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Biography

## Professor Emeritus Roy A. Norton and his outstanding contributions to our knowledge of systematics, evolution, morphology, ecology and behaviour of Oribatida and other mites

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Roy A. Norton (RAN), who is viewed by many as one of the most outstanding acarologists of today, a teacher, a mentor and a colleague to so many, was born 12 August 1947 in Rochester, New York, then a thriving industrial town and home of some of America's most iconic companies, such as Eastman Kodak, Xerox and Bausch & Lomb.

RAN's academic career is linked to the State University of New York-College of Environmental Science and Forestry in Syracuse, New York. Founded in 1911, SUNY-ESF is one of the oldest and most respected schools in the USA dedicated to the study of the environment, with strong interdisciplinary focus, a large cohort of graduate students, and a tranquil leafy campus. There, in Illick Hall, home to the Department of Environmental and Forest Biology, RAN studied and later worked as Technical Assistant (1970–1974), Research Assistant (1974–1977), Research Associate (1977–1985), Senior Research Associate (1985–1989), Associate Professor (1989–1991) and Professor (1991–2011), retiring as Professor Emeritus (2012–present). For 20 years (1985–2005) RAN was also a Research Associate at The Field Museum of Natural History in Chicago, Illinois.

After a B.Sc. in Wildlife Management *magna cum laude* (1969), RAN proceeded to do his M.Sc. (1973) focusing on arthropod communities in Lake Ontario beach debris. It was also the year when RAN described his first new mite species<sup>1</sup>, which surprisingly was not an oribatid mite, but the Mesostigmatan—*Macrocheles ontariensis* Norton, 1973. More publications on taxonomy, ecology and behaviour of mites and soil arthropods followed<sup>2–10</sup>. In 1977 RAN defended his Ph.D. dissertation “*The family Damaeidae (Acarina: Oribatei): systematics and review of biology*”, followed by a series of publications on systematics and biology of oribatid mites<sup>11–18</sup>. His most significant paper from that period is the review of F. Grandjean's system of leg chaetotaxy in the Oribatida<sup>13</sup>, which has had lasting importance for systematics and taxonomy of oribatid mites. Indeed, RAN's thorough absorption and clear interpretations of Grandjean's concepts are evident in all his systematic and morphological publications, for example<sup>122, 123, 131, 223, 228</sup>.

The same year (1977) RAN started teaching in The Acarology Summer Program at The Ohio State University, a series of week-long workshops on identification of mites and ticks which has been the longest running program of this kind in the world. RAN taught General Acarology and Soil Acarology annually or biennially until 2018, when the Acarology Summer Program moved to the University of Arkansas, Fayetteville. The generations of students who were privy to RAN's encyclopedic knowledge of oribatid systematics, behaviour and ecology included participants from 36 countries (Argentina, Australia, Austria, Belgium, Brazil, Canada, Chile, China, Columbia, Costa Rica, Egypt, England, Estonia, France, Germany, Israel, Japan, Kenya, Latvia, Mexico, Netherlands, New Zealand, Norway, Romania, Russia, Pakistan, Peru, Philippines, Puerto Rico, South Africa, Spain, Sweden, Taiwan, Thailand, Turkey, USA).

Since 1978–79 RAN has focused primarily on his favorite group—Oribatida—where he has reached towering heights of expertise, publishing to date over 200 research papers and book chapters on systematics, evolution, biogeography and ecology of oribatid mites. There have been also studies on Astigmata and Prostigmata<sup>19–21, 33, 71, 74</sup>, projects on impacts of natural and anthropogenic perturbations on soil animal communities<sup>23, 46, 51, 67, 126, 137, 140, 165</sup> and methodological contributions<sup>53, 54, 60</sup>. Most of RAN’s publications resulted from collaborative work, much of which was international in scope; more than 150 co-authors represent 60+ institutions worldwide.

There is hardly any aspect of oribatid mite biology that escaped RAN’s attention during his incredibly productive career. RAN has enriched our knowledge on such matters in Oribatida as: phoresy<sup>31, 200</sup>; courtship behaviour<sup>162, 204</sup>; sperm transfer<sup>104</sup>; food passage through the alimentary tract<sup>138</sup>; defecation mechanisms<sup>169</sup>; trophic relationships<sup>141, 146, 191</sup>—we now know that oribatid mites can eat rotifers<sup>103</sup> and are in turn eaten by newts<sup>8</sup>; general community ecology<sup>52, 145, 150, 159, 163, 174, 183, 210, 219, 222, 225, 229, 231, 232, 233</sup>; and chemical ecology<sup>125, 134, 194, 214, 224</sup>, including the fascinating topic of oribatid mites of certain families (Scheloribatidae, Parakalummidae, Drymobatidae, Mochlozetidae and Galumnidae) being a major dietary source of alkaloids in the skin of some poison dart frogs<sup>155, 189, 190, 206, 213</sup>.

In 1993 RAN started a laboratory strain of the trhypochthoniid *Archezogetes longisetosus* Aoki, 1965 from a single gravid female collected in Puerto Rico. He shared offspring of this female with scientists worldwide, and to date there are almost 100 publications dealing with taxonomy, ecology, phylogeny, morphology and development of this species, based on this strain<sup>125, 134, 138, 150, 153, 157, 169, 176, 178, 182, 187, 193, 194, 199, 202, 220</sup>. *Archezogetes longisetosus* is considered a chelicerate model species along with the ticks *Ixodes ricinus* (Linnaeus, 1758) and *I. scapularis* Say 1821, and the spider mite *Tetranychus urticae* Koch, 1836.

RAN’s interest in reproductive modes in Oribatida opened up a new field of evolutionary ecology in acarological research. His work with Sandra Palmer on parthenogenesis in oribatid mites<sup>62, 69, 75, 79, 80, 83</sup> was a scientific milestone, highlighting that evolutionary radiation occurred in the absence of sexual reproduction in a number of large fully parthenogenetic families of Oribatida, and suggesting that automictic thelytoky was the mechanism involved. This was followed by a book chapter<sup>85</sup> “Phylogenetic perspectives on genetic systems and reproductive modes of mites” in Wrensch & Ebbert (1993), which was particularly influential in providing an evolutionary framework for the existing knowledge on reproductive modes in mites. RAN’s collaboration with Dana Wrensch on inverted meiosis in holokinetic chromosomes<sup>91</sup> outlined mechanisms for DNA repair and genetic variability in thelytokous lineages, explaining how wholly thelytokous higher taxa can result. Work on early development and cytology of oribatid mites with Paavo Bergmann and Michael Laumann<sup>182, 187, 220</sup> provided first evidence for automixis (meiotic thelytoky) in Oribatida. Numerous other collaborative projects<sup>109, 133, 148, 149, 151, 153, 154, 156, 176, 198</sup> with Mark Maraun, Michael Heethoff and other colleagues investigated evolutionary, cytological and ecological aspects of reproduction and diversification in thelytokous oribatid mites.

A pivotal evolutionary question where RAN has made a significant contribution is that of the origin of Astigmata. RAN’s view, a hypothesis first raised by Aleksei Zachvatkin (1953) and endorsed by Barry OConnor (1984), was that Astigmata (*r*-strategist colonizers of ephemeral substrates) are highly derived oribatid mites that evolved as a paedomorphic clade from within the Desmonomata. The life-history patterns<sup>90</sup>, morphological characters<sup>113, 115</sup> and opisthotal oil gland chemistry data<sup>125</sup> were consistent with the hypothesis that Astigmata evolved from within the oribatid mites. In contrast to the evidence from morphology and oil gland chemistry, the early analysis of the 18S ribosomal and nuclear DNA did not support the origin of Astigmata within Oribatida<sup>157</sup>. The phylogenetic affinities of Astigmata remained unresolved, but not for long—further studies by other authors (e.g., Dabert *et al.* 2010; Klimov *et al.* 2018), using molecular

phylogenetic tools, again convincingly placed Astigmata as a highly derived clade within Oribatida, thus rendering Oribatida themselves paraphyletic.

Structural, evolutionary and ecological aspects of Oribatida morphology are a significant research interest for RAN, and he has demonstrated how morphology can provide a phylogenetically informative set of characters for oribatid mite systematics and contribute to our understanding of their phylogenetic relationships. In collaborative studies, RAN has investigated the functional morphology of porose integumental organs<sup>99-102</sup>; ptychoid defensive mechanism<sup>136, 177, 186, 205</sup>; fine structures of the gnathosoma<sup>193</sup>; bite force of the chelicerae<sup>178</sup>; cuticular calcification<sup>81, 82, 123</sup>; and ecdysial cleavage lines<sup>93, 120</sup>. Of particular significance has been RAN's work on morphology of juvenile stages in Oribatida<sup>87, 92, 98, 112, 144, 160, 208, 223, 230, 234</sup>, a topic replete with knowledge gaps, especially in groups where juveniles and adults are not easily associated. This work has culminated recently in the catalogue of all known oribatid mite juveniles<sup>203</sup> for 805 species in 310 genera, a massive effort—but still only a small fraction of Oribatida species described as adults.

RAN's interest in fossil Oribatida led to a series of collaborative projects<sup>41, 61, 68, 71, 106</sup>, the latter paper on mite-plant associations in Paleozoic coal swamps the winner of "Outstanding Paper of 1997" award from the Society for Sedimentary Geology. Work on Paleozoic mites was followed by research on oribatid mites from acarodomatia of Eocene fossil leaves<sup>78</sup>, from Tertiary amber<sup>88, 152, 170</sup> and from Holocene stalagmites<sup>121</sup>. Some years later, this interest led to a series of publications<sup>188, 192, 195</sup> on fossil oribatid mites from amber with Ekaterina Sidorchuk, which are outstanding in detail and quality.

RAN's 'favourite' taxa have been Damaeidae<sup>23, 27-29, 32, 35, 37, 47, 70, 86, 89, 94, 95, 127, 158, 185</sup> and Enarthronota<sup>24, 34, 42, 122, 123, 160, 180, 181, 201, 208</sup>, but other Oribatida groups have also benefitted from his attention. Significantly, he has documented<sup>59</sup>, clarified<sup>12, 18, 25, 26, 76, 77</sup> and revised<sup>76, 217, 234</sup> many of the Oribatida previously recorded from North America. RAN's descriptions of new species, often done in collaboration, are too numerous to present here individually, but two deserve a special mention. Of these, the description of *Collohmanna johnstoni* Norton & Sidorchuk, 2014 is an outstanding example of a modern species description, with precision and rich details in observations on development and biology<sup>204</sup>. Similarly rich in detail is the description<sup>208</sup> of *Nanohystrix hammerae* Norton & Fuangarworn, 2015—a single known species in the new family Nanohystricidae in Enarthronota, endemic to shrubland and forests of northern New Zealand. With an adult body length of 1–1.2 mm, *N. hammerae* is the largest known enarthronote mite outside Lohmanniidae and appears to be phylogenetically relictual. It has glassy, luminous erectile notogastral setae and unusual plesiomorphic traits (e.g., pigmented lateral eyes).

The publication that best captures RAN's breadth of thinking and his research philosophy is his 2007 Plenary Address to colleagues at the XI International Congress of Acarology in Mexico<sup>161</sup>. He uses examples from oribatid mites—their predator defenses, their high incidence of obligate female parthenogenesis, and the origin of the exploitative group Astigmata from the detritivorous Malaconothroidea—to advocate for diverse and holistic approaches to acarological research "that get to the heart of ultimate, evolutionary causes for large-scale patterns that we see in mite biology."

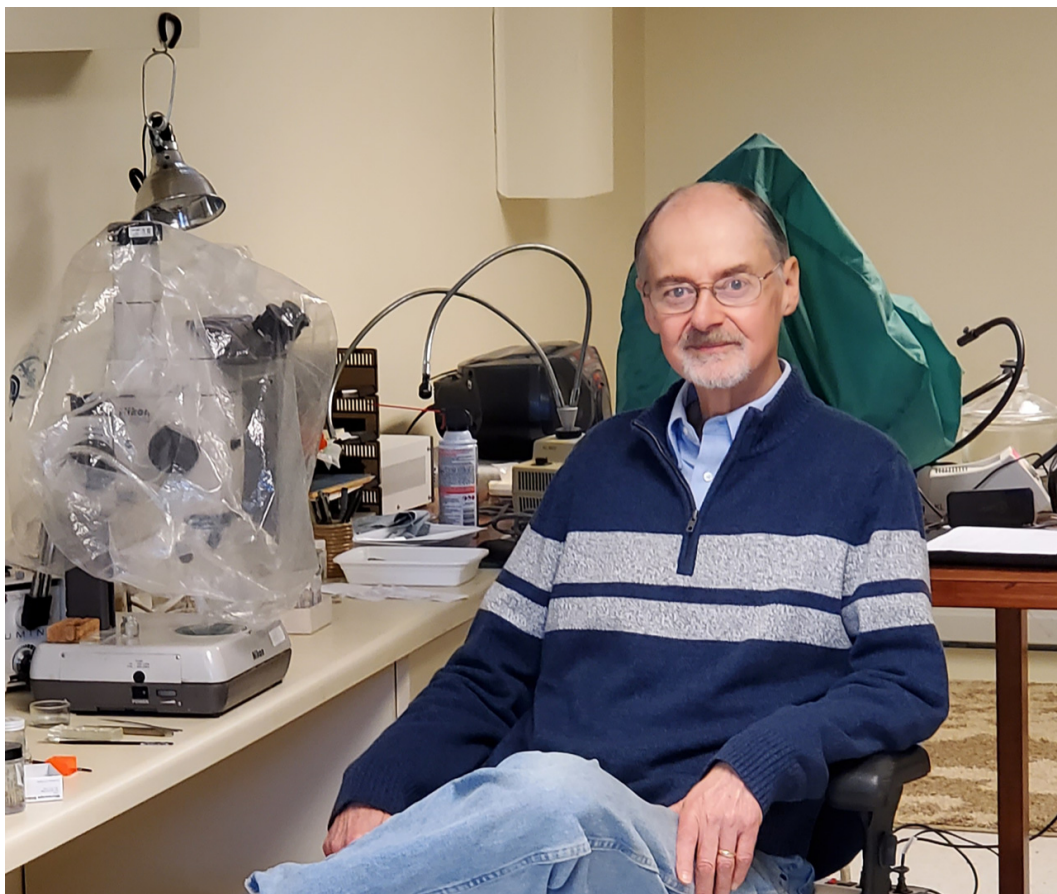
Over the course of his career, RAN held membership in a number of scientific societies, including the Acarological Society of America (charter and life member), Entomological Society of Mexico, European Association of Acarologists, and Systematic and Applied Acarology Society (China). He was the elected member of the Executive Committee of Acarological Society of America (1986–1990), member of Nominations Committee, Acarological Society of America (1990), elected member of the Executive Committee for the International Congresses of Acarology (1990–1994), and General Secretary of the Executive Committee, International Congresses of Acarology (1994–1998). Throughout his career, RAN had been an active member of editorial and advisory boards of acarological journals, including *Experimental and Applied Acarology*,

*International Journal of Acarology, Acarologia, Acta Zoologica Hungarica, Systematic and Applied Acarology, Acarina, Folia Entomologica Mexicana, Folia Entomologica Hungarica.* In 2001 RAN was awarded the honorary lifetime membership in the Hungarian Academy of Science.

As Professor Emeritus since retiring at the end of 2011, RAN continues to live in the Syracuse area with his wife, Georgiana, and to carry on research and collaboration, with over 30 papers in recent years. His lasting impact in acarology is much more than the sum total of his publications—he is a patient, helpful and generous mentor, and has influenced so many learners of acarology. A multitude of students and colleagues have benefitted from his truly encyclopedic knowledge and thoughtful advice. RAN's colleagues comment on his generous and knowledgeable guidance, his great accuracy, precision and self-criticism in scientific matters, but also on his unbiased openness in discussions, and his humbleness.

Of unparalleled benefit to all working with Oribatida has always been RAN's collection of literature on oribatid mites, which includes nearly everything ever published on the subject, and which he readily makes available to colleagues. Today, this collection has been digitized and has become the part of regularly updated PDF Library of all literature on Oribatida, which is of inestimable value to the global community of oribatologists.

With seven mite genera and 29 species named in his honour, the RAN name has been already woven into the fabric of acarological history. Here, we hope to have convinced you that Professor Emeritus Roy A. Norton is the most worthy recipient of the 2022 McMurtry Award for Lifetime Achievement in Acarology.



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