

Micro-terraforming by Antarctic springtails (Hexapoda: Entognatha)

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ABSTRACT

It has long been an axiom of Antarctic terrestrial ecology that interactions between terrestrial invertebrates and their abiotic environment are unidirectional: they are affected by their extreme environment in numerous ways, but they themselves do not affect their environment. Field observations in tandem with laboratory investigations of the exuvial refugia of the springtail *Gomphiocephalus hodgsoni* Carpenter, reported here, challenge this long-held assumption. These previously undescribed structures consist of minute lithic particulate matter that has been bound together by the accumulation of moult exuviae. Macrophotography, microscopy and manipulation assays demonstrated that the exuviae act as a kind of ‘cement’. Detachment of exuviae by emulsification indicated that this is mediated by the accumulation of cuticular hydrocarbons (retained in shed exuviae) at the lithic–exuvial interface. In addition to re-enforcing preferred microhabitat features by extending the hygrially buffered refuge phenotype, these structures contribute to primary soil formation processes through the structural cohesion of particulate matter. These by-products of moulting behaviour represent the first tangible evidence of environmental modification by terrestrial invertebrates on the Antarctic continent.

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Introduction

Isolation, environmental extremes and depauperate floral and faunal communities make polar habitats natural laboratories for investigating the minimal conditions capable of supporting biological interactions on Earth. Although some fundamental insights into ecological minima have been provided by the sophisticated manipulation of microcosms (e.g. Lawton et al. 1993, 1998), the importance of polar habitats is not only the presence of ‘real minima’, but also the presence of a set of environmental characteristics that are responsible for such ‘real minima’ (Convey 1996; Peck et al. 2006).

To date, most of what we know about the ecological interactions of minimal conditions in polar habitats is concentrated in the Arctic where, for example, the ‘simplicity’ of trophic interactions and the expected sequence of primary community assembly have been challenged (Hodkinson et al. 2001, 2002, 2003, 2004; Hodkinson and Coulson 2004;

Hawes 2008a; Hågvar and Ohlson 2013). A few studies have also specifically highlighted the potential for facilitation of ecological processes by invertebrates (Birkemoe and Liengen 2000; Hodkinson et al. 2001; Hågvar and Ohlson 2013). By comparison, traditionally, ecological interactions in Antarctica have been considered to be even more 'minimal' – although there is a general consensus that such a designation is based more on logical supposition than field evidence (Hogg and Stevens 2002; Hogg et al. 2006; references therein; Caruso et al. 2013).

Hence, the current view of ecological interactions for Antarctic terrestrial organisms might be summarized hierarchically: (1) abiotic→biotic (extensive interactions predicted, extensive interactions observed); (2) biotic↔biotic (few interactions predicted, few interactions observed); and (3) biotic→abiotic (no interactions predicted, no interactions observed). Although the relative ranking of each of these classes of interactions will probably not be altered by new information, it is clear that a more complicated and holistic picture of life histories and adaptations will continue to emerge as our knowledge of the biota grows. For example, recently examined abiotic→biotic relations in Collembola include the effect of ultraviolet radiation on physiology and behaviour (Hawes et al. 2012) and the stochastic effects of habitat hydrological regimens on survival (Hawes 2011). Similarly, recent investigations of the Antarctic fairy shrimp, *Branchinecta gaini*, have revealed evidence of biotic↔biotic interactions (cannibalism) and hinted at biotic→abiotic interactions through the mechanical breakdown of detritus in freshwater pools (which in turn sustains the food base of subsequent generations) (Hawes 2008b).

Indeed, ultimately, it is not the magnitude of contributions that makes polar biotic↔biotic and biotic→abiotic interactions interesting, but their existence in the first place – the presence of 'ecology' in what has often been considered to be an 'ecological vacuum'. For example, springtails (Collembola) are one of the most successful invertebrate taxa, flourishing in every terrestrial biome on the planet, from the tropics to Antarctica (Hopkin 1997). In Continental Antarctica they are the largest land animals of ice-free refugia. In tandem with mites, nematodes, tardigrades and rotifers they constitute the primary faunal elements of an ecosystem that is characterized by the extreme simplicity of its interactions (e.g. Block 1984; Convey 1996; Hogg and Stevens 2002; Velasco-Castrillón et al. 2014). Consequently, it has been assumed that the direction of interactions between this fauna and their abiotic environment is unidirectional: their environment affects them in numerous ways (e.g. Hawes, Bale, et al. 2008; Hawes, Worland, et al. 2008; Hawes 2011; Hawes et al. 2012), but not vice versa.

Gomphiocephalus hodgsoni Carpenter is named after Thomas Vere Hodgson, the biologist on Scott's *Discovery* Expedition of 1901–1904 (Carpenter 1908). The Expedition landed at Granite Harbour and collected samples of some of the first Antarctic 'aptera', which were ultimately described and named by Carpenter (1908). Over the intervening period of over a century, the taxonomic status of these hexapods has undergone various twists and turns, culminating recently with a reaffirmation of the endemic status of the genus and species by both morphological and molecular data (Greenslade et al. 2011). They are the most common and well-known species of Collembola in Continental Antarctica (Janetschek 1967; Peterson 1971; Stevens and

Hogg 2002), where they are found in ice-free areas in the soil and under the surface of stones (Peterson 1971).

In addition to its customary somatic functions (Hopkin 1997), the moult biology of Antarctic springtails has already been found to interact with, and/or facilitate, their occupation of Antarctica's extreme terrestrial habitats in a number of ways including increased survival and tolerance of low temperatures (Worland 2005; Worland and Convey 2008), the off-setting of starvation (Hawes, Worland, et al. 2008; Hawes 2011), the provision of 'rafts' for floating on water bodies (Hawes, Worland, et al. 2008), and the avoidance of ultraviolet radiation photic damage by preferentially moulting in a non-illuminated habitat space (Hawes et al. 2012). This paper describes how the by-products of *G. hodgsoni* moulting behaviour (aggregation, microhabitat selection and ecdysis) have material consequences for both its autecology and immediate micro-environment. Field observations revealed extensive temporal accumulation of exuviae in association with their moult sites – microclimatically buffered under-stone habitats. These exuvial accumulations were found to be responsible for the binding of lithic particulate material together: the first unequivocal documented evidence of structural habitat modification by terrestrial invertebrates in Antarctica.

Methods

Study site

Fieldwork was carried out in January 2010 during a field visit to Granite Harbour, Victoria Land (Hawes 2011; Hawes et al. 2012). The ASPA (Antarctic Specially Protected Area) adjacent to the field camp and study area is the type locality for *G. hodgsoni* (77°00'30"S, 162°34'00"E) (Carpenter 1908; Davidson and Broady 1996; Greenslade et al. 2011). The study area was a rocky shoreline extending to the moraines of the Mackay Glacier terminus, bounded on its northerly side by steep rock scree slopes that lead up to Mount England, and on its southerly side by sea ice. Supporting laboratory work (microscopy, assays, exuvial density) was carried out in New Zealand from February to March 2010. A subsample (c.10 g) of the particulate matter from each of 20 refugia was carefully brushed from the rock surfaces and collected and transported back to the laboratory. To randomize the subsequent examination and analysis of these microstructures (see below), all samples were pooled (c.200 g).

Field observations and survey

Representative photographs were taken of exuvial structural modifications and a macro-photographic survey of 57 rocks was undertaken over a 20-m² area in which springtail populations were found to be concentrated. Photographs were taken with a super-macro (1 : 1) lens (Canon Axiophot A480, Canon Inc., Tokyo, Japan). Each rock (c.10–45 × 10–45 cm) was photographed individually at different scales of magnitude. A two-category classification system was devised to describe the structures: (1) microstructures (small aggregations of < 20 particles held together by moult exuviae); and (2) macrostructures (aggregations of > 20 particles held together by moult exuviae). (The largest microstructure observed in the sample set was composed of 15 stone particles). The

former may be considered to include structures in embryonic form and/or peripheral materials that were cemented together but unconnected to a larger structure. These microstructures are therefore equally likely to represent future macrostructures (i.e. their building blocks) or an unknown arbitrary factor responsible for limiting the further growth of particle aggregation (e.g. rock preference of springtails, particle abundance beneath the rock, etc.). Macrostructures, by contrast, may be considered, the modification of habitat in its more developed form. The following parameters were quantified for both microstructures and macrostructures: percentage presence of structures; mean number of structures per stone; mean number of particles in the largest exemplar from each stone; association with exuviae; association with surface irregularities (e.g. grooves, depressions, in under-stone micro-topography); and association with algae or lichens.

Microscopy

Microstructures were examined under an Olympus C011 Dissecting Microscope with 10 × eyepieces and 1–4 × zoom (total magnification 10–40 ×) (Olympus Co. Ltd, Tokyo, Japan). The density of exuviae on particle surfaces was noted. Samples of aggregated particles were carefully teased apart using entomological forceps to identify the binding sites of the stone particles and establish whether the binding sites were the exuviae or the surface of the stones or some previously unseen alternative. Representative photographs were taken with a camera attached to the microscope eyepiece.

Bond strength assay

An assay to test the strength of the bond produced between the individual particles of the microstructures, provided further confirmation that the exuviae were responsible for cementing the particles together. Microstructures were teased apart as described for the microscope analysis. All individual particles were then pooled. Then five stone particles were chosen at random, pushed together so that the edges of all particle surfaces were touching those of another. A drop of water (c.1 ml) was pipetted on to the touching particles so that all particles were submerged. The five particles were then left to dry at room temperature. After the water had evaporated, the five particles were tested for the strength of their re-cohesion. The same submergence and cohesion test procedure was carried out simultaneously on five particles without moult exuviae. Replicates of 25 (25 × 5 particles) were tested for both particles with and without exuviae. The test for cohesion consisted of counting the number of ‘turn-overs’ it took for the five particles to separate. A fine paintbrush was used to turn-over (i.e. dorsal surface to ventral surface, ventral surface to dorsal surface, and so on) the five particles together. The number of turn-overs it took for each particle to separate from the rest was noted as t1 to t4 (where t1 represents the separation of the first particle and t4 represents the separation of the remaining fourth and fifth particles).

Emulsification assay

The role of hydrophobicity in the attachment of the exuviae to the lithic surface was assayed by the application of an emulsification agent. Individual particles ($n = 48$; size c.2–5 mm) with exuviae attached to their surfaces were placed in the wells of plastic multi-well cell culture plates (Sigma-Aldrich Ltd, St Louis, MO, USA). A second control treatment (no exuviae) was simultaneously established in another set of wells ($n = 48$; size c.2–5 mm). Every particle in each treatment was then individually submerged. The first treatment was submerged under a combination of water and liquid detergent (1 : 10 ml), the second control treatment was submerged under just water. All wells were left at room temperature and checked after 48 h for exuvial detachment.

Exuvial density

Forty-eight small stones were collected from a randomized pool of particulate matter with exuviae. These were used to provide a measure of exuvial density (number of exuvial skins per particle). Counts of detached exuviae represent samples that were, on visual inspection, > 75% 'entire', with 'parts' of exuviae and older amorphous material excluded.

Statistics

Pearson's correlation coefficient was used to test the association between exuviae and macrostructures and microstructures. Spearman's rank correlation was used to test for associations between macrostructures and microstructures and the presence of either lichen or rock surface irregularities. An unpaired *t*-test was used to compare the re-bonding ability of stone particles with and without exuviae. As n was > 30, a *z*-test was used to compare proportions of samples from water and detergent treatments in which exuviae detached from stones. Calculations were performed in Minitab 17 (Minitab Inc., State College, PA, USA).

Results

Field observations and survey

Springtail aggregations and/or moult exuviae were located underneath rocks in association with small piles of aggregated lithic and other particulate matter. These clusters or aggregations of small stones and particles were found to be directly associated with the remains of springtail exuvial casts. Closer inspection revealed that many of these small stones appeared to be 'cemented' together by the exuviae. These bound microstructures were often visibly occupied, or used as an interstitial lattice, by the springtails: [Figure 1](#) shows a well-developed macrostructure occupied by springtails and dismantled manually using a paintbrush to reveal a representative building block or micro-structure. A field survey confirmed that these structures were not an isolated occurrence confined to a few stones, but a widespread local phenomenon ([Table 1](#)). Macrostructures were rarer as a result of patchy populations, but their building blocks, the microstructures, were observed on all sampled rock surfaces where springtails and/or exuviae were

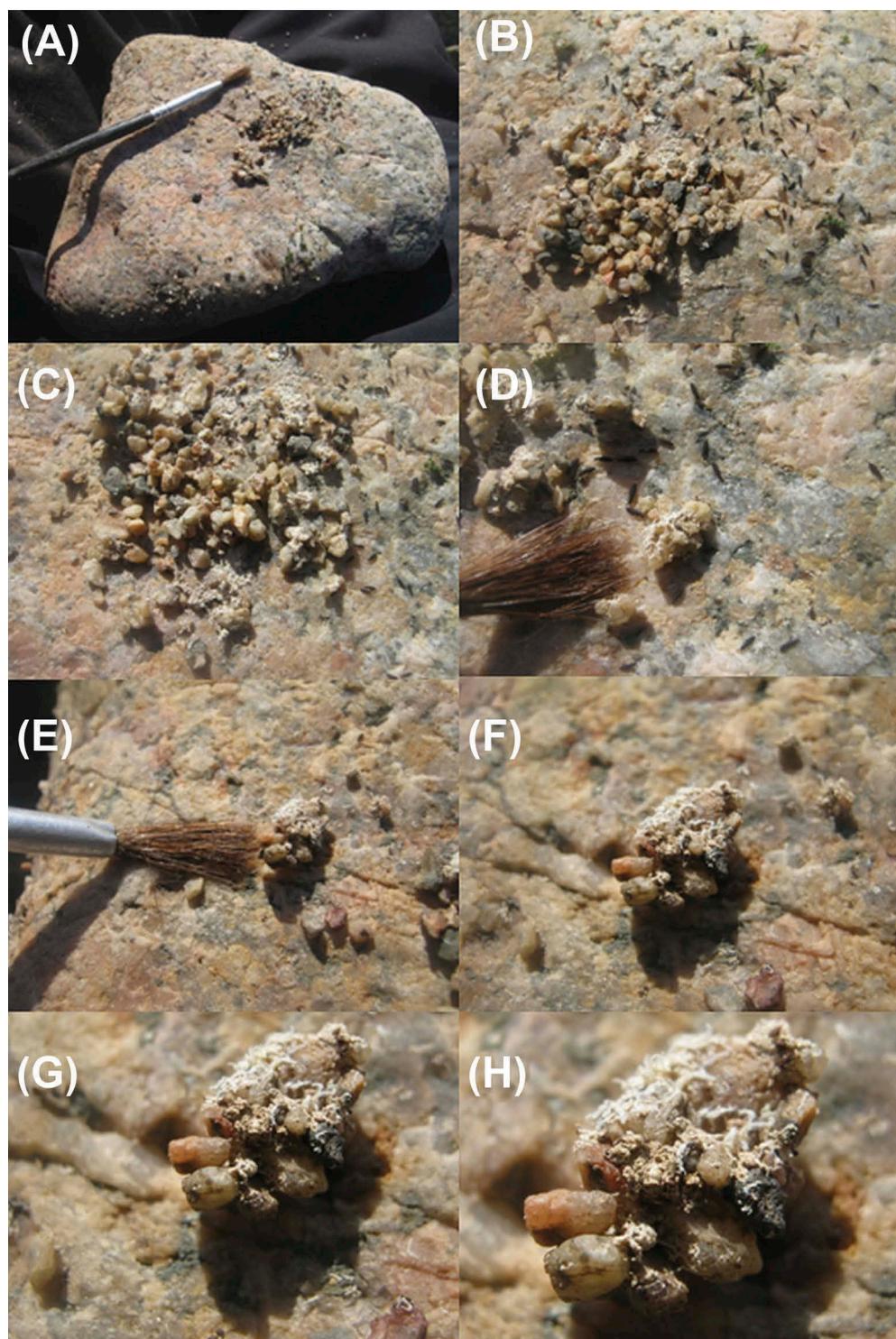


Figure 1. Dismantling of representative field macrostructure to reveal it is composed of microstructure building blocks: (A) undersurface of entire rock with paintbrush for scale (brush whisker

Table 1. Field survey of under-surfaces of stones ($n = 57$) for springtail habitat modification and associated variables.

	Percentage presence (%)	Mean number per stone	Mean number of particles in the largest structure from each undersurface	Association with exuviae (%)	Association with surface irregularities (grooves, depressions, etc.) (%)	Association with lichen (%)
Macrostructures	56.14	0.62 ± 0.11	51.96 ± 5.07	100	18.75	9.38
Microstructures	100	6.53 ± 0.67	6.95 ± 0.52	100	26.86	9.56

found. Pearson's correlation coefficient found a highly significant relation between the presence of exuviae and both macrostructures ($n = 57$; $r = 1$; $p < 0.001$) and microstructures ($n = 57$; $r = 1$; $p < 0.001$). Spearman's Rank correlation found no statistically significant association between number of microstructures per rock and the presence of surface micro-topographic irregularities ($r = -0.18$; $p = 0.19$; two-tailed test) or the presence of lichen on rock surfaces ($r = -0.26$; $p = 0.053$; two-tailed test); or between the presence of macrostructures and surface irregularities ($r = -0.37$; $p = 0.08$; two-tailed test) or lichen ($r = -0.34$; $p = 0.13$; two-tailed test).

Two 'unusual' observations are worthy of mention. For most observed instances of exuvially mediated aggregation of lithic matter, cohesion is achieved through the presence of many exuviae. However, one microstructure suggested that this may not be necessary: [Figure 2](#) shows a small quartz-like particle attached to its base with what appears to be only one exuvial skin. In contrast, photographs from another sample stone demonstrate that, given enough exuviae, the small stones cease to be the 'bricks' of the structure, and become instead the scaffolding or 'mortar' for a dense web of exuvial remains within which the springtails may seek refuge ([Figure 3](#)).

Microscopy

Observation of the nest particulate matter under a dissecting microscope confirmed the attachment of exuvial skins to the lithic surface and the extent to which nest matter was encrusted by exuviae ([Figure 4](#)). Stone surfaces also showed extensive evidence of temporal accretion: exuviae on the particle surfaces ranged in condition from amorphous almost powdery encrustations to fully identifiable, freshly shed skins. [Figure 4](#) shows a typical cemented microstructural 'unit' in the different stages of being teased apart into its constituent parts. The photo-sequence shows how the single encrusted unit is actually composed of six small stones: close-ups show representative exuvial attachments at different stages of separation, from extensive attachment ([Figure 4\(I\)](#)), to the late stages of separation ([Figure 4\(M\)](#)), to the final stages of separation ([Figure 4\(D, G\)](#)).

length = 11 mm); (B) close-up of moult refuge with springtails (body size c.1 mm) visibly dispersing around its periphery; (C) refuge after manual disturbance by paintbrush to identify microstructures; (D) a microstructure is selected for further examination; (E–H) progressive magnifications of microstructure demonstrate it is bound by a 'cement' of exuvial remains and is composed of many small stone particles.

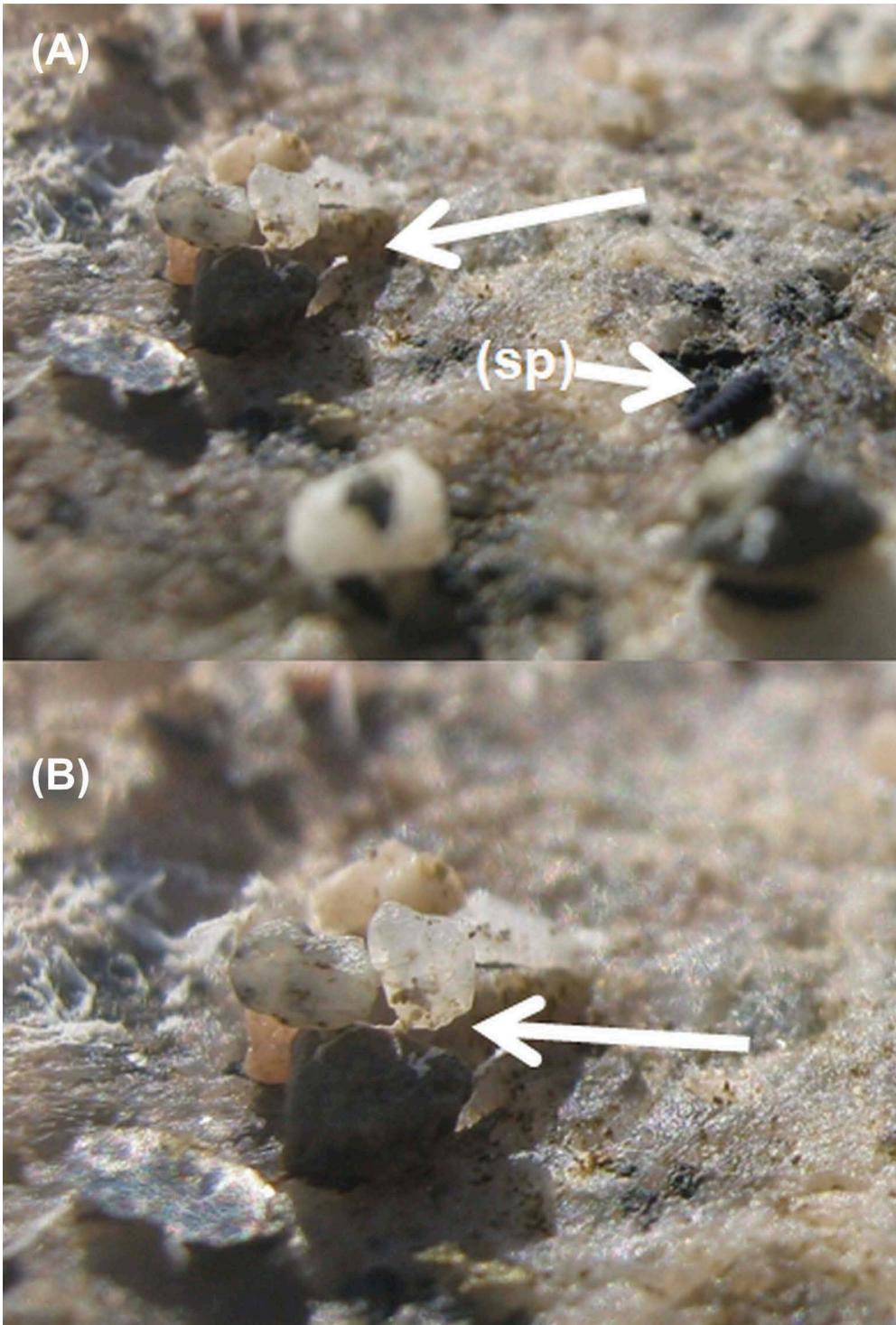


Figure 2. Microstructure unit from field survey rock #11: (A) with springtail in foreground ('sp.') for scale (body size c.1 mm); (B) further magnification reveals that the 'cement' is composed of only a single exuvial strand. (White arrows indicate site of 'microstructure' binding.)

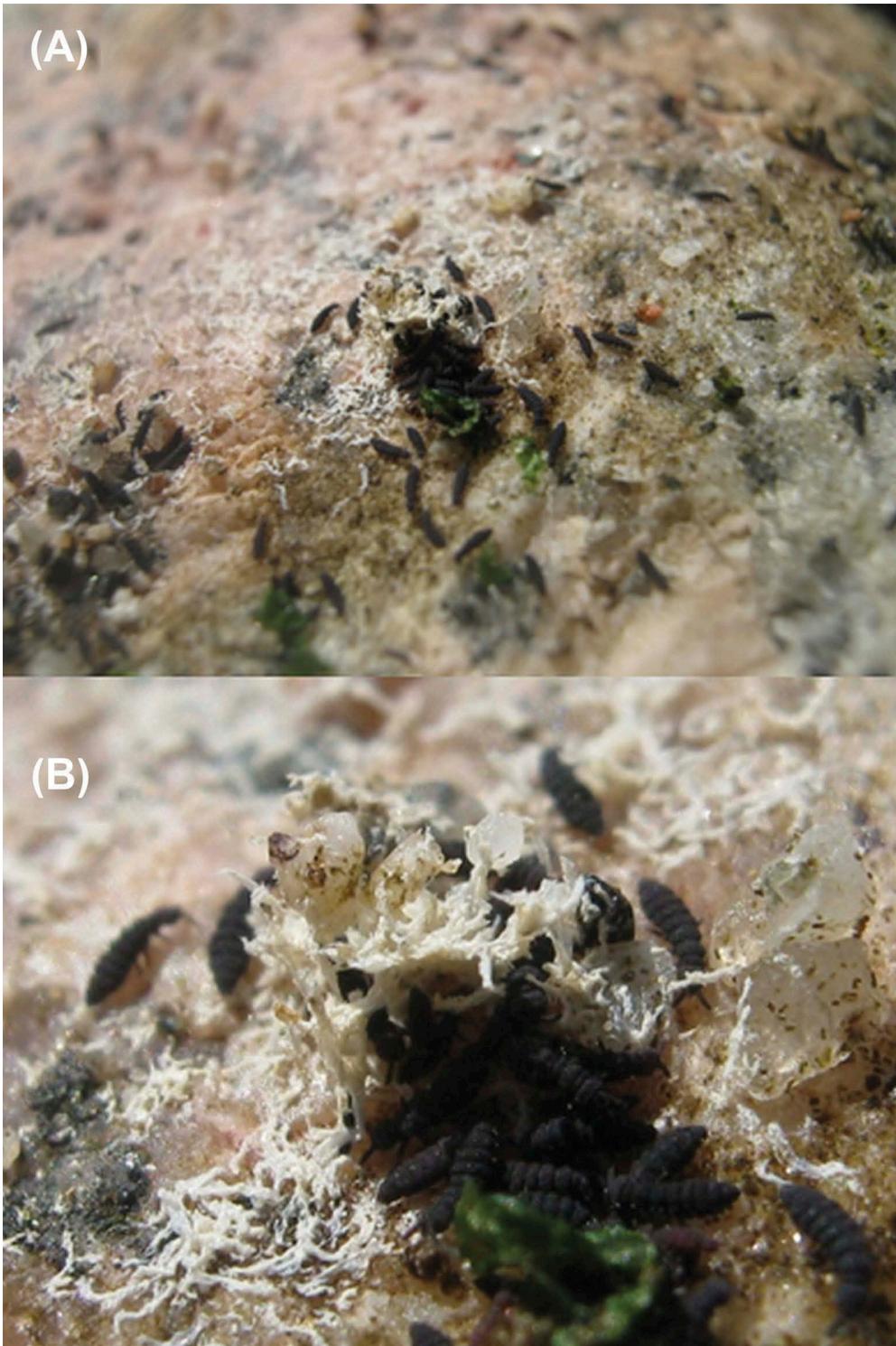


Figure 3. Extreme exuvial density of field survey rock #13 shows how the stone particles may become scaffolding for an exuvial 'web' composed of many exuviae joined together. Note the associated high density of springtails (body size c.1 mm) using it as a refuge.

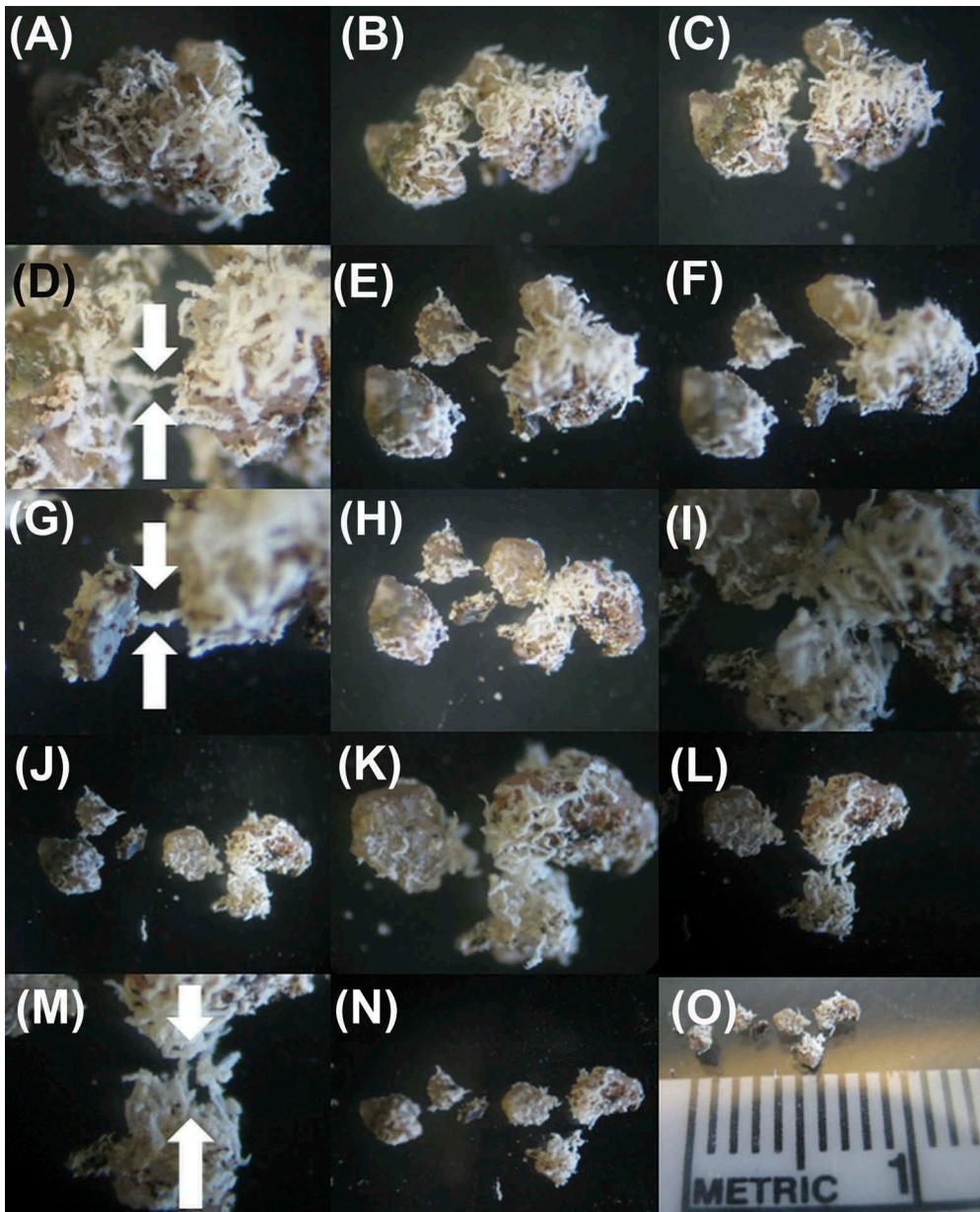


Figure 4. Microstructural unit 'cemented' together by exuviae and teased apart to reveal it is composed of six small stones (size c.1–2 mm). Images: (A) single 'cemented' unit; (B–D) first stone separated, with (D) close-up of separation; (E) a second stone is separated; (F–H) a third stone is separated, with (G) close-up of exuviae; (I–K) separation of fourth stone, with (I) close-up of exuviae; (K–M) fifth and sixth stones separated, with (M) close-up of exuviae; (N) all six stones separated; (O) all six stones beside the 1-cm mark of a ruler for scale. (White arrows highlight exuvial attachment on separating stones.)

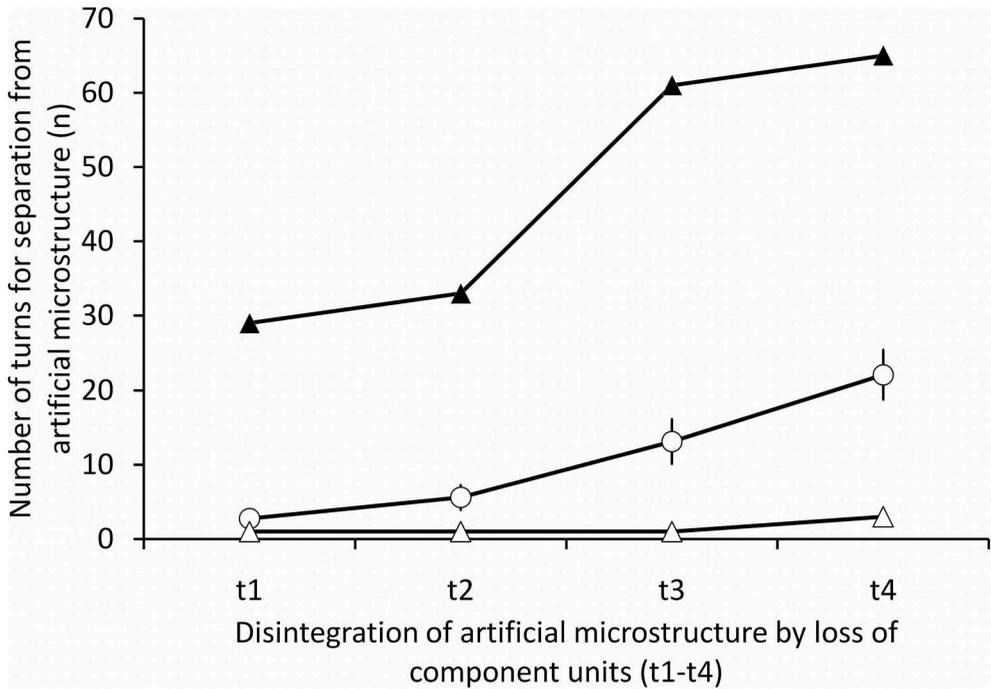


Figure 5. Disintegration of microstructures artificially created from component units of naturally occurring particle aggregations in response to turn-over test. Black triangles represent maxima; white triangles represent minima; white circles represent means. The symbols t1–t4 represent the sequential separation of stones from the artificial microstructure, where t1 represents the first particle to lose cohesion and t4 represents the separation of the final fourth and fifth particles.

Bond strength assay

The role of exuviae in mediating attachment and cohesion was further confirmed by the creation of artificial microstructures using separated component material. It was possible to re-bond exuvially encrusted particles together just by wetting, pressing them together, and leaving them to air dry. A turn-over test to assay the strength of the bonds in these artificial microstructures found a mean total cohesion of 22.08 (± 1.15) turns, with a minimum total cohesion of 3 (± 1.67) turns, and a maximum total cohesion was 65 (± 3) turns (Figure 5). In contrast, particles without exuviae that were treated to the same protocol disassembled immediately ($n = 25, 25; t = 0; p < 0.001$).

Emulsification assay

An emulsification assay demonstrated the role of cuticular hydrocarbons in mediating the attachment. Only stone particles submerged in dilute liquid detergent showed evidence of complete or partial exuvial detachment after 48 hours ($n = 48, 48; z = 9.8; p = < 0.001$).

Exuvial density

The potential extent of exuvial deposition is readily observed in [Figures 3](#) and [4](#). The mean number of exuviae counted from individually emulsified stone particles was 27.27 (\pm 3.51). The maximum number of exuviae counted on one stone particle was 113.

Discussion

The springtail *G. hodgsoni* is an autogenic engineer (*sensu* Jones et al. 1994): it uses its own organic material to modify its environment. Field and laboratory observations of the moult refugia of *G. hodgsoni* unambiguously demonstrate that their exuviae are responsible for aggregation of particulate matter. Likewise, observed active occupation of these sites ([Figures 1–3](#)), in tandem with evidence for temporal accumulation of exuviae, demonstrates that these moult refugia represent the products of repeated, site-specific aggregations.

Springtails, particularly in dry, desert-like polar landscapes – the site of observations was a habitat matrix of sand and gravel interspersed with larger rocks – actively seek out moist micro-sites for ecdysis (when they are most at risk of water loss) (Hopkin 1997). In addition to cementing the stones together, the exuviae may also contribute to preventing desiccation. As the exuviae are, in effect, the hydrofuge skins of the springtails, their deposition and layering around the moult-sites may be hypothesized to further reduce organismal water loss (and their consequent attractiveness as moult sites) by a kind of ‘wallpaper effect’. Hence, at the densities observed here, a semi-impermeable extended phenotype, composed of shed dermal excreta and stone, is formed around the springtails.

Although these refuges are passive by-products of moulting behaviour they are, nonetheless, actively mediated through behavioural re-enforcement. Research on other species of springtails has highlighted the tendency of springtails to aggregate and show moult-site fidelity during moulting (Hopkin 1997 and references therein), which is, in turn, re-enforced by pheromonal cues (e.g. Verhoef et al. 1977; Benoit et al. 2009). As springtails spend most of their lives individually foraging, both the hygric environment of these moult refugia and their promotion of aggregation, may also encourage the utilization of these sites for mating and egg-laying (e.g. see Schulte et al. 2008). It seems reasonable to infer that moulting feeds a positive feedback loop that facilitates further use and growth of the structures. Although, realistically, such feedback – in interaction with the patchy population dynamics typical of polar Collembola (e.g. Usher and Booth 1986; Stevens and Hogg 2003; Hayward et al. 2004; Hawes et al. 2010) – may serve to confine such temporal accretion to isolated spatial points in the suitable habitat matrix.

While not an act of sociality in the immediate sense (Wilson 1975), these constructions are nonetheless the products of a kind of abstract, indirect socializing of generations – a meeting of generational remains. Previous understanding of sociality in Collembola has noted only their ability to aggregate in a number of ways, including moulting and mass migrations (Hopkin 1997). That such aggregations may have more material significance is worthy of further consideration. In particular, the presence of Collembola at high latitude and alpine sites of community assembly – both geo-

historically and in association with Holocene ice-retreat (Davidson and Broady 1996; Hogg and Stevens 2002; Hodkinson et al. 2004; Convey and Stevens 2007; Hawes 2008a, 2015; Hågvar 2010; Ávila-Jiménez and Coulson 2011) has been assumed to facilitate soil formation primarily through allochthonous inputs (Hodkinson et al. 2002) and grazing (Birkemoe and Liengen 2000; Hågvar and Ohlson 2013). A structural contribution to assembly processes, reported here for a Continental Antarctic site, may be more widespread at the micro-scales at which Collembola live their lives. Further research to elucidate the ecological significance of these structures might profitably focus on both facilitation of soil formation itself, and the facilitation of floral and faunal assemblages in and around these structures.

'Terraforming' literally means the 'shaping' of 'earth'. The exuviae of the springtail *G. hodgsoni* are responsible for the 'shaping' of Continental Antarctica's primitive 'soil' at micro-scales: as a result of their presence and mediative 'cementing' of materials, minute particulate matter acquires a more cohesive and aggregated shape. This is the first evidence that members of Antarctica's terrestrial invertebrate fauna physically alter their abiotic environment.

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Disclosure statement

No potential conflict of interest was reported by the author.

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