. It is possible that mite SMF Be 1855c has

been surrounded by defensive setae after the death of the millipede. Even exuviae of bristly millipedes appear to retain their entangling ability, and the corpse may be capable of doing so as well.

2. Interaction while alive: If the bristly millipede specimen and the two glaesacarid mites became stuck into the tree resin while still alive, a possibility of being fossilized in close proximity is that the mites were using the *Polyxenus* as a host either of parasitism in a wide sense (using the host only as a mean of transportation, i.e. phoresy), or in a strict sense (in which feeding is involved). Parasitism and phoresy on animal hosts are widespread among mites (Seeman & Walter, 2023). In fact, mites are possibly the most frequently reported parasitic organism in amber (De Baets et al., 2021). To the best of our knowledge, there is only one record of parasitism of a bristly millipede by mites attributed to a larva of an erythraeoidean mite, an ingroup of Trombidiformes (Iniesta et al., 2024). According to records from modern fauna, most mites associated with small millipedes (< 3 cm) are astigmatans (Farfan & Klompen, 2012); nevertheless, none of these point to an association between astigmatan mites and polyxenids in particular. Although there are no records of modern representatives of Glaesacaridae, there is a potential extant astigmatan sister group, i.e. Lemanniellidae (Sidorchuk & Klimov, 2011). As in most astigmatans, phoretic behavior in this group is found in the deutonymphal stage (Wurst, 2001; O'Connor, 2009b), the typical morphology of which does not correspond with that of the mites here reported.

   Representatives of Lemanniellidae are associated with ant nests, where their adults feed on fungi (Wurst, 2001). The specimens of *G. rhombeus* could have been feeding on fungal hyphae and algal films growing on the surface of the bristly millipede body. Although the position of the mites facing their venter to the ventral side of the millipede would not support this hypothesis, since this would not be the natural position of the millipede, the flow of tree resin could have distorted the original placement of each specimen.

   A third possible interaction of the mites with the live bristly millipede is predation. Although astigmatan mites rarely prey on other euarthropodans (e.g. Meyer, 1962; Papadopoulou, 2006), it cannot be ruled out that the mites in SMF Be 1855 were in the act of preying on the bristly millipede or about to do so. Nevertheless, there are no signs of damaged body parts in the millipede (except seemingly degraded cuticle, Supp. Figure 1) that would lead to this interpretation, and as none of the reported mites are directly interacting with the bristly millipede this scenario seems to not be plausible.

3. Shared microhabitat: Rather than a direct interaction, the bristly millipede and mite specimens could have been using the same substrate when they became entrapped in the tree resin. In fact, although rarely investigated, frequent co-occurrence of mites in the same microhabitat as *Polyxenus*, such as snail shells, has been reported in extant fauna (Ebejer & Schembri, 2001). Some species of Lemanniellidae have been reported feeding on fungus hyphae growing on wood surfaces inside ant nests (Wurst, 2001). It is possible that a similar feeding habit was shared by representatives of *G. rhombeus*, who could have been feeding on fungi growing on tree bark. Therefore, both *Polyxenus* and *Glaesacarus* groups could have relied on the same food type: microalgal films and fungal hyphae. This has also been proposed as the explanation behind a syninclusion containing an aggregation of *G. rhombeus* in proximity to a fungus weevil in a piece of Rovno amber (Legalov et al., 2021).

In Polyxenida, detachable defensive setae are used as a defense mechanism against predators and they are also the only millipedes that do not rely on chemical defense (Makarov, 2015). In extant fauna, typical small-sized predators such as ants can get entangled in them (Eisner et al., 1996). However, these setae can be used as a passive defense mechanism, hence entangling any organism moving in proximity to them and of a certain size, similar to larvae of Dermestidae (Nutting & Spangler, 1969). Therefore, the fact that one of the mites is sitting on the terminal setae and potentially entangled does not necessarily mean that the mites were preying on this specimen. It does, however, offer a glimpse on the potential effectiveness of the defensive setae of polyxenids even as far back as the Eocene. Although microhabitat sharing could be common between mites and bristly millipedes (Ebejer & Schembri, 2001), the close proximity can lead to collateral death in mites as bristly millipedes release their setae in their habitat (e.g., oribatid larvae, pers. obs. by JLC); a similar case is found in the family of carrion beetles Dermestidae, where the larvae use detachable defensive setae (i.e., hastisetae) that can entangle other euarthropodans in the habitat (Ruzzier et al., 2021). Although *G. rhombeus* has been found before in syninclusions with other euarthropodans, it has also been found in the absence of any other organism, even in large numbers inside a single amber piece (Grünemaier, 2017; Perkovsky et al., 2007). This supports the possibility of a sap-feeding diet, as in *Histiogaster* species, another astigmatan lineage found in a piece of Eocene Rovno amber containing several adult specimens and no other euarthropodan inclusion (Kolesnikov et al., 2025).

All potential explanations for this common entrapment are plausible, but without any clear direct interaction between them, we can only conclude that the two specimens at least shared a microhabitat, which seems to be the most likely scenario. Yet, this reported syninclusion provides an exceptional insight into forests during the Eocene.

## Conclusions

Extinct bristly millipedes likely have lived in the same manner as today's species in and around tree bark. However, the intriguing close proximity with the two representatives of glaesacarid mites offers a glimpse on either their past competition for the same food resource as they share the same microhabitat or on the role of *Glaesacarus rhombeus* in the feeding on euarthropodan remains.

The reported syninclusion supports at least shared microhabitats between euarthropodans from 40 million years ago, which represent very different evolutionary scenarios in regard of their lineages trajectory in time:

1. The bristly millipede belongs to a lineage still present to these days and undistinguishable from an extant species, hence it is possibly a case of bradytely.
2. In contrast, the two glaesacarids belong to a lineage that has no modern representatives nor close relatives, thus a lineage that went extinct.

This discovery of a putative early representative of *Polyxenus lagurus* highlights the importance of reinvestigating the five fossil *Polyxenus* species described in Koch and Berendt (1854). These descriptions are 170 years old and are in dire need of revision, particularly through the application of modern microscopic tools to access morphological characteristics in detail. A proper and updated revision might lead to further clarification of the identity of the five species, as well as their close resemblance with the specimen investigated here and to *P. lagurus*.

## Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-025-00369-2.

Supplementary Material 1. Figure 1. Details of the *Polyxenus* aff. *lagurus* in the amber SMF Be 1855. **A.** Ventral view of the brisly millipede. **B.** Dorsal view of the bristly millipede. **C.** Anterior part of the specimen, with the head, collum, and two first body segments. **D.** Terminal end ornamental setae. **E.** View of the pairs of walking legs 6-11. **F.** Posterior sets of trichomes with, in the center, the bundle of ornamental setae. **G.** First three pairs of legs, with the vulva on the second pair of legs.

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### Author contributions

Conceptualization, JLC, SIA and RRM; methodology, JLC, JUH, RRM and SIA; investigation, JLC, SIA and MS; resources, JUH and RRM; writing—original draft preparation, JLC, RRM, SIA and JUH; writing—review and editing, JLC, JUH, RRM, MS and SIA; visualisation, JLC and SIA; supervision, JLC and SIA. All authors have read, reviewed and agreed to the published version of the manuscript.

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### Availability of data and materials

No datasets were generated or analysed during the current study.

## Declarations

### Ethics approval and consent to participate

Not applicable.

### Competing interests

The authors declare no competing interests.

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