How mites surprise us*

ROY A. NORTON
SUNY College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, New York, USA 13210
ranorton@esf.edu


It truly is an honor to be included among the recipients of the James Allen McMurtry Award, bestowed by the Systematic & Applied Acarology Society. I am grateful to Dr. Zhi-Qiang Zhang and the selection committee, and especially to Dr. Maria Minor, who nominated me, wrote the associated biography with Dr. Valerie Behan-Pelletier (Minor & Behan-Pelletier 2022), and recorded my oral presentation. The award was unexpected, since my career as a soil biologist seems rather unrelated to Jim’s field of biological control. But while acarologists occasionally have surprised me, mites do it constantly. One need not look far. Even our follicle mites, which certainly surprised our mid-19th century ancestors by their form and presence, continue to surprise us today: they have the lowest number of protein-coding genes known in arthropods, according to Smith et al. (2022). Having been asked by Dr. Zhang to offer some reflections on my half-century in acarology, I can think of no better premise than to give some examples of the numerous times and ways in which my focal group—oribatid mites—surprised, even astonished me.

Mites regularly surprise us with strange new morphologies, and it speaks to the incompleteness of our knowledge that the proposal of new families is not a rare thing. I’ve had such surprises a half-dozen times, but none was as astonishing as the discovery of a primitive family, Nanohystricidae, on the North Island of New Zealand (Norton & Fuangarworn 2015). This rather bizarre, extra-large (2 mm; Fig. 1A) mite can be found even in the Auckland region and is surface-active, having been collected from pitfall traps and sweeps of low vegetation. How could it have been missed?

Mites can surprise us with unusual chemical properties. These may relate to their integument, as in some early-derivative groups of oribatid mites that harden their cuticle in a manner unique among arthropods (Norton & Behan-Pelletier 1991a, b; Alberti et al. 2001). Crystals of whewellite (calcium oxalate) are formed in epicuticular chambers, which can make rather astonishing patterns when viewed under polarized light (Fig. 1B). Or the properties may relate to defensive chemistry: a surprising diversity of defensive compounds have been discovered in the opisthonotal glands of oribatid mites, including various terpenes, aromatics, hydrocarbons and even hydrogen cyanide (e.g., Sakata & Norton 2001, 2003; Raspotnig 2006, 2010; Heethoff 2012; Brückner et al. 2017). But most surprising was the discovery of diverse alkaloids, including types known from neotropical poison frogs, for which oribatid mites appear to be important prey (Takada et al. 2005; Saporito et al. 2007, 2015).

Mites surprise us by living in unexpected places. In the mid-19th century, skin pores were unexpected homes for mites, but acarologists have come to view such microhabitats as commonplace. My greatest surprise was learning that oribatid mites can live in what amounts to a small puddle of water, held in shallow weathering pits on barren sandstone in the high desert of southeastern Utah (Fig. 1C). Paraquanothrus grahami Norton and Franklin are active—feeding on microflora and rotifers—only during the short time that free water exists and can survive months of dryness entombed in calcareous sand deposits (Norton & Franklin 2018).

Mites can surprise us with unexpected behaviors. None surprised me more than a defensive behavior in a species of Oriobotritiidae that I first observed in the early 1990s in a soil sample from southern Florida. Oriobotritiid mites have a ptychoid body form, and the characteristic defensive reaction of such mites is to close like a jackknife, or more accurately like an operculate snail: legs and mouthparts are pulled into a temporary chamber capped by a hardened aspis (https://youtu.be/cGFcQbfjkTM). When disturbance is past, the mites open and resume their activity. But species of the genus Indotritia have an additional, startling reaction to being touched: these otherwise slow-moving mites can disappear as if by magic (https://youtu.be/c62PxR_T-G0). In fact, they leap a centimeter or more by means of internal hydraulic force and a releaser mechanism, analogous to the jumping of collembolans, as eventually described by Wauthy et al. (1997, 1998).
Mites can surprise us when we simply look at them more closely. Several years ago, Sergey Ermilov and I initiated what was intended to be a simple descriptive study of morphological ontogeny in *Eulohmannia ribagai* (Berlese). This is a common Holarctic species that is euedaphic, inhabiting fine humus under leaf litter or moss. It has also been considered an evolutionary relict—essentially the only species in its family and superfamily—and widely considered ‘parthenogenetic’ (actually, thelytokous). After studying specimens from just a small number of locations—all tentatively identified as *E. ribagai*—it became clear that Eulohmannidae was more diverse than...
previously thought, and in unexpected ways (Norton & Ermilov 2022). (1) We found that *E. ribagai* has sexual populations in glacial refugia of the northwestern Nearctic. (2) We found that a supposed subspecies, *E. ribagai bifurcatus* Fujikawa is clearly a distinct species. (3) We found two new species of *Eulohmannia*: a large sexual species from the Kolyma Highlands of the Russian Far East and a paedomorphic species from Kashmir. (4) We found and described a new species from the northwestern USA that is both sexual and paedomorphic, being only the second oribatid mite known to unequivocally curtail anamorphic development at the protonymph; for this, we proposed the second genus of Eulohmanniidae, *Paedolohmannia* (Fig. 1D). We have no doubt that other species will ‘appear’ within Eulohmanniidae when the group is viewed even more closely, through molecular studies. In recent years, when the ‘magnifying glass’ afforded by DNA has been directed toward oribatid mites, cryptic species seem to appear everywhere (e.g., Schäffer et al. 2019; Pfingstl et al. 2021, 2022).

Finally, mites can surprise us when fragmented knowledge congeals to illuminate previously mysterious or even unknown evolutionary patterns; *i.e.*, they can give us ‘Eureka!’ moments. My most significant such moment came early, when reading Graham Bell’s (1982) modern classic about reproductive biology. It highlighted the ‘queen of problems’ in evolutionary biology: why does sexual reproduction dominate multicellular life when asexuality has so many short-term advantages? Asked, conversely—why is asexuality so rare (<<1 % of animal species)—the assumed answer is that asexual species are not genetically flexible enough to adapt to changing conditions in the necessary time frame. As a result, asexual species should quickly become extinct and therefore appear isolated on the tree of life. Two commonly cited exceptions—the asexual bdelloid rotifers and darwinulid ostracods—where long-term success suggested that evolutionary radiation occurred without bisexuality, have earned the descriptor of ‘ancient asexual scandals.’

At the same time, I had an unrelated reason to read F. Grandjean’s (1941) short but seminal treatment of sex-ratio, in which asexuality was reported for the first time in oribatid mites. But most of the 30 species he identified as parthenogenetic were in early- to middle-derivative families for which no sexual species were reported. In other words, among oribatid mites, parthenogenesis appeared to be common and largely clustered: Eureka! Several years of focused research showed that nearly a tenth of oribatid mites are asexual, and that not only are there isolated asexual species but there are numerous examples of entire genera and entire families without known sexual species (Norton & Palmer 1991, Palmer & Norton 1991, 1992, Norton et al. 1993; Cianciolo & Norton 2006).

So, oribatid mites can be considered ‘super scandalous,’ but that also makes them ‘super interesting.’ Why are asexual oribatid mites not subject to quick extinction? Explanations relate to what might be considered their ‘permissive’ cytogenetics, as first posited by Wrensch et al. 1993 (recently put in modern context by Archetti 2021): they are meiotic, and in a way that permits extended existence and, ultimately, speciation. In the past two–three decades dozens of research papers have examined many aspects of oribatid mite asexuality, including cytology, genetics, selective forces, phylogeny, and ecological ramifications, many from the laboratories of Michael Heethoff, Mark Maraun, and their students (e.g., Heethoff et al. 2009, 2013; Maraun et al. 2019, 2022) and most recently by Pequeno et al. (2022).

These are but examples of how mites have kept one acarologist in a continual state of surprise for nearly a half-century. It seems unavoidable. So, if you are someone who dislikes surprises, acarology may be a field to avoid.

References


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