



The globe thistle habitat and attachment of *Macrolophus pygmaeus* on leaves of three *Echinops* species

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Abstract

Echinops plants, a genus of globe thistles, have proven to be highly attractive to various arthropods in the field. They offer a complex, three-dimensional, and pubescent terrain that is conducive to omnivorous predatory mirid bugs, such as *Macrolophus pygmaeus*, and related species within the subfamily Bryocorinae (Heteroptera, Miridae), where many other entomophagous insects may struggle. A microscopic examination of the leaf surfaces of 20 *Echinops* accessions across five species and one subspecies revealed differences in their microstructural features. *Echinops bannaticus*, *Echinops exaltatus*, and *Echinops sphaerocephalus* were selected for detailed evaluation and included in traction force measurements with female *M. pygmaeus* to compare the bug's attachment on different plant surfaces. These insects demonstrated significantly stronger attachment to the leaves compared to glass, generating forces that were 47 to 12 times their body weight, respectively. The abaxial leaf surfaces, which are covered by a dense layer of tomentous trichomes, provided superior footholds compared to the adaxial glabrous or pruinose leaves. The larger the area covered with tomentous trichomes, the higher the safety factor (attachment force normalised by the bug's body weight) for the insects. In addition, the number of pulling movements decreased on glandular trichomes, likely to avoid being trapped by glandular secretion. This study provides further evidence of the essential role of the interaction between plant surfaces and insect integuments in insect–plant relationships. Insect settlement on plants depends on having proper footholds, which are influenced by surface properties. Consequently, these factors warrant more attention in future research on insect evolution, ecology, and pest management.

Keywords Bryocorinae · Insect attachment · Miridae · Pest management · Plant surface · Traction force · Trichomes

Introduction

The genus *Echinops* L. comprises approximately 120 species of globe thistles found in Eurasia and Africa, including 12 species in Europe. These species belong to the monotypic subtribe Echinopsinae (Cardueae, Asteraceae) and grow in semi-humid, semi-arid, and temperate regions (Walter 1991; Jäger 1987). *Echinops* plants contain a variety of secondary metabolites that have attracted interest due to their potential medical properties. They have been traditionally used to treat pain, inflammation, respiratory diseases, and infections caused by various microorganisms, as an aphrodisiac, to expedite placental expulsion and post-partum care, to address stomachic and liver disorders, to assist in the removal of renal stones, and for diuretic and hypoglycemic effects (Bouzabata et al. 2018; Bitew and Hymete 2019). Alkaloids, flavonoids, terpenoids, steroids, lipids, and polyacetylenes have been isolated from various *Echinops* species (Shukla 2003). Recent

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efforts have focused on oil production, seed extraction, breeding, and cultivation (Horn 2007; Horn et al. 2008). In this context, *Echinops* crops have garnered some agricultural interest in recent decades, particularly due to their thermal resilience and adaptability to the rising temperatures associated with climate change.

Echinops plants are also recognised as valuable sources of forage for bees. Since the nineteenth century, several decorative species have been introduced from Southern to Central Europe for this purpose (Walter 1991). These biennial (hapaxanth) and perennial, herbaceous plants feature a rosette growth form, alternate, lobed pinnate leaves covered with trichomes, edged pubescent stem, and spherical inflorescences, creating a complex, three-dimensional terrain that supports a diverse range of arthropods beyond just pollinators, including members of Hemiptera, Diptera, Homoptera, and Neuroptera (Fig. 1; Supplementary information: sampling habitat survey).

The omnivorous mirid bug *Macrolophus pygmaeus* (Rambur, 1839) (Heteroptera, Miridae, Bryocorinae, Dicyphini) can reach an extraordinary abundance in *Echinops* crops, particularly in the glandular hairy species *E. sphaerocephalus* L., where it inflicts significant damage shortly after hibernation (Horn 2007; Supplementary information). Bugs, including their eggs, larvae, and adults, hibernate and become active early in the season before prey arthropods are abundant. Different developmental stages and generations

often coexist on the same host (Wagner 1952, 1955, 1970; Wachmann et al. 2004).

Macrolophus pygmaeus is one of 14 species within the genus *Macrolophus*, which inhabits a variety of environments, including forests, bushes, and both humid, shady and sunny, open areas. It lives on *Carduus* sp., *Cirsium* sp., *E. sphaerocephalus* (Asteraceae), *Cucubalus* sp. (Caryophyllaceae), *Pulmonaria* sp. (Boraginaceae), *Salvia glutinosa* L., and *Stachys sylvatica* L. (Lamiaceae), across much of Europe (Wagner 1955; Wachmann et al. 2004). This particular mirid bug has been known to prey on several crop-damaging arthropods, including whiteflies (Zybulskaja and Kryshanowskaja 1980; Ter Horst 2000; Hillert et al. 2002; Perdakis and Lykouressis 2002; Lykouressis et al. 2009; Leman et al. 2020), aphids (Mardzhanjan and Ustjan 1965; Ter Horst 2000; Hillert et al. 2002; Perdakis and Lykouressis 2003; Lykouressis et al. 2007; Fatinou et al. 2008), thrips (Hillert et al. 2002; Leman et al. 2020), leaf miners (Köhler and Hanke 2005; Urbaneja et al. 2012; Zappala et al. 2013; De Backer et al. 2014; Bouagga et al. 2018; Sanchez et al. 2018), moth eggs (Ter Horst 2000; Ebrahimi et al. 2018), and spider mites (Hillert et al. 2002; Ramzi et al. 2022). This zoophagous ability has led to *M. pygmaeus* being introduced into biological control programmes in over 20 countries since 1994, where it is commercially available to manage primarily whiteflies, aphids, and spider mites in crops (van Lenteren 2012; Lemanski and Herz 2025).

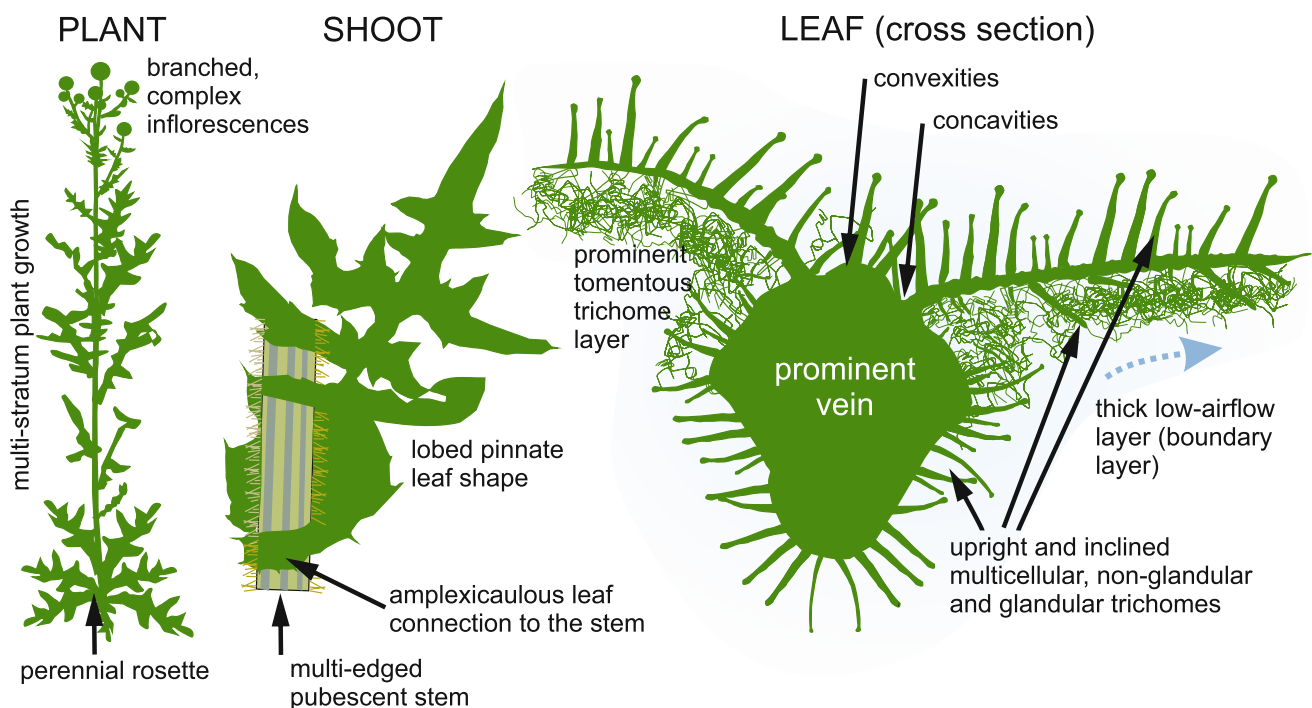


Fig. 1 The *Echinops sphaerocephalus* habitus at the plant, shoot, and leaf level provides highly suitable multidimensional terrains, shelters, and microclimatic conditions for arthropod inhabitants, such as *Macrolophus pygmaeus*

Like other plant bugs (Miridae), *M. pygmaeus* is closely associated with plants, which influence its oviposition and development (Ter Horst 2000; Lykouressis et al. 2001). They prefer pubescent plant species, where other entomophagous insects, such as lady beetles, parasitoids, and larvae of lacewings, minute pirate bugs, and syrphids, are hampered (Walters 1974; Dixon 1986; Obrycki 1986; Quilici and Ipertti 1986; Jervis and Kidd 1996; Dos Santos et al. 2003; Verheggen et al. 2009). Related omnivorous bugs like *Dicyphus errans* Wolff (Heteroptera, Miridae, Bryocorinae, Dicyphini) employ an avoidance strategy, keeping the light, slim bodies at a large distance from the hairy plant surface and the adhesive secretion of glandular trichomes by using long, slender legs (Southwood 1986; Voigt and Gorb 2010) and particular pretarsal structures (Wagner 1955; Seidenstücker 1967; Schuh 1976; Voigt et al. 2007). Is *M. pygmaeus* employing the same strategy? Although it shares a similar body structure with *D. errans*, the smaller *M. pygmaeus* (3.1–3.9 mm body length) holds its leg segments at wider angles and maintains a closer proximity to the substrate compared to *D. errans* (4.5–5.1 mm body length) (Wagner 1970; Wachmann et al. 2004; Voigt 2005). Additionally, the leg morphology differs between the two genera: *Macrolophus* has linear femora and tibiae and strongly curved, narrow claws with a small basal projection. In contrast, *Dicyphus* features elongated, linear legs that taper towards the apex, a long tarsus with a large pretarsus, and linear, apically recurved claws with a significant basal projection (Cassisi 1984). Are these differences in attachment ability to plant surfaces reflected in *M. pygmaeus*?

Foothold (i.e. tarsal attachment) is particularly important for plant-dwelling arthropods, as previously experimentally demonstrated for *D. errans*. Activities, such as walking, foraging, resting, grooming, feeding, mating, oviposition, hatching, and moulting, require a reliable grip, repulsion on plant surfaces, and the mechanical interlocking of claws with trichomes. This interlocking can occur both in the short term, with a high frequency (e.g. during walking), or in the long term, lasting for remarkable periods (e.g. during oviposition) (Voigt 2005, 2019). Females establish a stronger foothold, enabling them to anchor more effectively to plant surfaces while exerting force to insert their saw-like ovipositor into plant tissue, resulting in the implantation of significantly more eggs. Additionally, stronger attachment correlates with a higher consumption of prey individuals, as secure body postures facilitate effective handling of prey on plant substrates. This ability of animals to attach to various substrates can be measured quantitatively using traction (or pulling) force measurements (e.g. Stork 1980a; Betz 2002; Gorb and Gorb 2002; Voigt et al. 2007). In these measurements, the insect's abdominal thorax is tethered to a thin thread connected to a force sensor. As the insect walks and pulls horizontally, it generates a (traction) force laterally

against the surface. This force corresponds to the friction between the insect's pretarsi and the substrate. The force relative to body weight is referred to as the safety factor, indicating how many times the insect can support its body weight on the substrate during attachment. These quantitative values of force and safety factor allow for comparisons of attachment abilities within a single species across various substrates or among different species, influenced by both abiotic and biotic conditions.

Based on preliminary observations of high and stable abundance of *M. pygmaeus* populations in *Echinops* plantings, the question arises if this mirid bug species performs specifically on the surface of these plants, and if this is reflected in the bug's preference for abaxial leaves. That is why we investigated the attachment ability of *M. pygmaeus* on plant surfaces by conducting traction force experiments on the adaxial and abaxial leaves of three out of 20 *Echinops* accessions selected through micromorphological screening. The morphological characteristics of these plants may support the sectional classification of *Echinops*, which is often complicated by a high degree of macromorphological uniformity (Jäger 1987).

Our data on *M. pygmaeus* attachment contribute to a deeper understanding of plant–bug interactions in the context of evolution and biological control.

Materials and methods

Plants and bugs

Twenty accessions of different *Echinops* species were observed and sampled from a medical plant field in Zappendorf, Germany, in mid-June at the bud stage (51° 30' N, 11° 48' E; 70 m NN, mean annual temperature: 8.4–9.9 °C, annual precipitation: 460 mm, Fabig 2007; Fig. S1, Table S1, Supplementary surveys). The plants were sown directly or partially pre-grown in pots, then planted in rows spaced 50 cm apart. They were cultivated in fresh loamy soil using bio-organic methods and maintained on a biennial cycle without irrigation. Soil fertilisation was achieved by incorporating Persian clover into the crop rotation. The generative plants sampled were two years old and had heights ranging from 1.00 to 2.00 m. The upper, fully developed leaves measured 20–30 cm in length and 5–10 cm in width.

For laboratory studies, 20-cm-long stem pieces with 6–8 leaves were cut from the plant apex (Fig. S2) and transferred to the lab in plastic bags. Through photographic and microscopic screening of the 20 accessions and comparing leaf surfaces (Figs. S3, S4; Table S1), we selected three representative species/accessions for detailed studies and traction force experiments with *M. pygmaeus*: *Echinops bannaticus* Rochel ex Schrad., *Echinops exaltatus* Schrad.,

and *Echinops sphaerocephalus* L. These species exhibited marked differences in their leaf surface structures, including trichome types and epicuticular waxes (Tables 1 and S1, Figs. 3, S3, and S4), and provided reliable substrates for comparative studies with inhabiting mirid bugs.

Using an aspirator, mating adult *M. pygmaeus* were collected from *Echinops* populations at the same field location. They were kept in Exo Terra® Faunariums (plastic boxes, 360×170×220 mm with ventilated lids, HAGEN Deutschland GmbH & Co. KG, 25,488 Holm, Germany) on turgescient shoots of *Echinops* sp. under conditions of 23 °C, 70% relative humidity, and a 16-h light photoperiod (light sources: fluorescent lamps OSRAM 18W/640 cool white; OSRAM GmbH, Munich, Germany, and Philips Master TLD 18W/830; Philips Lighting, Suresnes Cedex, France, cold: warm light ratio of 1:1).

Imaging

Plant surfaces and bug body postures were observed using an Olympus SZX12 stereomicroscope with the DF PLAPO 1_PF lens (Olympus Corporation, Tokyo, Japan). Digital images were captured with a Nikon Coolpix E995 photo camera connected to the binocular via an MDC 2 relay lens

(Nikon Corporation, Tokyo, Japan). The same camera was used for photographing the plant samples.

The elastic protein resilin in the tarsus was localised using fluorescence microscopy, which targets this protein's auto-fluorescence at an emission maximum of 420 nm (Andersen and Weis-Fogh 1964). Fresh tarsi of a female bug were cut off with microscissors and mounted on glass slides in poly-vinyl alcohol (Mowiol). After being covered with glass coverslips, the samples were visualised using a Zeiss Axio-plan fluorescence microscope with an HBO 103 mercury vapour lamp and an XBO 75 xenon short-arc lamp (Carl Zeiss MicroImaging GmbH, Jena, Germany). The material composition of the cuticle, including the presence of resilin, was assessed by superimposing digital images obtained at green (excitation 512–546 nm, emission 600–640 nm), red (excitation 710–775 nm, emission 810–890 nm), and UV wavelengths (excitation 340–380 nm, emission 425 nm) (Gorb 1999).

Cryo-scanning electron microscopy (cryo-SEM) was carried out using the Hitachi S-4800 (Hitachi High-Technologies Corp., Tokyo, Japan) equipped with a Gatan ALTO 2500 cryo-preparation system (Gatan Inc., Abingdon, UK) as well as the Zeiss SUPRA 40VP-31-79 (Carl Zeiss SMT Ltd., Oberkochen, Germany), which was fitted with an EMITECH K250X cryo-preparation unit (Quorum

Table 1 Leaf surface morphometric characters of three *Echinops* species

Leaf side	Measured parameter	Plant species		
		<i>E. exaltatus</i>	<i>E. bannaticus</i>	<i>E. sphaerocephalus</i>
Abaxial	Living ng trichome length [μm]	294.8±54.44	143.9±24.87	n.a.
	Living ng trichome thickness (middle of the stalk) [μm]	30.8±3.47	28.5±4.53	n.a.
	Dead, twisted trichome thickness [μm]	3.9±0.64	6.5±0.63	8.8±3.75
	% of dead, twisted trichome-covered area (“tomentous layer”)	53.3±3.47	58.7±3.22	49.4±3.30
	Glandular trichome length [μm]	n.a.	n.a.	326.7±115.32
	Glandular trichome thickness [μm]	n.a.	n.a.	41.3±7.37
	No. of living ng trichomes [mm ⁻²]	9.6±13.61	2.6±3.31	n.a.
	No. of glandular trichomes [mm ⁻²]	n.a.	n.a.	9.3±3.09
Adaxial	Wax crystal width [μm]	0.5±0.09	0.8±0.18	n.a.
	Wax crystal thickness [μm]	0.1±0.01	0.1±0.02	n.a.
	No. of wax crystals [mm ⁻²]	91.6±19.82	56.6±2.70	n.a.
	Living ng trichome length [μm]	530.5±106.41	186.6±46.92	n.a.
	Living ng trichome thickness (middle of the stalk) [μm]	49.7±11.69	36.1±6.96	n.a.
	Glandular trichome length [μm]	n.a.	n.a.	210.1±66.92
	Glandular trichome thickness (middle of the stalk) [μm]	n.a.	n.a.	39.8±3.33
	Glandular head width [μm]	n.a.	n.a.	38.9±2.93
	No. of living ng and glandular trichomes [mm ⁻²]	4.6±1.07	7.9±2.28	n.a.
	No. of glandular trichomes [mm ⁻²]	n.a.	n.a.	6.5±1.18
	Cuticular fold distance [μm]	1.1±0.28	1.3±0.23	n.a.
	Cuticular fold width [μm]	0.2±0.03	0.6±0.12	n.a.
	Cuticular fold height [μm]	1.2±0.14	0.8±0.23	n.a.

Mean ± sd, *n* = 10 (randomly chosen from different sites of three distinct, 3rd fully developed leaves from the plant apex). ng, non-glandular

Technologies Ltd., Ashford, Kent, UK). Five by five mm pieces of leaves were cut using microscissors, mounted on metal holders with polyvinyl alcohol Tissue-Tek® OCT™ compound (Sakura Finetek Europe, Zoeterwoude, The Netherlands), frozen in the preparation chamber at -140°C , sputter coated with gold–palladium or platinum (6 nm), and examined in a frozen state in the cryo-SEM at 3 kV, maintaining temperatures between -90 and -120°C .

Leaf surface characters obtained from the images were morphometrically analysed with SigmaScan Pro 5 software (SPSS, Inc., Chicago, IL, USA), focusing on the number of trichomes and crystalline wax plates per unit area, the area covered with tomentous trichomes, and the dimensions of trichomes, wax platelets, and cuticle folds (Table 1).

Force measurements

Intercostal pieces ($5 \times 5 \text{ cm}^2$) of fresh, turgescient *Echinops* leaves (specifically the third fully developed leaf from the apex) were cut using microscissors and fixed to a horizontal glass plate using double-sided adhesive tape tesa® 05338 (tesa SE, Hamburg, Germany).

Ten female *M. pygmaeus* were weighed individually using an Ultra Microbalance UMX2 (Mettler Toledo GmbH, Greifensee, Switzerland) and kept in clean polystyrene tubes (16/68 ml, with air-permeable ceaprene stoppers; Greiner Bio-One GmbH, Frickenhausen, Germany). The bugs were anaesthetised with CO_2 and attached to a 10-cm-long human hair using a molten wax droplet, with their forewings glued together. After a 1-h recovery period, the free end of the hair was connected to a force sensor. Traction force measurements were conducted according to Voigt et al. (2007) using the FORT-10 force transducer (10 g capacity, World Precision Instruments Inc., Sarasota, USA). Each female was tested walking distally and horizontally on the adaxial and abaxial leaf surfaces of the three species and, for comparison, on a glass surface (with a water contact angle of 55° and a surface energy of 42.9 mN m^{-1}). Safety factors were calculated by normalising the traction force by the bug's body weight.

The sequence of different substrates was randomised. Prior to substrate exchange, the bugs were allowed to groom and walk over the glass surface. Force–time curves were recorded utilising AcqKnowledge 3.7.0 software (Biopac Systems Ltd, Goleta, CA, USA) to estimate the mean traction force exerted by a single bug during five consecutive runs on a test substrate. Ten females were tested individually on each plant surface. In total, 300 individual tests with 10 different individuals were carried out on leaves ($N_{\text{adaxial, abaxial leaves}} = 6$, $N_{\text{♀♀}} = 10$, $n_{\text{individual runs}} = 5$). This was compared to another set of 300 individual tests conducted on glass surfaces (before the plant surface). A two-way ANOVA followed by all pairwise multiple comparison procedures

(using the Holm–Sidak method) was employed to assess differences in force measurements between the various test surfaces (software SigmaPlot® 12, Systat Software, Inc., Richmond, California, USA). Additionally, pairwise *t*-tests were performed to compare the force and safety factor values between tests made on glass and plant surfaces.

Results

The *Echinops* plant surface

The sampled leaves exhibited differences in shape and characteristics (Figs. S2–S4, Table S1). Also, intraspecific differences in the presence of trichomes and epicuticular folds occurred. The leaf surface was textured due to epidermal cells and vein convexities, edge concavities, stomata, cuticular folds, epicuticular wax crystals, trichomes, and marginal spines (Figs. 1, 2). Four main types of trichomes were identified and classified according to Voigt et al. (2007): (1) uniseriate, multicellular, cone-shaped trichomes, transitioning from a bi- to multicellular base over 5–7 living, uniseriate cells to filamentous, twisted extensions (dead cells), which form the tomentous layer on abaxial leaves, (2) (living) multiseriate, multicellular tapered trichomes, (3) non-glandular, biseriate, multicellular trichomes, and (4) glandular, biseriate, multicellular trichomes with four- to five-celled glandular heads (Fig. 2).

The following *Echinops* plant species were analysed in detail (Fig. 3) and subsequently used in traction force experiments with *M. pygmaeus*.

Echinops bannaticus. Medium-sized leaves. The abaxial side shows a slightly sloped type-1 along with several type-3 trichomes on veins, where trichomes hide epidermal cells and stomata. The adaxial side features sloped type-2 and several type-1 trichomes distributed over the lamina, slightly undulated epidermal cells, scattered stomata, cuticular folds, and epicuticular crystalline wax platelets, along with multiseriate, multicellular spines at leaf edges.

Echinops exaltatus. Narrow leaves with a small lamina area. The abaxial side has sloped type-1 and very few type-3 trichomes, mainly on veins, with hidden epidermal cells and stomata obscured by trichomes. The adaxial side displays slightly sloped type-2 and several type-1 trichomes scattered over the lamina, slightly undulated epidermal cells, scattered stomata, cuticular folds, and epicuticular crystalline wax platelets.

Echinops sphaerocephalus. Leaves with large lamina area and large lobes. The abaxial side features perpendicularly oriented type-1 trichomes on veins and type-4 trichomes interspersed in the tomentous layer over the lamina. Epidermal cells, including stomata, are covered by trichomes. The adaxial side features perpendicularly oriented type-4

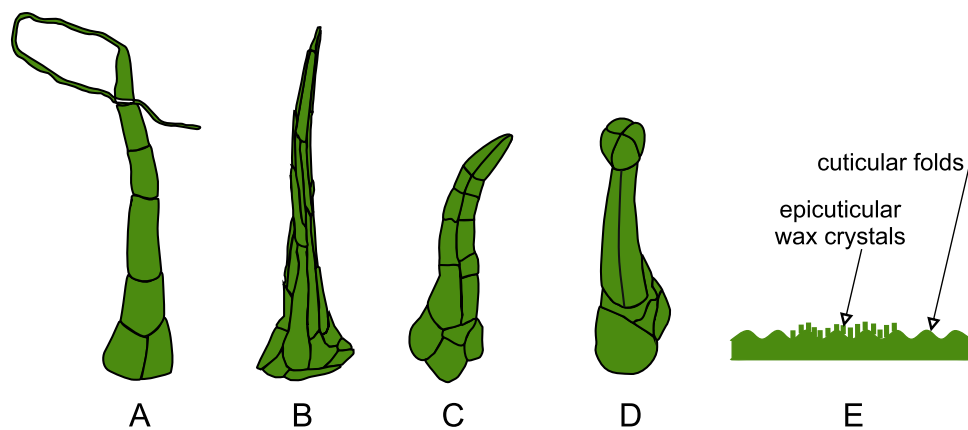
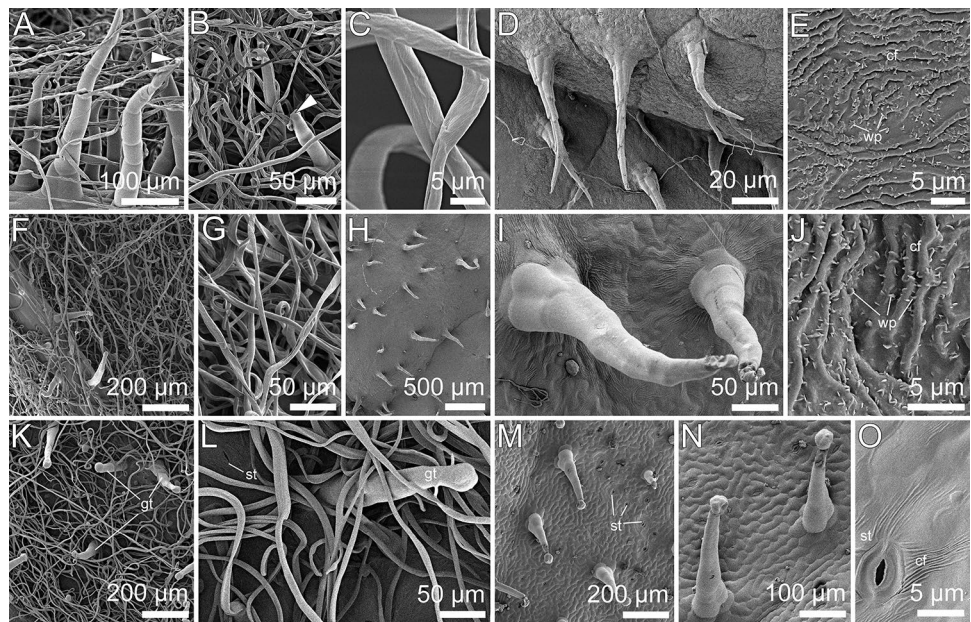


Fig. 2 *Echinops* trichome types, cuticular folds, and epicuticular crystalline wax plates observed in the present study. **A** Uniseriate, multicellular, cone-shaped trichome, transitioning from a bi- to multicellular base over 5–7 living, uniseriate cells to filamentous, twisted extension (dead cells). The latter form the tomentous layer on abaxial leaves. **B** Multiseriate, multicellular trichome (living cells). **C** Non-

glandular, biseriate, multicellular trichome. **D** Glandular, biseriate, multicellular trichome with a four- to five-celled glandular head. **E** Cuticular folds, superimposed with wax crystals on the epidermal cell surface. See Table 1 for morphometrics, Table S1 and Figs. S2, S3, S4 for the presence of various leaf surface characters in different *Echinops* species and accessions

Fig. 3 Abaxial (**A–C, F, G, K, L**) and adaxial leaf surfaces (**D, E, H–J, M–O**) of *Echinops exaltatus*, S 232 (**A–E**), *E. bannaticus*, S 237 (**F–J**), and *E. sphaerocephalus*, S320 (**K–O**). The arrowheads point to transitions of living trichome cells to dead, thread-shaped, twisted parts of trichomes, forming the abaxial felt-like coverage. cf, cuticular folds; gt, glandular trichome; st, stomata; wp, epicuticular crystalline wax platelets. See Table 1 for morphometrics



trichomes, evenly distributed over the lamina, slightly undulated epidermal cells, numerous stomata, cuticular folds surrounding the stomata, and epicuticular crystalline wax platelets.

Non-glandular trichomes on *E. exaltatus* were longer and thicker than those on *E. bannaticus* (295 μm , 31 μm , and 144 μm , 29 μm , respectively; Table 1). Abaxial glandular trichomes on *E. sphaerocephalus* were longer and thicker (327 μm , 41 μm) compared to abaxial non-glandular trichomes on the surfaces of two other species. However, adaxial glandular trichomes on *E. sphaerocephalus* had lengths and thicknesses that fell between the

non-glandular trichomes of the other species. The highest number of trichomes per unit area was observed on the abaxial leaves of *E. exaltatus* and *E. sphaerocephalus* (10 and 9 trichomes mm^{-2} , respectively), while the number was lower on the abaxial leaves of *E. bannaticus* (3 trichomes mm^{-2}) and the adaxial leaves of *E. exaltatus* (5 trichomes mm^{-2}). The abaxial leaves of *E. bannaticus* had the densest tomentous layer (59% covered area with dead, twisted trichomes), followed by *E. exaltatus* (52%) and *E. sphaerocephalus* (49%). The adaxial leaves of *E. exaltatus* and *E. bannaticus* were covered with cuticular folds

and epicuticular crystalline wax platelets, whereas these structures were absent on *E. sphaerocephalus*.

Tarsal morphology and attachment ability of *M. pygmaeus*

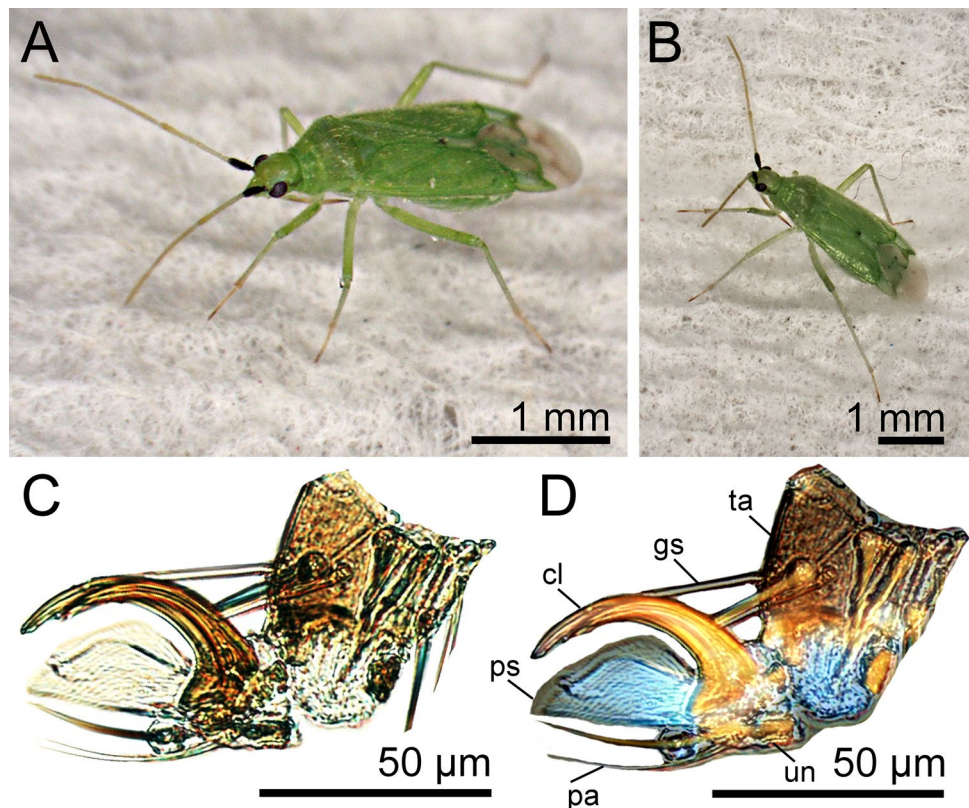
The female body is approximately three times as long as wide (3.2–1.1 mm), with a head width of 450 μm , and its legs measure 0.5–0.7 times the body length (Fig. 4A, B). The fore, mid-, and hind legs measure 1.6, 1.7, and 2.2 mm in length, respectively. Femora are the longest segments of the leg, measuring between 807 and 942 μm and exhibit the largest aspect ratio (14–15). The tarsi are 7 to 9 times longer (288–446 μm) than they are wide (43–56 μm). The pretarsal unguitractor plates bear paired, round, curved claws with superficial longitudinal striae (inner and outer claw lengths are 45 and 55 μm , respectively) (Fig. 4C). The slightly tapered claw tips (teeth) are 1.1 μm long. Trapezium-shaped pseudopulvilli arise at the claw base, and between these, there are two setiform parempodia measuring 37.5 μm in length. Fluorescence microscopy elucidated the presence of the elastic protein resilin in the pseudopulvilli, as well as in the connective arthrodistal membrane at the claw base and unguitractor plate, and the tip of the third tarsomere (Fig. 4C). There is a stronger dorsal guard seta present on the dorsal distal third tarsomere. The inner side of the claws is sharp edged. The average diameter of a circle that fits

the concavity of the claws is 15 μm , with an overall claw curvature of 35 μm .

The average body mass of female *M. pygmaeus* was 1.4 ± 0.3 mg (mean $\pm$ sd, $n = 10$). These females generated traction forces ranging from 164 to 636 μN , corresponding to 12 to 47 times their body weight, on glass and leaves, respectively. Notably, they demonstrated significantly stronger attachment to leaves compared to glass (Figs. 5, 6, Table S2). Force–time curves show similar plateaus on both glass and *E. sphaerocephalus* (Fig. 5A, B), indicating that the bugs maintained a steady force level for approximately 2 s. Differently, traction curves on *E. exaltatus* and *E. banaticus* show several peaks, which are produced by actively walking *M. pygmaeus* females during multiple short pulls (Fig. 5C, D).

In general, bugs attached significantly more strongly to the abaxial leaf surfaces of all three *Echinops* species (Figs. 5, 6, Table 2). This observation is further supported by normalised forces and safety factors, although the latter results were not statistically proven (Figs. 6, S5, Tables S2, S3). On abaxial leaves, the traction force was positively related (linear regression) to the number of living trichomes per unit area ($R = 0.6$, $R^2 = 0.3$, $p = 0.6$) and negatively associated with the thickness of dead, twisted trichomes ($R = 0.9$, $R^2 = 0.7$, $p = 0.3$) by trend. Moreover, the greater the abaxial leaf area that was covered with tomentous, dead, twisted trichomes, the higher the safety factor ($R = 1.0$, $R^2 = 1.0$,

Fig. 4 Light microscopic images of *Macrolophus pygmaeus*. **A, B** Different body postures and the positions of legs influence the body-substrate-distance on a fibrous filter paper. **C, D** Lateral view of the pretarsus under transmission light (**C**) and fluorescence microscope (**D**) (background is removed). The shiny blue areas in (**D**) demonstrate the presence of resilin in the pseudopulvilli, the membranous areas surrounding the unguitractor plate, and the claw–tarsomere connection. cl, claw; gs, guard setae; pa, parempodium; ps, pseudopulvillus; ta, 3rd tarsomere; un, unguitractor



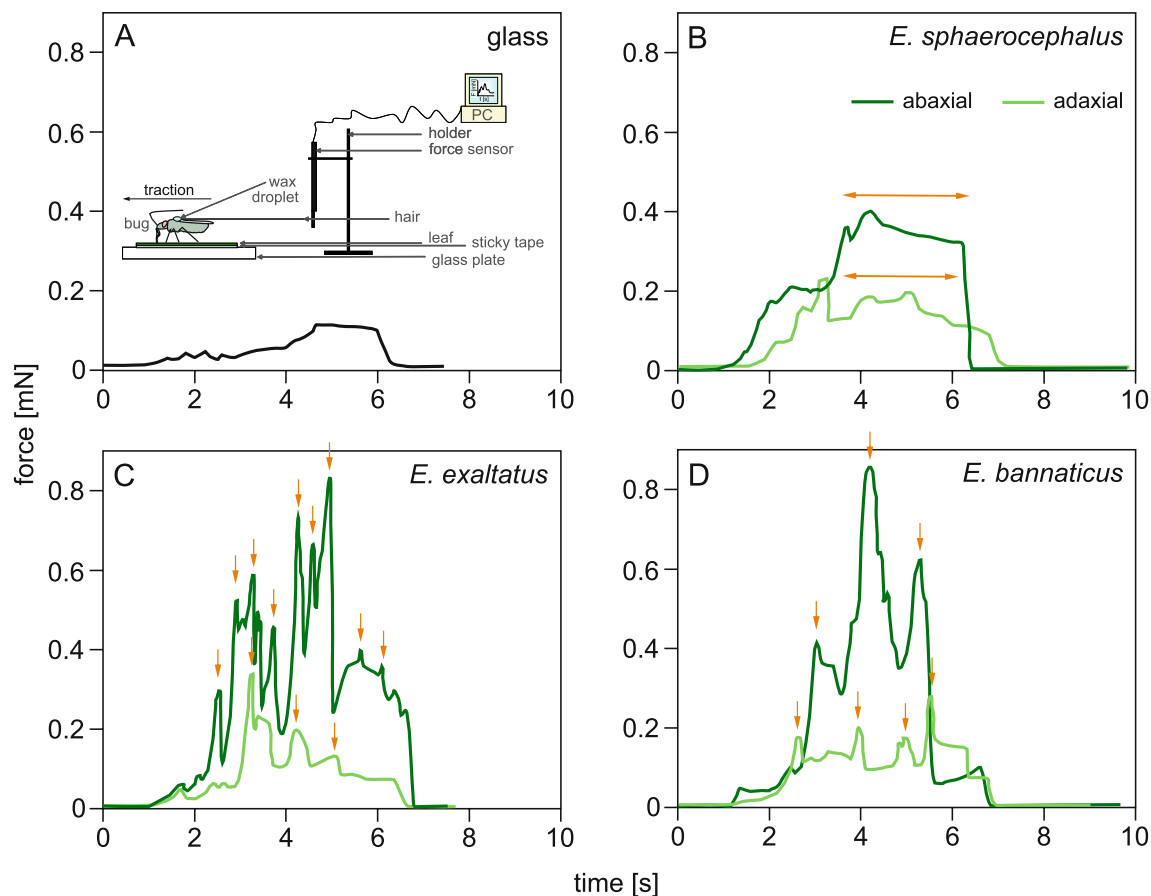


Fig. 5 Force–time curves obtained during traction experiments with *Macrolophus pygmaeus* females on glass (A) and adaxial and abaxial leaves of *Echinops sphaerocephalus* (B), *E. exaltatus* (C), and

E. bannaticus (D). The inset in A illustrates the experimental setup. Double arrows indicate a force plateau. Single arrows point to the multiple force peaks

$p=0.08$). No other relationships were found among the data evaluated in this study.

Discussion

The plant surface

The *Echinops* plants examined exhibit highly complex, three-dimensional growth and various surface structures that differ in arrangement, shape, and dimension. Each species has distinct plant habits and size. The leaf shape and dimension also vary slightly between species and accessions. For example, the narrow, delicately lobed leaves of *E. ritro* ssp. *ruthenicus* have a smaller area compared to the slightly larger leaves in *E. exaltatus*, medium-sized leaves in *E. bannaticus* and broad-lobed leaves in *E. sphaerocephalus* (Fig. S2). Reconsidering the micromorphological differences can help overcome the considerable macromorphological uniformity that complicates sectional classification (Jäger 1987). Differences in the presence and abundance

of various trichome types, epicuticular wax crystals, and cuticular folds can be observed on the adaxial and abaxial leaf surfaces among species and accessions (Figs. 3, S3, S4; Table S1). All observed abaxial leaves of *Echinops* exhibit a dense layer of tomentous trichomes; however, the percentage of leaf area covered and the thickness of the trichomes vary between species (Tables 1, S1). Multicellular, non-glandular trichomes and irregularly dispersed epicuticular crystalline wax plates are regularly found in *E. ritro* ssp. *ruthenicus*, *E. exaltatus*, and *E. bannaticus*. In contrast, *E. sphaerocephalus* largely lacks this trichome type and wax, instead being predominantly covered with glandular trichomes, which are mostly absent in other species. Interestingly, variations in surface structures can also be detected between accessions of the same species, a fact that requires further systematic exploration.

Trichomes, which are common in this plant genus and family, serve multiple functions, including reflecting radiation, reducing water loss, providing insulation, preventing heat loss, retaining nutrients, increasing boundary layer thickness, minimising wind impact on energy budget, and

Fig. 6 Traction forces (**A**) and safety factors (**B**) measured during traction force tests with *Macrolophus pygmaeus* females on glass and *Echinops* leaves (adaxial, abaxial side). Means and error bars, $N=10$ females, $n=5$ runs per female per substrate. The asterisks indicate statistical differences between the adaxial and abaxial leaf sides; two-way ANOVA followed by all pairwise multiple comparison procedures, Holm–Sidak method, $t=2.5$, $P=0.014$. Glass differs significantly from all plant substrates in traction force and safety factor (paired t -test; $P\leq 0.001$; $t=16.8$, $t=15.5$, respectively). See Tables 2 and S3 for statistics

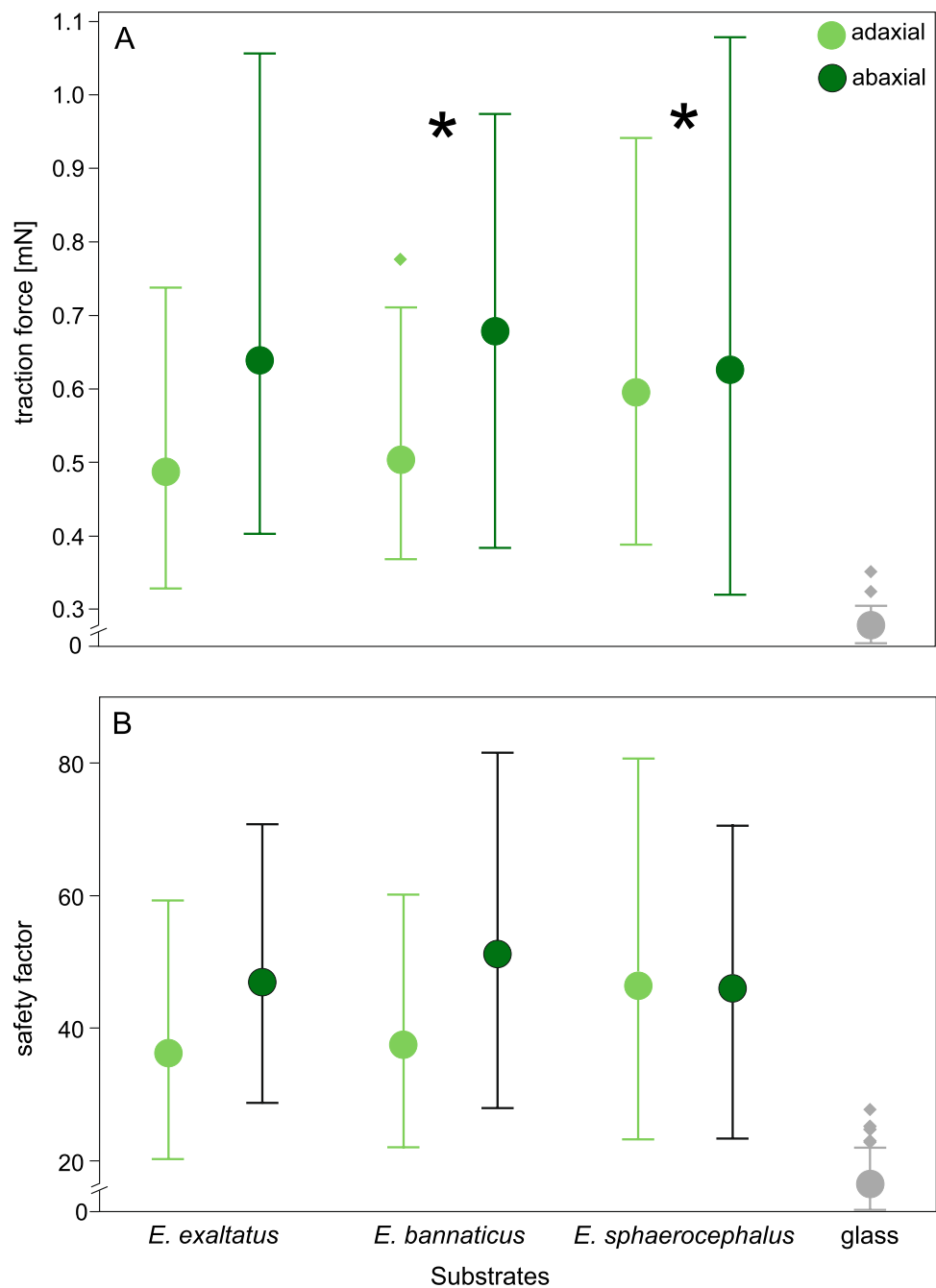


Table 2 Results obtained by a two-way analysis of variance (general linear model) comparing the traction force of *Macrolophus pygmaeus* females between *Echinops* species and leaf sides

Source of variation	DF	SS	MS	F	P
Plant	2	0.03	0.01	0.41	0.67
Leaf side	1	0.21	0.21	6.47	0.01
Plant $\times$ leaf side	2	0.06	0.03	0.90	0.41
Residual	53	1.68	0.03		
Total	58	1.97	0.03		

DF, degree of freedom; SS, square sum; MS, mean square; F , F statistics; P , probability value

establishing a microclimate (Tsukaya et al. 2002; Aschenbrenner et al. 2013; Li et al. 2022; Katinas 2025). They also aid in dispersal through climbing and interlocking mechanisms, such as hook-shaped or sticky structures (Johnson 1975; Press 1999).

Plant surface–bug interactions

A primary role of trichomes is defence, acting as both physical and chemical barriers against herbivores. They impose various nutritional, mechanical, and allelochemical

constraints (Levin 1973; Price et al. 2011). The influence of trichomes on arthropods, particularly families such as Chrysomelidae, Aphididae, Aleurodidae, Cicadellidae, Sphingidae, Noctuidae, and Tetranychidae, has mainly been attributed to the presence of trichomes (Lee et al. 1986; Haddad and Hicks 2000), their density (e.g. Fordyce and Agrawal 2001; Kowalewski and Robinson 1978; Zvereva et al. 1998; Rudgers et al. 2004), shape (Andres and Connor 2003), length (Hoxie et al. 1975; Hoffmann and McEvoy 1985; Dalin et al. 2004), and glandular function (e.g. Duffey 1986). Plant pubescence is known to affect various aspects of arthropod population dynamics, including abundance, mobility, oviposition, development, mortality, body mass, behaviour, host–plant choice and acceptance, and overall performance and fitness (e.g. Ringlund and Everson 1968; Gibson 1971; Hoxie et al. 1975; Benedict et al. 1983; Roberts and Foster 1983; Zvereva et al. 1998; Malakar and Tingey 2000; Valverde et al. 2001; Ranger and Hower 2002; Andres and Connor 2003). Research by Shanower et al. (1996) indicated that a greater length of trichomes results in fewer phytophagous insects. In addition, natural enemies of these insects are often chemically repelled, leading to increased searching and consumption times. Further studies have shown that the walking speed, searching efficiency, and encounter rates of Coccinellid larvae decrease on hairy plant substrates (Shah 1980, 1982; Belcher and Thurston 1982; Obrycki and Tauber 1984; Carter et al. 1984; Grevstad and Klepetka 1992). The ladybird beetles themselves, along with their integument, may be harmed by hook-shaped trichomes (Putman 1955; Walters 1974; Dixon 1986; Quilici and Ipertti 1986; Obrycki 1986; Eisner et al. 1998). Several species of Chrysopidae are hindered by a highly dense pubescence (Arzet 1972; Elsey 1974; Dos Santos et al. 2003; Simmons and Gurr 2004, 2005). Predatory thrips have also been found to become impaled by hooked trichomes (Sengonca and Gerlach 1984). Furthermore, parasitoids are frequently deterred and harmed by the complex pubescence of plant surfaces (Rabb and Bradley 1968; Keller 1987; Andow and Prokrym 1990; Kashyap et al. 1991; Jervis and Kidd 1996; Gingras and Boivin 2002).

However, some arthropods, like the omnivorous predatory mirid bugs *M. pygmaeus*, are not adversely affected by trichomes (Perdikis and Lykouressis 1997, 2000, 2001; Ter Horst 2000). The present study confirms that these bugs prefer and perform better in pubescent terrains, likely due to trichome characteristics. This preference, alongside the provision of niches, shelters, and enemy-free spaces, may help explain the high abundance of *M. pygmaeus* in *Echinops* crops.

In related *D. errans* mirid bugs, longer and thicker (living) trichomes resulted in higher traction forces. This finding does not apply to *M. pygmaeus*, which generates lower forces on thicker, dead, twisted trichomes. However, larger

leaf areas covered with these types of trichomes tend to correlate with higher safety factors, which is reflected in significantly higher traction forces on abaxial leaves, where the layer of tomentous trichomes, composed of dead twisted trichomes, is predominant. Therefore, reliable footholds could be another reason, in addition to microclimate and shelter, why ‘thin-skinned’ mirid bugs are mostly found on the undersides of leaves in fields.

Contrary to previous reports suggesting that high trichome density can hinder insects in their prey search (Belcher and Thurston 1982; Obrycki 1986; Kauffman and Kennedy 1989; De Clercq 2008; Adedipe and Park 2012), the number of trichomes per unit area is slightly positively related to *M. pygmaeus*' traction force, while no relation was found in studies with *D. errans*. The interspecific differences in attachment ability may be attributed to morphometric divergence. Comparisons of female traction forces on glass turned out that, generally, larger mirid bug species generate higher forces: 3.2-mm-long *M. pygmaeus*: 164 μN (12.1 times body weight), 4.7-mm-long *Dicyphus errans*: 230 μN (6.1 times body weight), and 4.9-mm-long *Pameridea roridulae* Reuter (Heteroptera, Miridae, Bryocorinae, Dicyphini): 692 μN (47 times body weight) (Voigt et al. 2007; Voigt and Gorb 2010). It is noteworthy that the latter species resides on the glandular hairy carnivorous plant *Roridula gorgonias* Planch. (Roridulaceae), relying on a defence strategy and possessing an anti-adhesive epicuticular layer, which, along with its behaviour and strong traction, allows it to navigate among sticky trichomes. In contrast, *M. pygmaeus* and *D. errans* maintain distance between the fragile body and pubescent plant surfaces by using longer legs and specialised claws. The body length-to-width ratio is lower in the smaller *M. pygmaeus* (3.0) than in *D. errans* (3.9), corresponding to body length-to-leg length ratios of 0.9 and 0.5, respectively (Wagner 1970; Voigt and Gorb 2010). Thus, *M. pygmaeus* appears more compact, with relatively thicker and shorter legs, leading to a shorter distance between its body and the substrate. These physical characteristics may affect the bug's ability to navigate plant surfaces, potentially causing it to move less or more gently on glandular hairy leaves (Fig. 5B) to avoid sticking. Additionally, *M. pygmaeus* spends more time grooming on glandular substrates (Hillert et al. 2002; Ter Horst 2000). Sarmah et al. (2019) noted that these bugs tended to fall off leaves densely covered with glandular trichomes, which could hinder their movement. Similarly, for *D. errans*, the traction force has been shown to decrease with increasing substrate adhesion force, and the pretarsi became contaminated when walking over glandular surfaces (Voigt et al. 2007). However, the Bryocorinae mirid bugs may overcome the sticky plant substrate, unlike true bug larvae from the family Anthocoridae, which have been observed getting caught in hooked and glandular trichomes (Evans 1976; Coll et al. 1997).

On the surfaces of *Echinops* species, *Macrolophus* mirid bugs produce mean traction forces ranging from 485 to 636 μN , which corresponds to 37–47 times their body weight. In contrast, *D. errans* generates higher traction forces on pubescent plants, ranging from 720 to 1213 μN , but with lower safety factors (2 and 33). The claw shape and dimension differ between the two mirid bug species: *M. pygmaeus* has shorter claws (55 μm) with a round shape, while *D. errans* has shepherd's-hook-shaped claws that are 75- μm -long (Southwood 1986; Voigt and Gorb 2010). Interestingly, the diameter of the circle fitting the claw concavity is similar in both species (15–16 μm). However, *M. pygmaeus* lacks the pronounced, interlocking claw base found in *D. errans*. This functional deficiency may be compensated for by the obviously elastic distal part of the third tarsomere, which has not been observed in other species so far, making the tarsus–claw connection flexible and adaptable (Fig. 4D).

Similar to other arthropods, both mirid bug species face challenges on glabrous and pruinose substrates, as indicated by significantly lower traction forces on the waxy adaxial *Echinops* leaf surfaces. Nevertheless, they can still achieve reliable safety factors due to the presence of interspersed trichomes, which may be advantageous for generating grip (Figs. 5C, D, 6, Table 2). Previous research has shown that crystalline waxy surfaces interfere with attachment in various insect families, including Anthocoridae and Miridae (Lauenstein 1976, 1980; Voigt et al. 2007), Chrysopidae (Eigenbrode 2004), Coccinellidae (Eigenbrode et al. 2009), and Chrysomelidae (Gorb and Gorb 2002), among others (Stork 1980b; Jeffree 1986; White and Eigenbrode 2000). The combination of minor cuticular folds and superimposed wax crystals on the adaxial leaves of *E. exaltatus* and *E. bannaticus* poses particular challenges for honeybees and green bottle flies regarding foothold (Bräuer et al. 2017). On these surfaces, insect claws are unable to interlock, and adhesive pads are hindered by minimised contact, contamination, or the formation of slippery films (Gorb and Gorb 2002). Given that effective attachment significantly correlates with ontogeny and prey consumption, which ultimately influences fitness (Southwood 1986; Voigt 2002, 2005, 2019), it may explain why *M. pygmaeus* struggled to control established aphid populations on predominantly glabrous *Capsicum annuum* and perished before moulting to adult (Messelink et al. 2015).

Conclusion

The mechanical interactions between plant surfaces and the feet of *M. pygmaeus* are particularly relevant to biological control, especially considering the predatory activity of mirid bugs in croplands, such as fields and greenhouses (Schewket Bey 1930; Geiler 1963; Kolbe and Bruns 1988;

Aviron et al. 2016; Saulich and Musolin 2019). This study confirms the significance of insects' foothold on plant substrates, as previously demonstrated for life history and prey consumption in *D. errans* (Voigt 2019). When insects make contact with plants, diverse traits of the plant surfaces meet diverse traits of the insect surfaces, leading to a diversity of interactions based on the species involved. These aspects should be thoroughly considered in future studies and strategies related to biological control, as bio-control agents are most effective when released onto suitable substrates. The ability of Bryocorinae mirid bugs to navigate on glandular hairy plants makes them promising predatory candidates for biological control of herbivores on plant substrates, which are challenging for other natural enemies.

The omnivorous lifestyle of predatory mirid bugs, such as *M. pygmaeus*, implies complex interactions across multiple trophic levels as they serve as 'intermediate agents' within food chains (Costanzi and Pini 1991; Benuzzi and Mosti 1994; Alomar and Wiedenmann 1996; Eubanks et al. 2003; Voigt 2019). This ecological role places mirid bugs between predators *sensu stricto* and other entomophagous arthropods such as parasitoids, thus stabilising ecosystem networks. This context must be carefully taken into account when planning biological control, as 'intermediate agents' function effectively when they are part of multispecies communities.

The interactive role of plants in biological pest control (Cortesero et al. 2000; Maselou et al. 2014) and the potential of *Echinops* species as long-term habitats for mirid bugs suggest their use as banker plants for sustained establishment in commercial fields and greenhouses. The longer crops are established, the higher the population density and dispersal in cultivated areas, ultimately leading to increased consumption rates (Agustí et al. 2020; Sánchez et al. 2021). These findings stimulate long-term banker plant management in agricultural systems, which can ensure the long-term settlement and timely presence of natural enemies.

In summary, the ability of insects to attach, the characteristics of plant surfaces, and the interactions at their interface require more attention and further investigation. Understanding these factors is crucial for assessing life history, prey consumption, and multitrophic plant–insect associations in relation to evolution, ecology, and sustainable pest management.

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Author contributions Dagmar Voigt contributed to conceptualisation, data curation, formal analysis, investigation, methodology, resources, software, validation, visualisation, writing—original draft, and writing—review and editing. Gert Horn contributed to resources and writing—review and editing. Stanislav Gorb was involved in methodology and writing—review and editing.

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Data availability All data needed to evaluate the conclusions in the paper are present in the article and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Declarations

Conflict of interest The authors declare no conflict of interest.

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