



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](mailto:ranorton@esf.edu)

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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 grahmi* 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 Oribotritiidae that I first observed in the early 1990s in a soil sample from southern Florida. Oribotritiid 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).

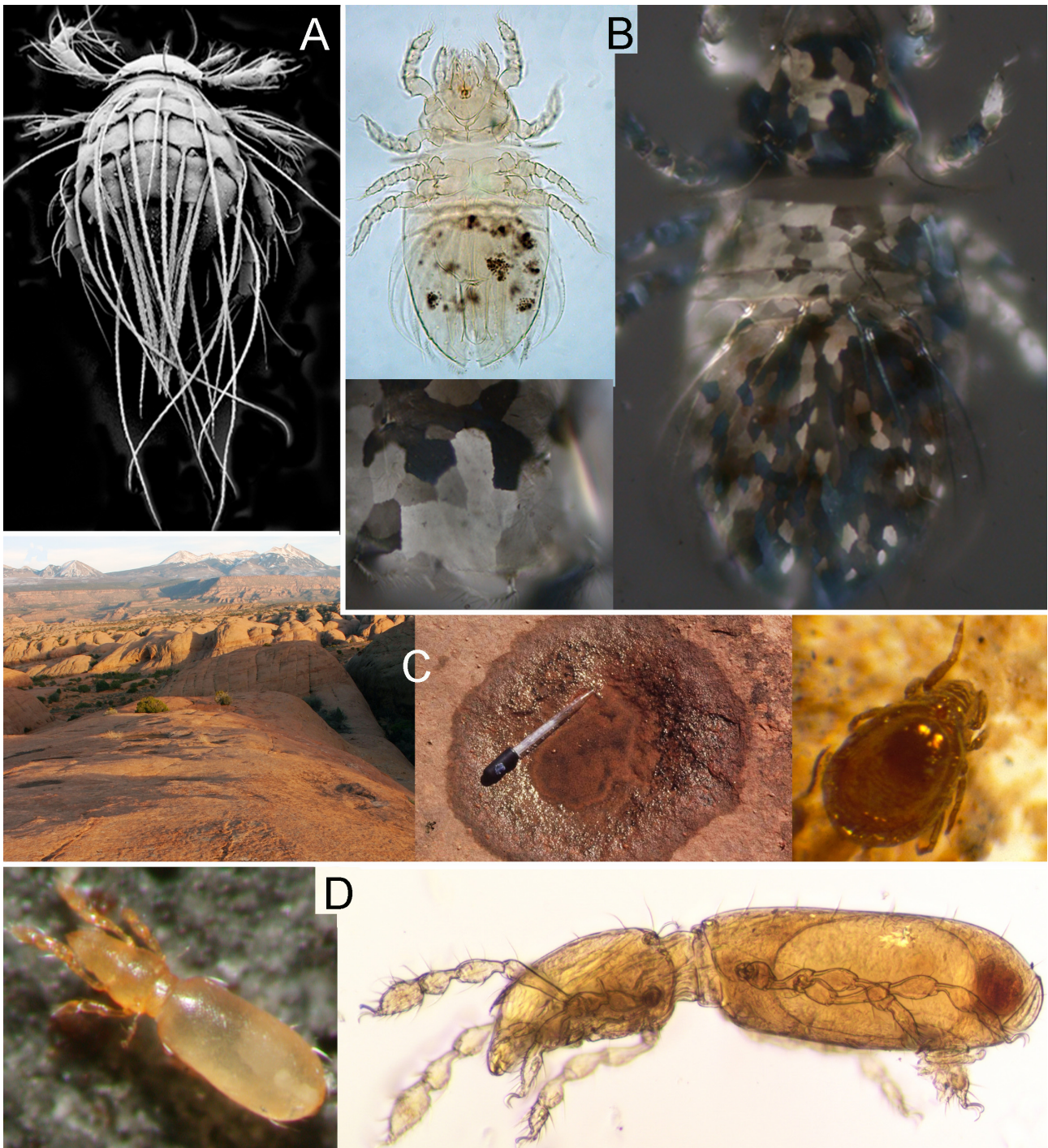


FIGURE 1. A—*Nanohystrix hammerae*, dorsal view (SEM); B—*Phyllozetes* sp., bright-field illumination (upper left), polarized light showing epicuticular crystals (right) and magnification (lower left); C—*Paraquanothrus grahmi*, habitat in Utah (left), microhabitat (center) and active specimen (right); D—*Eulohmannia ribagai* on left (photo by D.E. Walter), *Paedolohmannia metzi* on right.

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; Pfungstl *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

- Alberti, G., Norton, R.A. & Kasbohm, J. (2001) Fine structure and mineralisation of cuticle in Enarthronota and Lohmannioidea. *In: Halliday R.B., Walter D.E., Proctor H.C., Norton R.A. & Colloff, M.J. (Eds) Acarology: Proceedings of the 10th International Congress*. CSIRO Publishing, Melbourne, pp. 230–241.
- Archetti, M. (2021) Evidence from automixis with inverted meiosis for the maintenance of sex by loss of complementation. *Journal of Evolutionary Biology* (2022), 35, 40–50.
<https://doi.org/10.1111/jeb.13975>
- Bell, G. (1982) *The Masterpiece of Nature: The Evolution and Genetics of Sexuality*. The University of California Press, Oakland, 635 pp.
- Brückner, A., Raspotnig, G., Wehner, K., Meusinger, R., Norton, R.A. & Heethoff, M. (2017) Storage and release of hydrogen cyanide in a chelicerate (*Oribatula tibialis*). *Proceedings of the National Academy of Sciences*, 114(13), 3469–3472.
<https://doi.org/10.1073/pnas.1618327114>
- Grandjean, F. (1941) Statistique sexuelle et parthénogenèse chez les Oribates (Acaris). *Comptes rendus des séances de l’Académie des Sciences*, 212, 463–467.

- Heethoff, M. (2012) Regeneration of complex oil-gland secretions and its importance for chemical defense in an oribatid mite. *Journal of Chemical Ecology*, 38, 1116–1123.
<https://doi.org/10.1007/s10886-012-0169-8>
- Heethoff, M., Bergmann, P., Laumann, M. & Norton, R.A. (2013) The 20th anniversary of a model mite: a review of current knowledge about *Archezogozetes longisetosus* (Acari, Oribatida). *Acarologia*, 53, 353–368.
<https://doi.org/10.1051/acarologia/20132108>
- Heethoff, M., Norton, R.A., Scheu, S. & Maraun, M. (2009) Parthenogenesis in oribatid mites (Acari, Oribatida): Evolution without sex. In: Schön I., Martens K. & Dijk P. (Eds) *Lost Sex. The Evolutionary Biology of Parthenogenesis*. Springer-Science + Business Media B.V., Dordrecht, pp. 241–257.
https://doi.org/10.1007/978-90-481-2770-2_12
- Maraun, M., Bischof P.S.P., Klemp F.L., Pollack J., Raab L., Schmerbach J., Schaefer I., Scheu S. & Caruso T. (2022) “Jack-of-all-trades” is parthenogenetic. *Ecology and Evolution*, 12, e9036, 10 pp.
<https://doi.org/10.1002/ece3.9036>
- Maraun, M., Caruso T., Hense J., Lehmitz R., Mumladze L., Murvanidze M., Nae J., Schulz J., Seniczak A. & Scheu S. (2019) Parthenogenetic vs. sexual reproduction in oribatid mite communities. *Ecology and Evolution*, 9, 7324–7332.
<https://doi.org/10.1002/ece3.5303>
- Minor, M. & Behan-Pelletier, V. (2022) Professor Emeritus Roy A. Norton and his outstanding contributions to our knowledge of systematics, evolution, morphology, ecology and behaviour of Oribatida and other mites. *Systematic & Applied Acarology*, 27, 1189–1206.
<https://doi.org/10.11158/saa.27.6.16>
- Norton, R.A. & Behan-Pelletier, V.M. (1991) Epicuticular calcification in *Phyllozetes* (Acari: Oribatida). In: Dusbabek F. & Bukva V. (Eds) *Modern Acarology, vol. 2*. Academia, Prague, pp. 323–324.
- Norton, R.A. & Ermilov, S.G. (2022) Paedomorphosis and sexuality in Eulohmanniidae (Acari, Oribatida): surprising diversity in a relictual family of oribatid mites. *Acarologia*, 62, 989–1069.
<https://doi.org/10.24349/p0b0-usvs>
- Norton, R.A. & Franklin, E. (2018) *Paraquanothrus* n. gen. from freshwater rock pools in the USA, with new diagnoses of *Aquanothrus*, *Aquanothrinae*, and *Ameronothridae* (Acari, Oribatida). *Acarologia*, 58, 557–627.
<https://doi.org/10.24349/acarologia/20184258>
- Norton, R.A. & Fuangarworn, M. (2015) Nanohystricidae n. fam., an unusual, plesiomorphic enarthronote mite family endemic to New Zealand (Acari, Oribatida). *Zootaxa*, 4027(2), 151–204.
<https://doi.org/10.11646/zootaxa.4027.2.1>
- Norton, R.A. & Palmer, S.C. (1991) The distribution, mechanisms and evolutionary significance of parthenogenesis in oribatid mites. In: Schuster R. & Murphy P.W. (Eds) *The Acari - Reproduction, Development and Life-history Strategies*. Chapman and Hall, London-New York, 107–136.
https://doi.org/10.1007/978-94-011-3102-5_7
- Norton, R.A., Kethley, J.B., Johnston, D.E. & OConnor, B.M. (1993) Phylogenetic perspectives on genetic systems and reproductive modes of mites. In: Wrensch D.L. & Ebbert M.A. (Eds) *Evolution and Diversity of Sex Ratio in Insects and Mites*. Chapman and Hall, New York, pp. 8–99.
https://doi.org/10.1007/978-1-4684-1402-8_2
- Palmer, S. & Norton, R.A. (1991) Taxonomic, geographic and seasonal distribution of thelytokous parthenogenesis in the Desmonomata (Acari: Oribatida). *Experimental and Applied Acarology*, 12, 67–81.
<https://doi.org/10.1007/BF01204401>
- Palmer, S.C. & Norton, R.A. (1992) Genetic diversity in thelytokous oribatid mites (Acari, Acariformes, Desmonomata). *Biochemical Systematics and Ecology*, 20, 219–231.
[https://doi.org/10.1016/0305-1978\(92\)90056-J](https://doi.org/10.1016/0305-1978(92)90056-J)
- Pequeno, P.A.C.L., Franklin, E. & Norton R.A. (2022) Hunger for sex: Abundant, heterogeneous resources select for sexual reproduction in the field. *Journal of Evolutionary Biology*, 35, 1387–1395.
<https://doi.org/10.1111/jeb.14091>
- Pfingstl, T., Lienhard, A., Baumann, J. & Koblmüller, S. (2021) A taxonomist’s nightmare – Cryptic diversity in Caribbean intertidal arthropods (Arachnida, Acari, Oribatida). *Molecular Phylogenetics and Evolution*, 163, 107240, 19 pp.
<https://doi.org/10.1016/j.ympev.2021.107240>
- Pfingstl, T., Schäffer S., Bardel-Kahr, I & Baumann, J. (2022) A closer look reveals hidden diversity in the intertidal Caribbean Fortuyniidae (Acari, Oribatida). *Plos One*, online, 22 pp.
<https://doi.org/10.1371/journal.pone.0268964>
- Raspotnig, G. (2006) Characterisation of monophyletic oribatid groups by oil gland chemistry - a novel systematic approach in Oribatida (Acari). *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, 78, 31–46.
- Raspotnig, G. (2010) Oil gland secretions in Oribatida (Acari). In: Sabelis M.W. & Bruin J. (Eds) *Trends in Acarology, Proceedings of the XII International Congress of Acarology, Amsterdam (2006)*. Springer-Science + Business Media B.V., Dordrecht, pp. 235–239.
https://doi.org/10.1007/978-90-481-9837-5_38
- Sakata, T. & Norton, R.A. (2001) Opisthotal gland chemistry of early-derivate oribatid mites (Acari) and its relevance to

- systematic relationships of Astigmata. *International Journal of Acarology*, 27, 281–291.
<https://doi.org/10.1080/01647950108684268>
- Sakata, T. & Norton, R.A. (2003) Opisthonal gland chemistry of a middle-derivative oribatid mite, *Archeogozetes longisetosus* (Acari: Trhypochthoniidae). *International Journal of Acarology*, 29, 345–350.
<https://doi.org/10.1080/01647950308684351>
- Saporito, R.A., Donnelly, M.A., Norton, R.A., Garraffo, H.M., Spande, T.F. & Daly, J.W. (2007) Oribatid mites as a major dietary source for alkaloids in poison frogs. *Proceedings of the National Academy of Sciences*, 104, 8885–8890.
<https://doi.org/10.1073/pnas.0702851104>
- Saporito, R.A., Norton, R.A., Garraffo, M.H. & Spande, T.F. (2015) Taxonomic distribution of defensive alkaloids in Nearctic oribatid mites (Acari, Oribatida). *Experimental and Applied Acarology*, 67, 317–333.
<https://doi.org/10.1007/s10493-015-9962-8>
- Schäffer, S., Kerschbaumer, M. & Koblmüller, S. (2019) Multiple new species: Cryptic diversity in the widespread mite species *Cymbaeremaeus cymba* (Oribatida, Cymbaeremaeidae). *Molecular Phylogenetics and Evolution*, 135, 185–192.
<https://doi.org/10.1016/j.ympev.2019.03.008>
- Smith, G., Manzano-Marin, A., Reyes-Prieto, M., Antunes, C.S.R., Ashworth, V., Goselle, O.N., Jan, A.A.A., Moya, A., Latorre, A., Perotti, M.A. & Braig, H.R. (2022) Human follicular mites: Ectoparasites becoming symbionts. *Molecular Biology and Evolution*, 39, msac125.
<https://doi.org/10.1093/molbev/msac125>
- Takada, W., Sakata, T., Shimano, S., Enami, Y., Mori, N., Nishida, R. & Kuwahara, Y. (2005) Scheloribatid mites as the source of pumiliotoxins in dendrobatid frogs. *Journal of Chemical Ecology*, 31, 2403–2415.
<https://doi.org/10.1007/s10886-005-7109-9>
- Wauthy, G., Leponce, M., Banai, N., Sylin, G. & Lions, J.C. (1997) Un Acarien qui saute et qui se met en boule. *Comptes rendus des séances de l'Académie des Sciences, Paris, Sciences de la vie*, 320, 315–317.
[https://doi.org/10.1016/S0764-4469\(97\)82773-4](https://doi.org/10.1016/S0764-4469(97)82773-4)
- Wauthy, G., Leponce, M., Banai, N., Sylin, G. & Lions, J.C. (1998) The backward jump of a box moss mite. *Proceedings of the Royal Society London, B, Biological Sciences*, 265, 2235–2242.
<https://doi.org/10.1098/rspb.1998.0565>
- Wensch, D.L., Kethley, J.B. & Norton, R.A. (1994) Cytogenetics of holokinetic chromosomes and inverted meiosis: Keys to the evolutionary success of mites, with generalizations on Eucaryotes. In: Houck M.A. (Ed.) *Ecological and Evolutionary Analyses of Life-history Patterns*. Chapman and Hall, New York, pp. 282–343.
https://doi.org/10.1007/978-1-4615-2389-5_11