



Maurice W. Sabelis · Jan Bruin *Editors*

Trends in Acarology

Proceedings of the
12th International Congress

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Maurice W. Sabelis
University of Amsterdam
Institute for Biodiversity and Ecosystem Dynamics (IBED)
Section Population Biology
P.O. Box 94248
1090 GE Amsterdam
The Netherlands
M.W.Sabelis@uva.nl

Jan Bruin
University of Amsterdam
Institute for Biodiversity and Ecosystem Dynamics (IBED)
Section Population Biology
P.O. Box 94248
1090 GE Amsterdam
The Netherlands
bruinjan@tiscali.nl

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Cover illustration: A female of the predatory mite *Gaeolaelaps (Hypoaspis) aculeifer*, feeding on a female of the bulb mite *Rhizoglyphus robini*, both cultured by Dr. Izabela Lesna (University of Amsterdam) (Photo: Bert Mans)

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Preface

For the past 50 years, the International Congress of Acarology has been the foremost forum for worldwide communication on the knowledge of mites and ticks. This group of very small arthropods exhibits a bewildering diversity of species that live in many different habitats, in association with the land, freshwater and marine organisms with which they interact. Many mites and ticks have economic consequences as they are pests of agricultural, veterinary and medical importance, and several species have become model organisms for studies in modern biology. While acarologists pur sang focus on evolution and phylogeny of the Acari, they may learn from insights emerging from fundamental and applied biological experiments in which selected species of Acari are the focal object of study. Experimental and applied biologists, on the other hand, may learn from insight in how their pet organism is positioned amidst the diversity of Acari. In this sense the International Congress of Acarology may stimulate biologists to look beyond the borders of their disciplines.

The 12th International Congress of Acarology, held from 21-26 August 2006 in Amsterdam, The Netherlands, succeeded in bringing together scientists that share an innate fondness for mites and ticks, yet differ widely in scientific specialisation. The congress was truly international and well attended, with 386 participants from 59 countries: Australia, Austria, Benin, Belgium, Brazil, Bulgaria, Cameroon, Canada, China, Colombia, Costa Rica, Croatia, Cuba, Czech Republic, Denmark, Egypt, Finland, France, Georgia, Germany, Ghana, Greece, India, Iran, Ireland, Israel, Italy, Japan, Kenya, Latvia, Mexico, Netherlands, New Zealand, Nigeria, Norway, Pakistan, Philippines, Poland, Portugal, Russian Federation, Serbia and Montenegro, Slovak Republic, South Korea, Spain, Sri Lanka, St. Vincent and the Grenadines, South Africa, Sudan, Switzerland, Taiwan, Thailand, Tasmania, Trinidad, Tunisia, Turkey, UK, Ukraine, USA, and Venezuela. Moreover, a wide variety of disciplines were represented, such as molecular biology, biochemistry, physiology, microbiology, pathology, ecology, evolutionary biology, systematic biology, soil biology, plant protection, pest control and epidemiology. As shown in Table 1, there were 14 symposia with invited speakers, 8 regular sessions with submitted

papers, and 8 workshops for small groups of specialists. In total, there were 469 presentations/posters with accompanying abstracts, published in an abstract volume edited by Jan Bruin. The keynote address on Molecular Acarology was given by Dr Hans Klompen (Ohio State University, Columbus, OH, USA) and a special invited lecture on Tick Genomics was presented by Dr Catherine Hill (Purdue University, West Lafayette, IN, USA).

Several of the papers presented and some of the sessions held during the congress have been published elsewhere. Most notably are two special issues of the journal *Experimental and Applied Acarology*, resulting from sessions on the Control of Poultry Mites (volume 48, issues 1-2, 2009; editor: Dr. O.A.E. Sparagano) and on Forensic Acarology (volume 49, issues 1-2, 2009; editor: Dr. M.A. Perotti). In total, 114 papers were submitted for publication in the Congress Proceedings, 18 of which had to be rejected for various reasons. The remaining 96 contributions have all been reviewed and carefully edited. The editors are confident that the Proceedings of the 12th International Congress of Acarology reflect current trends in acarology as a field of science. We sincerely hope that the volume will promote communication throughout the scientific community and may stimulate research for many years to come.

Maurice W. Sabelis & Jan Bruin

December, 2009, Amsterdam, The Netherlands

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Table 1 Symposia with invited speakers, regular sessions with submitted papers, and workshops at the 12th International Congress of Acarology, August 2006, Amsterdam, The Netherlands.

Symposia	Regular Sessions	Workshops
Molecular Phylogeny	Taxonomy	Coconut Mites
Tick Physiology	Morphology	Tomato Mites
Evolutionary Ecology	Ecology	Water Mites
Chemical Ecology	Soil Acarology	Soil Mites
Canopy Acari	Biogeography	Disease Transmission
Mites on Arthropods	Veterinary Acarology	House Dust Mites
Mites on Vertebrates	Agricultural Acarology	Pesticide Resistance
Biological Control	Videographic Acarology	Forensic Acarology
Invasive Acari		
Recognition Systems		
Host Race Formation		
Diseases of Mites and Ticks		
Symbionts of Mites and Ticks		
Non-target Effects of Pesticides		

Plenary Opening Lecture

From sequence to phoresy – molecular biology in acarology

Hans Klompen

Ohio State University Acarology Collection, Museum of Biological Diversity, 1315 Kinnear Road, Columbus, OH 43212, USA.
E-mail: klompen.1@osu.edu

First of all, I would like to thank Maurice Sabelis and the organizing committee of the International Congress for the honor of being invited to present this address. When Maurice invited me to give this address he suggested I stick with the general theme of this congress, ecology and genomics. I had a brief moment of doubt, I do not actually work on either genomics or ecology, and so I decided to broaden the topic to the impact of molecular biology on acarology. More specifically, to use this occasion to emphasize and celebrate some areas where molecular biology has allowed us to make significant advances. Acarology is clearly following in the footsteps of other disciplines in rapidly integrating molecular data and methods in all aspects of research. Anybody doubting this should check the listing of presentations at this congress. In presenting these comments I should stress that in selecting developments to highlight, I have tried to cover a range, but I lay no claim to being comprehensive. These are my choices, reflecting my biases.

I will deal with three main areas, each with a different focus (and different tools). First, population or species level issues. This includes issues of species delimitations, dispersal patterns, and population structure – basic scientific issues which also have considerable relevance in agriculture and medicine. This area relates most directly to the bread and butter research that makes knowledge of mites so important. In terms of techniques this used to be an area for allozymes and RAPD's, techniques partially replaced by sequencing of rapidly evolving markers and analysis of microsatellites. Second, my personal interest: higher-order systematics. This area goes beyond straightforward analyses of relationships. Hypotheses in systematics are often (and correctly) considered indispensable for testing broad evolutionary hypotheses, and in setting the parameters within which any such hypotheses have to operate. Sequencing of slowly evolving markers, such as nuclear rRNA and nuclear protein coding genes, is the main tool, but there are additional options, such as mitochondrial gene order. Finally, in genomics the focus is on the structure of the genome and the function and regulation of the various genes. This will be the area where eventually we might approach the holy grail of complete vertical integration from DNA to phenotype.

POPULATIONS AND SPECIES

Dispersal

How well are mites really getting around? What are average distances for dispersal, and what factors may influence this? Eight years ago Evert Lindquist in a similar keynote speech for the Canberra congress listed these types of questions as a possible priority area for research. A range of molecular techniques is allowing us to get a better handle on these questions. Previously employed molecular methods, such as

RAPD's and sequencing of relatively fast evolving loci can be used in this area, but they have clear limits. Analysis of microsatellites, often combined with sequencing or PCR-RFLP, appears to be more powerful. Microsatellites have been used to establish dispersal patterns and gene flow in a wide range of mite taxa, including the mesostigmatic mite *Varroa destructor* Anderson & Trueman (Solignac et al., 2003), the eriophyoid *Colomerus vitis* (Pagenstecher) (Carew et al., 2004), the spider mite *Tetranychus turkestani* Ugarov & Nikolski (Bailly et al., 2004), and the tick *Ixodes uriae* White (McCoy et al., 2003). One would hope that in the near future these techniques would be applied to an even wider range of taxa. For example, they might help provide insights in dispersal patterns of taxa such as Bdelloidea and Raphignathoidea, taxa of potential use in biocontrol, but whose dispersal abilities are quite poorly known. Moving into the soil ecosystem, these techniques may help elucidate dispersal patterns and population structure in oribatid mites.

But there is certainly no need to wait for future developments. Molecular techniques are already proving to be very powerful in current issues such as tracking invasive species. Recent work on *Aceria guerreronis* Keifer, a worldwide pest of coconuts (Navia et al., 2005), demonstrated a New World, probably Neotropical, origin of this mite. The direct importance of that research is that it allows a much more focused search for potential predators. Similarly tracking *V. destructor* invasions of North America and dispersal of *Raoiella indica* Hirst around the world may lead to improved management strategies. As an aside, it is interesting to note the current prominence of research on Tenuipalpidae. Often regarded as a minor player compared to the family Tetranychidae, the group has come into prominence in several areas in the last decade. *Brevipalpus phoenicis* (Geijskes) populations feature some very odd reproductive systems, including all-haploid populations (Weeks et al., 2001), *R. indica* has become yet another major pest of coconuts (<http://www.doacs.state.fl.us/pi/enpp/ento/r.indica.html>), and tenuipalps in general have emerged as vectors of major plant diseases (e.g., citrus leprosis) (Childers et al., 2003). We clearly have not exhausted the potential for scientifically and/or economically important discoveries, even in relatively well-known groups of mites.

Development of host races and species limits

The literature is filled with claims and counterclaims of host specificity and host races. Testing such claims is often difficult and very laborious using standard methods. Molecular techniques allow quicker and often more accurate assessments of separation between 'host races' by measuring actual gene flow. Such approaches have shown cryptic species in the genus *Varroa* (Anderson & Trueman, 2000) and significant indicators of host race formation in the

Sarcoptes scabiei complex (Walton et al., 2004) and in the tick *I. uriae* (McCoy et al., 2005). Meanwhile other molecular-based studies showed a lack of host specificity in *Psoroptes* (Ramey et al., 2000; Zahler et al., 2000; Pegler et al., 2005) and some *Tetranychus* species (Tsagkarakou et al., 1999; Bailly et al., 2004). A mtDNA-based study of genetic variability in *Myialges* spp. on the Galapagos Islands rejected the conventional wisdom that a single species, *Myialges caulotoon* Speiser, was associated with both Galapagos hawks and cormorants (Whiteman et al., 2006, 2007). In fact, the mites associated with the two bird hosts [and with members of two genera of louseflies (Hippoboscidae)] were genetically distinct. A re-examination of morphology showed small, but consistent, morphological differences between members of the two host races, reinforcing the molecular-based conclusions. This is a good example of how morphology and molecular data can be synergistic.

A broader issue is identification of species by molecular methods. In this context it is worthwhile to note the ongoing efforts in DNA barcoding. The idea here is to sequence a small piece of DNA that is species specific, thus providing the equivalent of a 'barcode'. To make this system work, some issues need to be worked out, including assessments of within species variability and the ability of the chosen sequence to distinguish closely related species. Neither issue can be assumed solved for mites until some experimentation has been conducted for a wide range of taxa. Such tests take on extra significance because of the dramatic range of evolutionary rates among mite taxa (Murrell et al., 2005; Klompen et al., 2007). Assuming these problems are solved, this approach can be very useful in specific situations. One example would be border inspections, where quick identifications are needed and experts are not always available. The practical problems in this type of situation should be limited, because such inspections often concentrate on a limited number of target species. Assuming those target species can be tested as needed, it should be possible to make molecular identification feasible soon. Eventually the same could be done for ecological studies of soils, etc., but that would require a much larger set of reference sequences. Of course it is not always necessary to identify specimens to species in ecological studies, but this merely shifts the problem to developing reference sequences for genera, families, or whatever grouping is needed. Some work is already being done in this area, and it is certainly worth exploring. Still I do not expect widespread application of these techniques in this field for some years. I stress that using 'molecular barcode' identifications is not the same as DNA taxonomy, the idea of defining new species based solely on (usually small) bits of DNA sequence. That 'shortcut' to the backlog of species descriptions has great potential for disrupting existing taxonomy, while the benefits are at best unclear.

Mite associates

Molecular techniques, combined with broader interest in the matter, have also expanded knowledge on associates of mites. We generally think of mites as small and being associates of other, larger organisms, but that view is incomplete. Mites themselves are also habitats for even smaller organisms. This includes well-known associations with tapeworms (Denegri, 1993), entomopathogenic nematodes (Samish et al., 2000), and fungi (Hofstetter et al., 2006), but investigations of associations with bacteria and protozoa have largely been limited to medically or veterinary impor-

tant taxa vectored by ticks or chiggers. Only a few mite associates outside of that setting have been studied in detail. The most prominent example in that category is *Wolbachia*, which in some (but not all) hosts can cause sex ratio distortion and cytoplasmic incompatibility (e.g., Breeuwer & Jacobs, 1996; Vala et al., 2000, 2002, 2003; Gotoh et al., 2003, 2005).

However, it is clear that the number of bacterial or fungal associations of mites is much larger than that, and we are seeing a growing interest in a wider range of microorganisms, especially those that affect the mites themselves (see Samish & Reháček, 1999; van der Geest et al., 2000). The use of a variety of molecular techniques (e.g., Jeyaprakash & Hoy, 2004), including PCR assays (Hoy & Jeyaprakash, 2005; Reeves et al., 2006), is allowing considerable progress in reliably detecting even very small numbers of microorganisms. This makes it feasible to quickly (and cost-effectively) search for such organisms in a much wider range of mite taxa, and to cover a wider range of microorganisms (not just pathogens). Many of the associations detected in this manner may well be accidental and have little biological significance, but others may provide some real insights. For example, reports of *Anaplasma* nr. *phagocytophilum*, agent of human granulocytic anaplasmosis, in various dermanyssoid Mesostigmata (Reeves et al., 2006) and in syringophilid quill mites (Skoracki et al., 2006) suggest a fairly wide distribution of this pathogen. The impact for epidemiology is not yet clear, but the Dermanysoidea are potential vectors or reservoir hosts. As for the presence of *A. phagocytophilum* in permanent parasites such as Syringophilidae, the authors found that often the bird hosts did not register as positive, which brings up the possibility that infected mites may provide evidence of past infections (Skoracki et al., 2006). Another area of potential interest is the interaction of various microorganisms in the mite host, for example the potential for facilitation or competition. This general area of microorganisms associated with mites should see lots of exciting developments in coming years, some of which were already shown at a symposium on 'Symbionts of mites and ticks' during this congress.

HIGHER-ORDER SYSTEMATICS

This area has not been exceptionally well developed in the Acari because of the great difficulties in establishing homologies among members of distant lineages. It is simply quite difficult to find characters that can be scored across all Acari, or even across a single order (Acariformes or Parasitiformes). With respect to homology issues, a summary of ongoing efforts to homologize setal designations across all Acariformes is included in the third edition of 'A Manual of Acarology' (Krantz & Walter 2009). There are also some excellent morphology-based studies, such as those by OConnor (1984) and Norton (1998) for Sarcoptiformes, Haumann (1991) for early-derivative oribatid mites, and Lindquist (1986) for Heterostigmata, but equivalent analyses are lacking for most other acarine lineages. The analysis by Lindquist (1984) is still the only phylogenetic analysis of relationships across acarine orders, and even that analysis includes only a relatively small character set. As with the intra-specific issues noted above, molecular biology can make, and is making, a major contribution in this area. It does so mainly by allowing the generation of large new data sets. The ultimate goal will be combined analyses of mor-

phology and molecules, but such studies have so far been limited to relatively small lineages (e.g., Klompen et al., 2000; Dabert et al., 2001).

A critical consideration in deep phylogeny analyses of mites is the choice of marker. Cruickshank (2002) noted that nuclear rRNA's (both 18S and 28S) appear among the best candidates for deep phylogeny in the Acari, whereas nuclear protein coding genes might be most useful at an intermediate level, e.g., from family to subordinal levels. So far, most molecular-based studies looking at higher-order relationships in groups of Acari have indeed been based on nuclear rRNA, mostly 18S small subunit rRNA, but increasingly sections of, or whole, 28S, or on the nuclear protein-coding gene Elongation Factor-1 alpha (EF-1 α) (Cruickshank & Thomas, 1999; Klompen, 2000; Lekveishvili & Klompen, 2004; Murrell et al., 2005; Schaefer et al., 2006; Klompen et al., 2007). Again, rate variation among lineages can be substantial, so relatively variable loci, such as the D3 variable region of 28S rRNA, may be relatively informative at higher levels in oribatid mites (Maraun et al., 2004), whereas the very conserved 18S is informative at the genus level in basal Mesostigmata (Lekveishvili & Klompen, 2004). As evidenced in this congress, multiple research groups are working in this area and it is likely that we will see substantial progress on higher-order systematics of Acari in the coming years. Additional molecular markers would be very welcome, and that area is also being addressed (e.g., Xu et al., 2003, 2004; Schaefer et al., 2006). Thus, we can expect not only more data for established markers, but also a considerable increase in diversity of markers over the next few years.

The ultimate goal for much of systematic research is to use acquired insights in relationships among groups to test evolutionary hypotheses on those groups. Such hypotheses cover diverse areas, from parthenogenesis to feeding modes, coloration, and host associations.

Parthenogenesis

Parthenogenesis is common among Acari, but particularly within basal lineages of oribatid mites ('Macropylina') (Norton & Palmer, 1991; Palmer & Norton, 1991). This despite the wide-held notion that all-female parthenogenesis (thelytoky) is an evolutionary dead-end. The long-term existence of thelytoky in bdelloid rotifers (Welch & Meselson, 2000) and darwinulid ostracods (Martens et al., 2003) has attracted a lot of attention, but thelytokous radiation in oribatid mites may be more common, and even more ancient (Heethoff et al., 2002). More astonishingly, we are seeing evidence of repeated reversal to sexuality, both within smaller oribatid lineages (this congress), and perhaps even the entire infraorder Astigmata (Norton, 1994, 1998).

Feeding modes

Most mites are fluid feeding, a feeding mode assumed to be ancestral in the Arachnida. There are exceptions, including Opilioacarida and a few genera of Mesostigmata (e.g., *Asternolaelaps*) among Parasitiformes, and the majority of Sarcoptiform Acariformes. But are they true exceptions, or is ingesting solid food the primitive condition for Acari? To determine this, we need more data on relationships in Chelicerata. Interestingly, molecular data so far have not been able to resolve order-level relationships in Chelicerata with any confidence (Giribet et al., 2001, 2002). Meanwhile, detailed studies of morphology continue to support a close

association of the fluid-feeding Ricinulei with Acari, but perhaps as sistergroup to Parasitiformes (that is within Acari), rather than as sistergroup to Acari (Shultz, 2007).

Coloration in water mites

Did the spectacular colors of water mites evolve as UV protectant, aposomatic warning colors, or other? Many Trombidiformes are red in color due to an accumulation of carotenoids in the cuticle, quite possibly as a UV protectant. However it is unclear whether the function of coloration has changed in water mites relative to their terrestrial relatives. Feeding experiments show that fish often reject water mites as prey, suggesting an aposomatic function of color (Proctor & Garga, 2004). Unfortunately observations comparing ponds with fish vs. ponds without generally show more bright-colored water mites in the fish-less ponds. One way to study this is to plot coloration and habitat data on a phylogeny of water mites / Parasitengona. Efforts are underway to generate a molecular phylogeny for Parasitengona, and the first results of these efforts were presented by Heather Proctor et al., during this congress.

Host-parasite associations

Acari are clearly one of the best, if not the best, groups to study host associations. Host associations have evolved numerous times, they include a wide range of association types (from phoresy to permanent parasitism), and involve a stunning diversity of hosts. Although most studies of host association patterns involve slightly smaller lineages than discussed above, molecular-based phylogenies are improving our understanding of mite and host phylogenies, thereby allowing more sophisticated hypotheses of evolution of the associations. Examples of host-parasite systems examined in just this congress include Cheyletoidea (Bochkov), Dermanysoidea (Dowling, OConnor), and Astigmata (Klimov, OConnor). In most of these cases results have not yet been published, but we can expect whole series of publications quite soon (e.g. Bochkov et al., 2008; Klimov & OConnor, 2008). And it is not only co-evolution scenarios that can be tested, there are additional questions such as the origin (and possible reversal) of parasitism and the notion that phoresy might be a facilitating condition for the evolution of parasitism (Athias-Binche & Morand, 1993; Houck & Cohen, 1995).

GENOMICS

How many coding regions are present in a given organism, what do these genes code for, how are they regulated, what is their distribution? These are just some of the questions asked in genomics research. This is a young field, and it may take some time before we can answer them for mites, but considerable progress is being made in some areas. Worth noting here is research on the sialome of ticks, the set of proteins in tick saliva involved in preventing blood clotting and in interfering with the host immune systems (Valenzuela, 2004). Other areas where similar but smaller-scale studies have been done include dust mite allergens, and Sarcoptiform alarm pheromones.

As for entire genomes, it is worth to briefly look at a relatively simple system, the mitochondrion. The mitochondrial genome of arthropods is relatively small (14-19,000 bp) and considered quite variable in nucleotide sequence, but

conserved in organization, that is in genes present and gene order (Boore, 1999). As with many areas, most early work in the Acari has been done for ticks (Campbell & Barker, 1998; Black & Roehrdanz, 1999). These studies found that the 'hypothetical ancestral pattern' for arthropods is retained in *Limulus*, derived *Ixodes*, and all Argasidae examined so far (Shao et al., 2004). However, although ticks are a morphologically conservative group, mitochondrial rearrangements have been demonstrated for several lineages of Ixodidae, including the addition of a second control region in some Australian *Ixodes* (Shao et al., 2005b), and re-arrangements of a considerable part of the genome in all Metastriata (Black & Roehrdanz, 1999). The only other Parasitiform for which the entire mitochondrial genome is known, *V. destructor*, again shows considerable changes (Evans & Lopez, 2002; Navajas et al., 2002), specifically a different position of several tRNA's and of the small subunit rRNA (12S rRNA). Recently the first Acariform mitochondrial genome was published, suggesting that observed deviations from the hypothetical ancestral pattern in Parasitiformes may be relatively minor. The genome of the chigger *Leptotrombidium pallidum* Nagayo et al. features several rearrangements of tRNA's, four control regions, plus an apparent doubling of a major section that includes a complete copy of the large subunit rRNA (16S), and a partial one for 12S rRNA (Shao et al., 2005a). Of course it is currently unclear whether this result is just an aberration, or whether it is representative of mitochondrial genome structure in Acariformes as a whole. Clearly we will need complete mitochondrial genomes for more Acariformes to evaluate that question.

The main area of excitement in mite genomics is certainly represented by projects focusing on the nuclear genome. Overall this type of research in Chelicerata is well behind similar efforts in insects, but acarology is doing quite well. We are already seeing the first results of the *Ixodes scapularis* Say genome project (<http://www.entm.purdue.edu/igp/>), and we can now add another, the *Tetranychus urticae* Koch project (approval announced during this congress). This means that complete genomes will soon be available for representatives of both Parasitiformes and Acariformes. Again, it will take some time before results of these projects will filter down to a wider range of projects, but it will happen, and it will be a major boost for our field, even if I do not dare speculate where the main impact will be.

CONCLUSION

In conclusion, molecular biology has a lot to offer for acarology, whether by itself or integrated with existing morphology- or ecology-based research. As a group, acarologists may complain about the decline in our numbers, the lack of funding, the scarceness of positions in the field, etc., all of which legitimate issues, but I am optimistic. The field attracted us because there are so many truly remarkable things left to be discovered, whether it is in systematics, physiology, ecology, or genetics. Molecular biology will be no different. What little we know so far has included a host of exciting and unanticipated results, and there is no reason to expect that we will not find many more. The ongoing genome projects will just add more possibilities to discover something amazing. So go out and dig.

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Phylogeny and Taxonomy of Acari

Systematic relationships of Lohmanniidae (Acari: Oribatida)

Roy A. Norton

S.U.N.Y. College of Environmental Science and Forestry, Syracuse, NY 13210, USA. E-mail: ranorton@esf.edu

Lohmanniidae is a moderately diverse family of macropylid oribatid mites that is usually grouped with taxa having opisthotal glands, even though they themselves lack these glands. Morphological traits are examined for evidence that lohmanniids are instead members of Enarthronota, particularly the superfamily Hypochthonioidea. Six traits are consistent with membership in Enarthronota, eight support a relationship with Hypochthonioidea and its close out-group Arborichthoniidae, seven support membership in Hypochthoniidae, and five others support a sister-group relationship with its subfamily Nothrolohmanniinae. Two alternative classifications are suggested to accommodate this relationship.

Key words: Oribatid mites, Enarthronota, Hypochthoniidae, Hypochthonioidea, *Malacoangelia*, *Nothrolohmannia*

Lohmanniidae is a moderate-size family comprising 21 nominal genera and 179 species (Subias, 2004), most with tropical or subtropical distributions (Hammer & Wallwork, 1979; Balogh & Balogh, 1992). Its present composition was attained gradually, as several fundamentally different mites (now in Epilohmanniidae, Eulohmanniidae, Perlohmanniidae, and the enarthronote *Malacoangelia*) were removed from Berlese's (1916) original tribe Lohmanniini.

Adults have a characteristic facies (Fig. 1A-C): elliptical to ovate shape in dorsoventral view, convex dorsum, flat venter, and pedofossae that receive retracted legs when an individual is disturbed. A large anterior notogastral tectum, unique among dichoid mites, covers the sejugal articulation dorsally. Their biology also seems rather uniform: they consume decomposing leaves and often woody substrates, within which they feed as endophages (Shereef, 1976; Haq, 1984; Ramani & Haq, 1991). Males are unknown (Grandjean, 1950) and parthenogenesis has been proven in the laboratory (Shereef, 1976). They are one of several families of early to middle derivative oribatid mites that show modest evolutionary radiation in the absence of sexual reproduction (Norton & Palmer, 1991; Maraun et al., 2004).

In a foundational paper, Grandjean (1950) considered Lohmanniidae an isolated family that exhibits interesting contrasts. It is specialized, yet rich in primitive characters and despite its homogeneous facies some traits show high variation. The latter include a wide range of dorsal setations (holotrichy to extreme neotrichy) and many combinations of shapes, subdivisions and fusions in plates of the anogenital region that, as Grandjean predicted, underlie the current multitude of recognized genera. He first expressed this isolation by listing Lohmanniidae as one of 11 distinct groups of oribatid mites (Grandjean, 1954a), then merged it with several others to form Mixonomata, one of six major groups in a later classification (Grandjean, 1969) that continues to be

used (e.g., Subias, 2004). Mixonomata is probably a paraphyletic group (Norton, 1998) that ancestrally has opisthotal glands (see below). Haumann (1991) had a similar view: his cladogram included Lohmanniidae between Eulohmanniidae and Perlohmanniidae (both mixonomatans) in a pectinate part of Novoribatida – the sister-group of Enarthronota in his study.

Lee (1984, 1985) first closely linked Lohmanniidae with taxa usually included in Enarthronota, although his unique terminology partly masked this insight (see Norton, 2001). He thought ancestral transverse scissures were lost from Lohmanniidae (essentially his cohort Affisurina), but thought its sister-group included all enarthronotes but Protoplophoroidea. Instead, Norton (2001) and Alberti et al. (2001) suggested that Lohmanniidae represents a derived family of Hypochthonioidea. This enarthronote superfamily exhibits much evolutionary plasticity, with both ptychoid (Mesoplophoridae) and holonotic (*Nothrolohmannia*) clades. Woas (2002) subsequently included Lohmanniidae within Hypochthonioidea, a classification followed by Weigmann (2006). However, the original suggestion was based on few traits, and no overview of morphological support exists. A preliminary DNA analysis is consistent with this hypothesis (Maraun et al., 2004), but lacks taxa important for testing it.

My objective is to examine how traits of Lohmanniidae fit the phylogeny proposed earlier for Hypochthonioidea (Norton, 1984, 2001). Lohmanniidae is included as the sister group of Nothrolohmanniinae (Fig. 2), where the weight of evidence seems to place it, and various branches are numbered for discussion. This is a preliminary study, because few new characters are considered and some alternative relationships are not yet examined. Still, traits of many taxa have been examined, particularly those of mixonomatan families, and no more plausible relationship was uncovered.

MATERIALS AND METHODS

The overall approach is to climb the tree from bottom to top, testing Lohmanniidae against characters that support relevant clades, as linked by numbers to Figure 2. Except for the first section (below) the apomorphic state is given, followed by the plesiomorphic state (pl) in parentheses. Principal sources are Grandjean (1950) for Lohmanniidae, Grandjean (1935) for *Malacoangelia*, Norton (2003) for *Nothroloh-*

mannia, and Fernandez (1984) for *Eohypochthonius*; the latter also summarizes traits of *Hypochthonius* and *Eniochthonius*. Traits of Endeostigmata and Palaeosomata are from Grandjean (1939, 1954b, respectively). Other sources are indicated where relevant. *Arborichthonius styosetosus*, in the monotypic Arborichthoniidae (Norton, 1982), was chosen as the outgroup of Hypochthonioidea, for reasons noted below. New developmental data for *Malacoangelia*

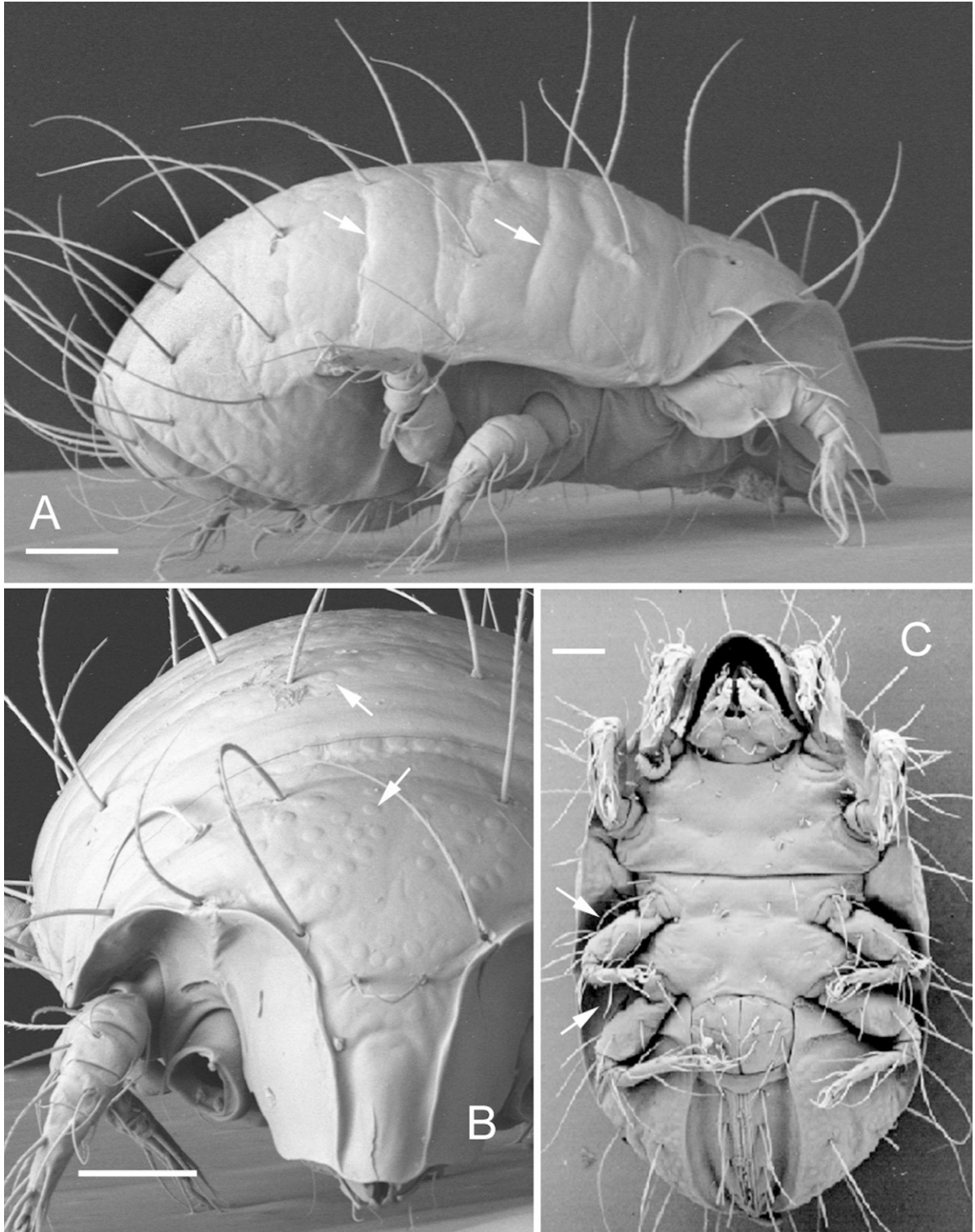


Figure 1 *Meristacarus* sp. A. Lateral aspect (arrows on mineralized bands). B. Anterior aspect (arrows on porose areas). C. Ventral aspect (arrows on pedofossae). Scales: 100 μ m. (Australian specimen, images by Sue Lindsay).

remigera came from specimens and exuviae collected in Quintana Roo, Mexico, by the author, and protonymphal data for *Nothrolohmannia calcarata* came from a topotypic specimen donated by the late János Balogh.

Are Lohmanniidae members of Enarthronota?

As Lohmanniidae are holonotic (have a one-piece notogaster), the most diagnostic trait of Enarthronota – one or more transverse notogastral scissures (Grandjean, 1947) – is absent, but most other traits are consistent with this placement. Except scissures, and the first two characters below, there are no recognized synapomorphies of Enarthronota. Other listed traits are plesiomorphies that help exclude Lohmanniidae from derived oribatid mite groups with apomorphic states.

Subcapitular anarthry. The subcapitulum of known Enarthronota is anarthric, i.e., it lacks a labiogenal articulation (Grandjean, 1957). By contrast, species in more derived macropyline groups (Parhyposomata, Mixonomata, Desmonomata) are stenarthric, i.e., they have an oblique articulation between mentum and genae. Lohmanniidae are all anarthric. Some have a pair of oblique lines on the subcapitular venter, but these are ridges or changes in cuticular structure, not articulations. Weigmann (1996) considered anarthry a synapomorphy of Enarthronota.

Immature instars with moderately sclerotized hysterosomal cuticle. This is a common trait of Enarthronota (Grandjean, 1969) that is most easily seen in the rather rigid exuviae (see below). Except for some Brachypylina, glandulate taxa have immatures with unsclerotized, weak hysterosomal cuticle that easily crumples during molting.

Absence of opisthonotal gland. Of the six major groups recognized by Grandjean (1969), members of Palaeosomata and Enarthronota lack opisthonotal glands, like Lohmanniidae. Nearly all Parhyposomata, Mixonomata, Desmonomata, and Brachypylina (Circumdehiscenciae) have them, and are referred to below as ‘glandulate’ taxa (Norton, 1998).

Plesiomorphic rutellum. The rutellum of Lohmanniidae clearly shows its setal origin (Grandjean, 1950, 1957). Although it is broader distally than those of Enarthronota, its

narrow base does not overlap the lateral lips and is not incorporated with the gena in the manner of glandulate taxa.

Absence of lyrifissures *iad* and *ian*. Grandjean (1950) considered their absence in Lohmanniidae a regression. However, all Enarthronota and Palaeosomata lack these lyrifissures, as do Endeostigmata. They are present in glandulate taxa, except most Brachypylina lack *ian*.

Ten pairs of genital setae. The plesiomorphic number of genital setae in oribatid mites seems to be 10 pairs. This is the common number in Palaeosomata and Enarthronota, and lesser setations seem attributable to losses (Grandjean, 1949, 1961b). Lohmanniidae have 10 pairs, but no glandulate group has more than nine.

Arborichthoniidae as an outgroup of Hypochthonioidea

Arborichthoniidae shares three apomorphies with Hypochthonioidea and Lohmanniidae that are not known in other Enarthronota.

1. **Adoral seta *or*₂ medially with deep notch and tooth** (pl = without notch). In Lohmanniidae, this apomorphy is present only in some genera (e.g., *Meristacarus*, *Torpacarus*). Hypochthonioidea have additional cilia distal to the tooth that are not known in Lohmanniidae.

2. **Subcapitular genae with paired dorsal rasps** (pl = rasp absent). A patch of rasp-like teeth arranged in transverse rows lies on the dorsal face of each gena, posterolateral to the rutellum and close to the mouth opening (Fig. 3A). It is not known from other oribatid mite taxa.

3. **Lyrifissure *im* on *notaspis*** (pl = *im* on pleuraspis or soft lateral cuticle). In Hypochthonioidea, *im* is anterior to setal row *e*, but is behind it in Arborichthoniidae. In Lohmanniidae *im* is above the suprupleural scissure, essentially aligned with row *e*.

Are Lohmanniidae members of Hypochthonioidea (clade I)?

Several synapomorphies proposed earlier (Norton, 1984, 2001) to distinguish Hypochthonioidea from other Enarthronota were based on the assumption that ancestors had the plesiomorphic enarthronote body architecture in which setal rows *e* and *f* are enlarged, erectile, and inserted on paired intercalary sclerites in two respective transverse notogastral scissures (type-S scissures of Grandjean, 1947). Arborichthoniidae has an autapomorphic arrangement in which setae *f* are erectile, but insert in a pair of soft cuticular patches rather than a single scissure.

4. **Loss of erectile function in setal rows *e* and *f***; i.e., full or partial incorporation of intercalary sclerites bearing setal row *e* and *f* into notogaster and size regression of setae (pl = *e* and *f* setae enlarged, erectile, on independent sclerites). Lohmanniidae have the apomorphic state but, unlike Nothrolohmannia, they have no vestige of ancestral scissures, so the ‘loss’ is equivocal.

5. **Sternal apodeme present** (pl = sternal apodeme absent). A distinct linear apodeme runs along the midline of fused epimera III and IV; it may be long, short, or in two parts. (lost in the ptychoid Mesoplophoridae). In Lohmanniidae it is relatively short and approximately centered in the plate.

6. **Aggenital plates fused with epimere IV** (pl = aggenital plates articulated with epimere IV). In Hypochthonioidea aggenital plates form what appear to be triangular extensions of the coxisternum that frame the genital plates anteriorly. Some Lohmanniidae have this state (e.g., *Torpacarus gramineus* and *Heptacarus graminosus*), but in most species the plates articulate with epimere IV.

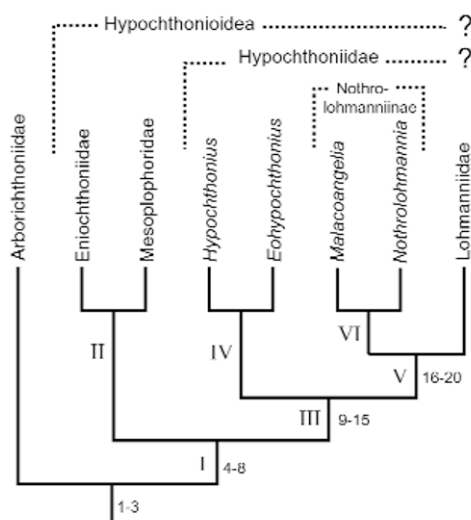


Figure 2 Hypothesis of cladistic relationships in Hypochthonioidea and Lohmanniidae, with Arborichthoniidae as outgroup. Roman numerals indicate clades referred to in text; arabic numerals indicate apomorphic traits for the clade as discussed in text. See Norton (2001) for support of clades II, IV, and VI. See text for discussion of indicated classification.

7. *Trochanter II glabrous* (pl = trochanter II with one seta). Trochanters I and II have one seta each in Arborichthoniidae and in most glandulate taxa. But trochanter I is glabrous in the majority of Enarthronota, perhaps in all Palaeosomata, and in many Endeostigmata. In contrast, trochanter II has one seta in most Endeostigmata, all Palaeosomata, and most Enarthronota. Hypochthonioidea is unusual, with trochanter II also glabrous: the typical setal formula is 0-0-2-2 (I to IV). Trochanter II is also glabrous in the distant enarthronote lineage Brachychthoniidae, and in a paedomorphic clade of Protoplophoroidea (Norton et al., 1983), but only Lohmanniidae share the 0-0-2-2 formula.

8. *Proximal part of chelicera inserted into body* (pl = chelicera not inserted). In Endeostigmata, Palaeosomata, Parhyposomata, Mixonomata, and most Enarthronota the entire chelicera projects from the body wall like other appendages. In Desmonomata and Brachypylina (Norton, 1998), and independently in Hypochthonioidea, the wall attachment encroaches such that part of the chelicera proj-

ects internally. The internal part comprises only about 5-6% in *Eniochthonius*, but 20-30% in other hypochthonioid genera, and in Lohmanniidae (Fig. 3B).

Are Lohmanniidae members of Hypochthoniidae (clade III)?

Apomorphies 9-15 characterize Hypochthoniidae, which currently includes *Hypochthonius*, *Eohypochthonius*, *Malacoangelia*, and *Nothrolohmannia*. In 2001 the loss of lyrifissure *ip* was listed, but this character appears to be incorrect and is deleted here. The lyrifissure exists along with the other four typical lyrifissures at least in *Hypochthonius* and *Eniochthonius* (Fujikawa, 2003 and RA Norton, unpubl. observations) and dense spicules make finding lyrifissures in Nothrolohmanniinae difficult. Members of Lohmanniidae retain all five lyrifissures

9. *Epicuticular chambers form as indentations over pore canals* and contain nonbirefringent calcium-potassium mineral, probably apatite (pl = chambers form as caverns within epicuticle and contain birefringent calcium oxalate).

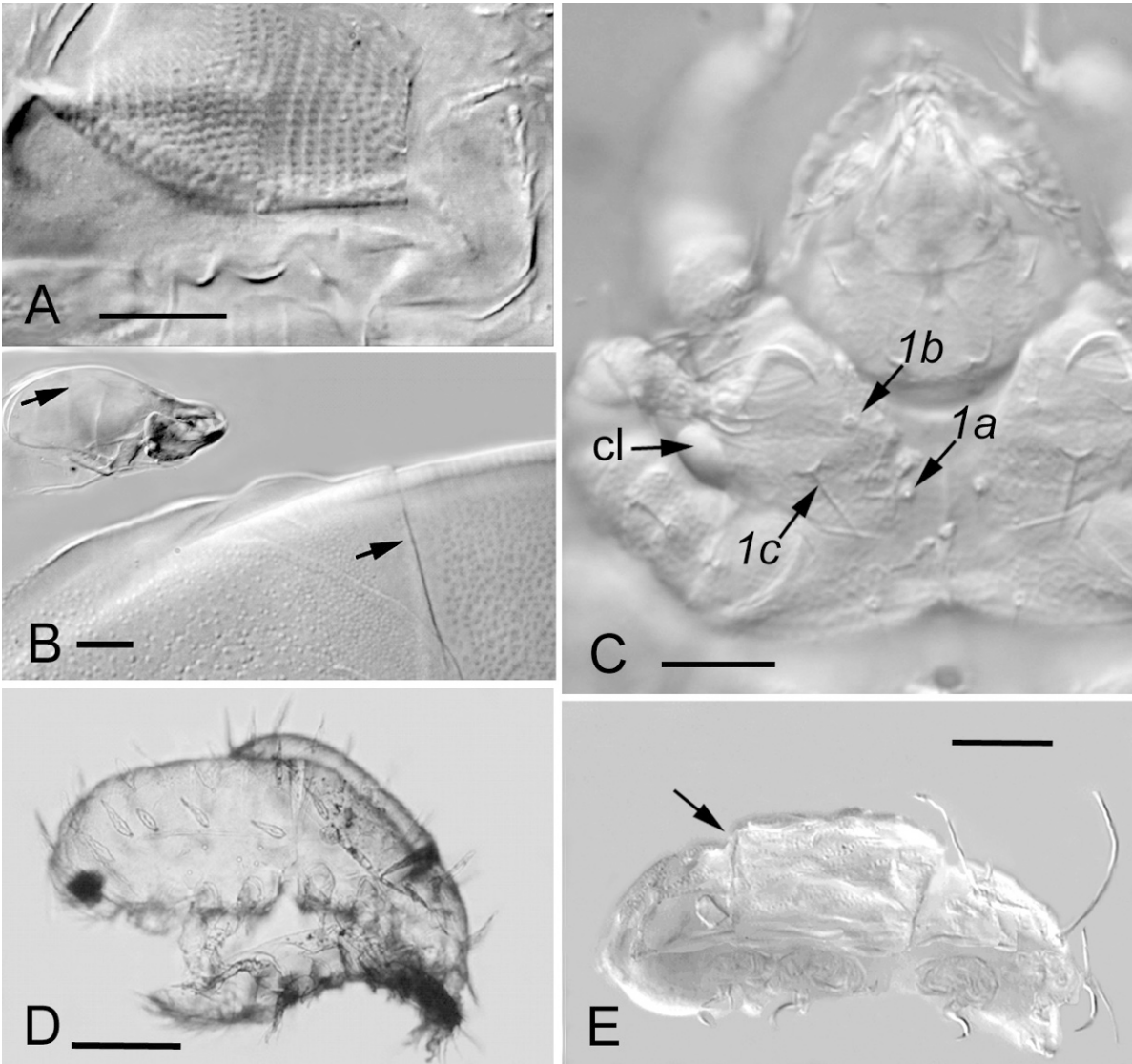


Figure 3 A. *Lohmannia carolinensis*, rasp on gena of subcapitulum. B. *L. carolinensis*, chelicera (insert) and enlargement of body wall attachment (arrows). C. *Malacoangelia remigera* larva, ventral proterosoma. D. *Lohmannia banksi*, molting deutonymph. E. *Nothrolohmannia calcarata*, protonymph (layered image: arrow on transverse scissure). Abbreviations: cl, Claparède's organ (stalk out of focus); 1a, 1b, 1c, epimere I setae. Scales: 10 µm (A-C), and 50 µm (D, E).

Table 1 Setation of adult legs (I to IV) of Hypochthonioidea (Mesoplophoridae excluded), Arborichthoniidae and representative Lohmanniidae.^a

	Trochanter	Femur ^b	Genu	Tibia	Tarsus ^c
Arborichthoniidae					
<i>Arborichthonius styosetosus</i> Norton ^d	1-1-2-2	5-6-3-3	5-5-4-4	5-4-4-4	18-16-13-13
Eniochthoniidae					
<i>Eniochthonius minutissimus</i> (Berl.) ^e	0-0-2-2	3-5-3-3	5-3-3-3	5-4-3-3	18-16-13-13
Hypochthoniidae					
<i>Hypochthonius rufulus</i> C. Koch	0-0-2-2	5-5-3-3	3-3-2-2	5-5-3-3	19-15-13-13
<i>Eohypochthonius</i> spp.	0-0-2-2	5-5-3-3	3-3-2-2	5-5-3-3	19-15-13-13
<i>Malacoangelia remigera</i> Berlese	0-0-2-2	5-5-3-3	3-3-2-2	5-5-3-3	19-13-11-12
<i>Nothrolohmanna baloghi</i> Norton	0-0-2-2	5-5-3-3	3-3-2-2	5-5-3-3	19-13-11-12
Lohmanniidae					
<i>Lohmannia lanceolata</i> Grandjean	0-0-2-2	5-6-3-3	3-3-2-2	5-5-3-2	17-13-12-12
<i>Torpacarum omittens</i> Grandjean	0-0-2-2	4-5-4-3	3-3-2-2	4-4-2-2	15-13-11-10
<i>Annectacarus mucronatus</i> Grandjean	0-0-2-2	5-6-4-3	3-3-2-2	5-5-2-2	17-13-10-10
<i>Cryptacarus promecus</i> Grandjean	0-0-2-2	5-6-3-3	3-3-2-2	5-5-1-1	17-11-9-9

^aData from Grandjean (1950), Fernandez (1984), Norton (1982, 2003), and new observations. ^bCounts in boldface exceed those of Hypochthonioidea. ^cFamulus included in count. ^dAncestral seta *m*" (monotrope) is absent (regressed) from tarsus I of *A. styosetosus* but retained in other listed taxa; *bv*" was inadvertently omitted from Figure 7 of Norton (1982). ^eSeta *it*" is absent (regressed) from tarsus I, present in Arborichthoniidae and Hypochthoniidae.

Lohmanniidae have chambers of the derived type (Alberti et al., 2001) that form the transverse bands previously thought to indicate primitive segmentation (Grandjean, 1950; Wallwork, 1963). The suggested plesiomorphic state is found in clade II, but not in Arborichthoniidae. This is problematic, since similar chambers probably also occur in some Protolophoroidea: *Phyllozetes* (Cosmochthoniidae) has large chambers with birefringent contents, but the mineral is unidentified; *Prototritia* (Protolophoridae) has calcium oxalate (Norton & Behan-Pelletier, 1991), but its epicuticle has not been studied. Mineralized epicuticular chambers are not known from other superfamilies.

10. *Aggenital setae absent* (pl = at least one pair present). Clade II ancestrally has aggenital setae, as does Arborichthoniidae, but all Hypochthoniidae lack them. Lohmanniidae also lack aggenital setae, but so do various families or genera throughout oribatid mites (Grandjean, 1949), so the character is homoplasious.

11. *Ontogeny of genital setae accelerated; deutonymph with five pairs of setae* (pl = deutonymph with four pairs). All adult Hypochthoniidae have the ancestral complement of 10 pairs, but the specific ontogeny of this setation is shared only by Lohmanniidae: 1-5-8-10 (protonymph to adult). All oribatid mites have a single protonymphal seta, and 10 adult pairs is common, but the unusual deutonymphal (5) and tritonymphal (8) setations presented problems for Grandjean's (1949, 1961b) interpretation of evolution in genital setation. Since deutonymphs of other enarthronotes and Palaeosomata have a maximum of four pairs, the fifth pair probably results from accelerated development. Having eight tritonymphal setae may be correlated with the deutonymphal acceleration, but not necessarily. *Palaeacarus* and the enarthronote *Gozmanyina* (Marshall & Reeves, 1970) have eight pairs in the tritonymph, but no other known oribatid mite has more than seven.

12. *Tarsus I famulus simple* (pl = famulus with lateral bract-like branch). Like Hypochthoniidae, Lohmanniidae has a simple famulus, but it has become short and peg-like. Simplification seems highly homoplasious (Haumann, 1991) and of little value.

13. *Iternal setae lost from tarsi II-IV* (pl = iteral setae retained on at least some of tarsi II-IV). Grandjean (1961a, 1964a) reported many patterns for iteral setae on leg tarsi,

and among the rarest is to have a pair on adult tarsus I, but none on tarsi II-IV. All four hypochthoniid genera have this pattern. The single pair first forms in the protonymph; under Grandjean's model, they have strongly 'resisted' regression, whereas those of other tarsi were gradually delayed to the point of loss. Studied Lohmanniidae either lack iterals altogether or only *it'* forms on tarsus I. Total loss of iterals is convergent in many lineages; however, when *it'* is present in Lohmanniidae it forms unusually early, in the deutonymph, which suggests that past resistance to regression was greater on tarsus I than on II-IV. In this sense, the iteral ontogeny is considered a derivative of the hypochthoniid type.

14. *Ventral setae absent from all leg genua* (pl = at least some ventral setae present). In contrast to the ancestral state in clade II, Hypochthoniidae have only fundamental genual setae (larval on I-III, deutonymphal on IV; Grandjean, 1942). The resulting formula (I-IV) is 3-3-2-2 in all known species (*d*, *l'* and *l'* on genua I and II; *d* and *l'* on III and IV). Ventral setae have been lost in parallel in Mesoplophoridae and several other groups of Enarthronota, but with formulas other than 3-3-2-2. Lohmanniidae share the rare genual setation of Hypochthoniidae (Table 1), which otherwise is known only for some Brachychthoniidae.

15. *Palp tarsus with distal setiform organ trifid* (pl = distal setiform organ bifid). All hypochthoniid mites have the ultimate pair of palp setae fused basally. This is common in Enarthronota, and found in some species of Palaeosomata, Parhyposomata, and Brachypylina. Clade II retains this form, but in Hypochthoniidae the unpaired subultimate seta joins the ultimals to form a trifid structure, and this is true of Lohmanniidae. Since the trifid state is also found in both close (Arborichthoniidae) and distant (*Gozmanyina*, *Nipponiella*) enarthronote outgroups, the character is homoplasious.

Are Lohmanniidae and Nothrolohmanniinae sister-groups (clade V)?

Of the many apomorphies proposed earlier for Nothrolohmanniinae (Norton, 2001, 2003), the following five (16-20) are shared by Lohmanniidae. *Papillacarus* possibly has another one, spicules developed from epicuticular chambers, but the ultrastructure of its spicules is unknown and they are distributed in areas *other* than the mineral-containing transverse bands.

16. *With pedofossae for accommodation of folded legs* (pl = pedofossae absent). Many Brachypylina have defensive reactions in which legs are folded into concave niches in the body wall. In macropylina taxa this behavior and the associated niches, or pedofossae, are known only from clade VI and Lohmanniidae.

17. *Seta p" absent from tarsus IV* (pl = p" present). Proral setae are rarely lost from tarsus IV in oribatid mites, but only in clade VI and Lohmanniidae is one lost unilaterally; p" is absent from all studied species. This loss is most obvious on the highly regressed protonymphal leg IV, where the normal count of seven tarsal setae is reduced to six. All studied Lohmanniidae have the rare protonymphal leg IV setation of 0-0-0-0-6 (Grandjean, 1946a, 1950), and the same is true of *Malacoangelia* and *Nothrolohmannia*.

18. *Coxisternal seta 1c setiform in larva, independent of Claparède's organ* (pl = seta 1c scaliform, covers retracted Claparède's organ). Ancestrally in acariform mites coxisternal seta 1c is modified to form a protective cap over Claparède's organ when the latter is retracted (Grandjean, 1933, 1939, 1954b). Concomitant with the disappearance of that organ in the protonymph, 1c transforms to a normal seta. Rarely 1c is setiform in the larva of oribatid mites: previously known examples were *Epilohmanniidae* and *Lohmanniidae* (Grandjean, 1946b, 1950), but *Malacoangelia* shares the trait (Fig. 3C; the larva of *Nothrolohmannia* is unknown). Grandjean (1955) considered the setiform larval state primitive and strongly believed that reversion from scaliform to setiform was impossible, but since 1c is consistently scaliform in basal acariform groups (Endeostigmata and Palaeosomata) it must be the plesiomorphic larval form within Enarthronota. The genetic-epigenetic mechanism producing the scale form is probably disabled in these rare cases, and I interpret setiform 1c as an acceleration of the protonymphal transformation, rather than a reversion. The acceleration in *Epilohmannia* is convergent.

19. *Anal plate regressed, strap-like* (pl = anal plate well formed, independent of adanal plate). In clade V adanal plates comprise most of the adult paraproctal valves, with the anal plate reduced to a narrow band at their medial edge. *Malacoangelia* has complete paraproctal atrichosy (At3 of Grandjean, 1954a), and the anal plate is not delineated from the adanal until the adult. Lohmanniidae have no such setal delays, but anal setae can lack altogether. A convergent internal lineage of *Eohypochthonius* also has the apomorphy (Fernandez, 1984).

20. *Porose organs present on notogaster* (pl = porose organs absent). Discrete porose organs are rare on the notogaster of macropylina mites, but they occur in clade VI and in some Lohmanniidae. Their ultrastructure and distribution differ between the two groups (Alberti et al., 1997, 2001), so this apomorphy is equivocal.

Characters states incongruent with Figure 2

If Figure 2 is correct, four traits listed above (1, 6, 13, and 20) are variable within Lohmanniidae and represent autapomorphies or homoplasies. Eight other problematic trait distributions (a-h) are not known to be variable: (a), (b), and (g) seem to be autapomorphic, the others are homoplasious.

a. *Molting*. In studied Hypochthonioidea molting is prodehiscent (Norton & Kethley, 1994): exuviae of immatures split anteriorly above the appendages in a U-shape and the animal emerges forward (new observations show *M. remigera* is also prodehiscent). The cuticle of immature Lohmanniidae splits posteriorly in a U-shape, and the animal

emerges backward (Fig. 3D), as in Brachypylina. A transition from prodehiscence is difficult to explain.

b. *Rutellum expanded distally into hyaline, thin, apparently flexible lobe* (pl = rutellum without distal expansion). The distal projection of Lohmanniidae is thumb-like, not a hyaline lobe.

c. *Notogastral fusion*. If Figure 2 is correct, the holonotic state of *Nothrolohmannia* and Lohmanniidae would be convergent, or the scissure in *Malacoangelia* would represent a reversal. Based on a single known protonymph, immatures of *Nothrolohmannia* have a functional transverse scissure (Fig. 3E) that bears small setae of row e, so the fusion occurs only in the adult instar. Immatures of Lohmanniidae show no evidence of a scissure.

d. *Proterasomal structure*. In *Malacoangelia*, *Nothrolohmannia*, and *Eohypochthonius* the prodorsal aspis is isolated from fused epimera I-II by articulating soft cuticle (a plesiomorphy). *Hypochthonius* and Lohmanniidae share the derived fusion of aspis and epimera I-II into a single proterasomal unit.

e. *Setation of femora*. The femoral chaetome of Lohmanniidae (Table 1) seems too rich to be consistent with the hypothesis in Fig. 2. Hypochthoniidae all have a setation (I to IV) of 5-5-3-3. But some lohmanniids have six setae on femur II, greater than any member of Hypochthonioidea, and some have four setae on femur III, greater than any known member of Enarthronota. If the hypothesis is correct, and if the rich femoral setations of Palaeosomata are ancestral in oribatid mites, then setae previously lost by regression have reappeared in Lohmanniidae. In contrast, the tibial and tarsal setations of Lohmanniidae are never richer than those of Hypochthoniidae, and all could have been derived by simple regressive losses.

f. *Solenidial complements* (Grandjean, 1964b). Lohmanniidae have solenidial formulae for tibiae and tarsi that are similar to those of Hypochthoniidae: 1-1-1-0 and 2-[1,2]-0-0, respectively [brackets indicate interspecific variation]. Lohmanniidae have a second genu I solenidion (2-1-1-1) that is absent from Hypochthoniidae (1-1-1-1), but not from Eniochthoniidae or Arborichthoniidae (each with 2-1-1-1). Figure 2 requires independent losses of the second solenidion in clades IV and VI, or its reappearance in Lohmanniidae.

g. *Coupling of solenidia with seta d on genua*. Overall, the distribution of seta/solenidion coupling within Enarthronota is complex, but it is rather uniform within Hypochthonioidea. Hypochthoniidae, Eniochthoniidae, and early derivative Mesoplophoridae (*Archoplophora*) have seta d independent of solenidia on all genua. Arborichthoniidae shares the pattern on genua I-III, but coupling occurs on genu IV. In Lohmanniidae d couples to a solenidion on all genua.

h. *Pretarsal claw structure*. *Malacoangelia*, *Nothrolohmannia*, and *Eohypochthonius* have a tooth along the dorsal marginal of the claw, but none on the ventral edge. *Hypochthonius* has a proximoventral claw, but none on the dorsal margin. Claws in Lohmanniidae are often smooth, but if a tooth is present it is proximoventral.

Conclusions

The weight of evidence suggests that Figure 2 is correct, and that Lohmanniidae should be included in Hypochthonioidea. Particularly convincing are progressive apomorphies 2, 3, 5, 9, 11, 16, and 18, and rare regressive apomorphies 14 and 17. Incongruencies exist, yet none is exceptional, and similar levels and types of homoplasy are found in other mite taxa.

Feeding biology is perhaps the most striking incongruence with Figure 2. Enarthronotes are primarily fungivores or scavenger/necrophages (Schneider et al., 2005). Loh-

manniidae are unique among them in being saprophages of higher plant structural material (see above). Their strong, broad rutella and robust chelicerae are quite similar to those of more derived groups with the same feeding biology (e.g., Mixonomata, Desmonomata), but the primitive rutellar base and anarthric subcapitulum reveal an enarthronote origin.

If Figure 2 is correct, a classification problem arises of a type discussed previously (Norton, 2001). Cladistically, Lohmanniidae form a clade within Hypochthoniidae and would fit well at the subfamily rank (Lohmanniinae) in a sequenced classification. But its divergent morphology and species diversity argues for retaining family rank, restricting Hypochthoniidae to the genera *Hypochthonius* and *Eohypochthonius*, and once again recognizing Nothrolohmanniidae for the sister-genera *Malacoangelia* and *Nothrolohmannia*. No classification change is recommended at this time, pending the results of an ongoing molecular study (with K. Domes, M. Maraun and S. Scheu)

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Anomalies of notogastral structures in poronotic oribatid mites (Oribatida: Poronota) interpreted as cryptic ancestral characters modulated by regulatory genes

Gerd Weigmann

Institute of Biology, Zoology, Freie Universität Berlin, Koenigin-Luise-Str. 1-3, 14195 Berlin, Germany.

E-mail: weigmann@zedat.fu-berlin.de

Occasionally, specimens of oribatid mites have abnormal asymmetric characters, e.g., regarding notogastral setation or the porose areas of the octotaxic system, similar to those in other more or less related taxa, or similar to those in ancestors. Exemplarily, anomalies in specimens of Schelorbitidae and Phenopelopidae are presented. A model is proposed involving chains of regulatory genes that explains evolutionary changes within branches of poronotic Oribatida as well as the notogastral anomalies discussed. This model may contribute towards a revised strategy for taxonomy and phylogenetical systematics.

Key words: Phylogenetic systematics, taxonomy, regulatory genes, Schelorbitidae, Phenopelopidae

Occasionally, specimens of oribatid mites have asymmetric characters, e.g. regarding notogastral setation or the porose areas of the octotaxic system. Often, the character expression of the aberrant side is strongly suggestive of the normal character expression in other more or less related taxa. Are such anomalies negligible mutations or developmental defects? Can we interpret them as an atavistic reminiscence of ancestors or should we maintain the view that they are reversal mutations? Grandjean (1948a,b, 1952) discussed anomalies ('écarts') within clones of *Platynothrus peltifer*, mostly concerning losses of setae, whether asymmetric or not, as well as their frequency of occurrence in populations. He concluded that these types of anomalies are not small mutations (Grandjean, 1948b, p.882: '...les écarts ne sont pas de petite mutations'), but phenotypical expressions in the context of evolution in the number of organs.

Some simple notogastral characters, as loss of centrodorsal setae (*da*, *dm*, *dp*), loss of setae *c*₁ or *c*₃, or realization of the octotaxic system either as areae porosae or as sacculi, seem to be widely distributed within the families of poronotic oribatid mites. The mosaic-like distribution of these characters in the systematic branches makes a cladistic analysis nearly impossible without assuming several convergent disappearances; patterns of above mentioned, presumably 'homologous' character expressions contradict other characters which are assumed to be of systematic relevance.

In the following, I discuss some examples of notogastral anomalies in the light of phylogeny, ontogeny and I introduce a model of regulatory gene complexes influencing morphogenesis and gene expression in the instars of oribatid mites to explain these anomalies. The results may help to critically revise taxonomy and systematics of oribatid mites, based on knowledge of modern molecular genetic processes underlying phenotypical character expression. A similar

approach regarding enzymatic patterns in *Platynothrus peltifer* has been proposed earlier as a 'new concept of evolution' by Ziegler & Wauthy (1987).

Abnormal patterns of notogastral setation and areae porosae in Phenopelopidae

Eupelops acromios

Within the genus *Eupelops* there are two well-known groups of species with different notogastral setation pattern: (A) the setae *h*₃ are very close to the areae porosae *A1* and the associated setae *lp*; (B) the setae *h*₃ are in normal lateral position and distant from setae *lp*, which are associated with areae porosae *A1*.

Eupelops acromios (Hermann) belongs to the species group B; its diagnostic characters are: short club-like sensillus, notogastral setae of median length and distally broadened, setae *h*₃ in normal lateral position. It is the most common arboreal bark-dwelling *Eupelops* species in Europe. Surprisingly, I recognized three single specimens with asymmetric setation pattern, two of them within populations of normal specimens and one specimen in a microscopical slide in the Willmann-Collection. The abnormality in all three specimens is the setation type A on the right side (with juxtaposed setae *h*₃ and *lp*; Fig. 1a) and the 'normal' setation type B on the left side. Using a determination key (Willmann, 1931; Weigmann, 2006) we must decide to follow either the right or the left side pattern. The left side morphology leads without any doubt to *E. acromios*.

Willmann (1931) ignored the asymmetry of his specimen, he regarded the right side as relevant and described his single specimen as '*Pelops geminus* Berlese'. Examining the mounted specimen (collected by C. Willmann on 25 July 1919 from Stoteler Forest, near Bremen, Germany), I

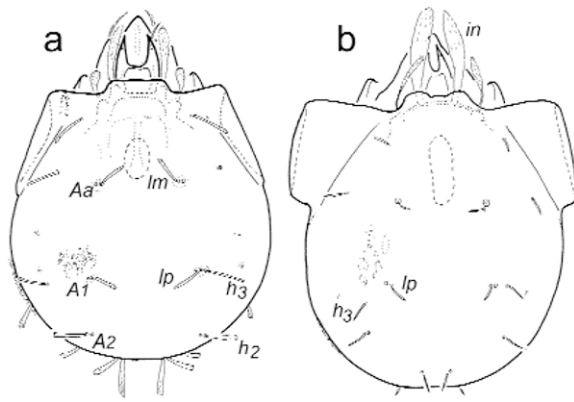


Figure 1 Abnormal *Eupelops* specimens. (a) *E. acromios*: left side with normal notogastral setation pattern, right side abnormal. (b) *E. occultus*: left side abnormal. Abbreviations: *in*, interlamellar seta; *Aa*, *A1*, *A2*, Areae porosae; *lm*, *lp*, *h2*, *h3*, notogastral setae.

assumed the specimen as probably belonging to *Eupelops claviger* (Berlese) (see Weigmann, 2006, p. 344). But now, compared with the other two abnormal *E. acromios*, the Willmann-specimen is most probably conspecific.

The second specimen with this asymmetry (drawing in Fig. 1a) has been collected by Stephanie Sobek in 2001 from a canopy branch of an oak tree, near Basel in Switzerland (Weigmann et al., 2004), together with several normal and symmetric specimens of *E. acromios*. The third specimen has been found in a dune area on the Isle of Sylt, Northern Germany (in 2005; G Weigmann, unpubl.), together with some normal *E. acromios*. These three independent findings from three distinct populations give rise to the assumption of a common cause for the misdevelopment, possibly a unilateral defect in the morphogenesis of the adult. The first idea was that the right side with the juxtaposed setae *h3* and *lp* should be a special apomorphy. In that case, the disjunct position of *h3* (as represented in nearly all other families of poronotic Oribatida) should be plesiomorphous: this seems to be a misinterpretation as will be discussed below.

Eupelops occultus

Eupelops occultus (CL Koch) is quite common in meadows. It belongs to the species group A as characterized in the previous section; the setae *h3* and *lp* are juxtaposed and form a complex together with *A1*. In 2005, I got some specimens collected by Andreas Toschki (Aachen, Germany) to verify the species identity. There was one specimen with abnormal notogastral setation (together with a normal specimen) which shows imperfect juxtaposition on the right side and far distant position of *h3* on the left (Fig. 1b). This observation seems to support the idea of a plesiomorphous character expression, representing an abnormal atavistic regression towards disjunct setae, yet with asymmetric configuration.

The described anomalies in *E. acromios* on the one hand and in *E. occultus* on the other seem to be incompatible and antagonistic: in *E. acromios* the setae *h3* and *lp* are juxtaposed abnormally, whereas in *E. occultus* the setae *h3* and *lp* are separated abnormally! Is a common explanatory model conceivable? This phenomenon begs for detailed phylogenetical discussion.

Abnormal patterns of notogastral setation in Scheloribatidae

In *Schelorbates* species and in most other genera of the family the notogastral setation is 'multideficient', following the terminology of Grandjean (1954), i.e., there are 10 pairs of notogastral setae in the adults. Some taxa, as *Topobates*, which is related to *Schelorbates*, have 12-14 pairs of notogastral setae in the adults, representing an intermediate status between 'unideficient' (15 pairs) and 'multideficient' (10 pairs). Some species with intermediate setation have been described as further genera, which seems to be punctilious splitting, based only on a character of minor taxonomic value (discussed in Weigmann & Miko, 1998). In this context, it is of highest importance that the third nymphs of all Scheloribatidae and related families (as far as I know) represent the unideficient status, i.e., with all 15 pairs of notogastral setae (the 16th seta f_1 in basic Oribatida is lost in all poronotic Oribatida).

Looking through the literature I discovered a lot of individual abnormalities in the notogastral setation of *Schelorbates* and *Topobates* species. In the following only some examples will be presented, constricted to both taxa, but the same phenomenon can be observed in some other genera and families as well; for instance, cf. Seniczak et al. (1990) on the ceratozetid *Fuscozetes fuscipes*. The first described *Topobates* was *T. granifer* Grandjean. It has 14 pairs of notogastral setae in the adult; compared with *Schelorbates* we find the mediadorsal setae c_3 , da , dm , and dp in addition. Yet, even the first author marked a unilateral vestigial seta c_3 , which represents the 15th seta of the unideficient pattern (Grandjean, 1958). Adult *Topobates holsaticus* Weigmann have 13 pairs of notogastral setae (without c_1 and c_3), but in one individual out of ca. 200, the unilateral seta c_3 was present and stronger than all other setae (as normally observed in some *Oribatula* species). In a Spanish *T. holsaticus* population, Subias & Arillo (2000) found a unilateral seta c_1 in a single specimen. Csizsar & Jeleva (1962) published a new species, *Schelorbates labyrinthicus* Jeleva, which differs from the widespread *S. laevigatus* (CL Koch) only by bilateral expression of hypertrophied c_3 -setae: *S. labyrinthicus* is assumed a junior synonym of *S. laevigatus* (Weigmann & Miko, 1998). Ingrid Wunderle has found a specimen of the arboreal *Schelorbates ascendens* Weigmann et Wunderle, with additional alveoles of notogastral setae c_3 and the centrodorsal da , dm , dp , partly unilateral, though all other studied adults have 10 pairs as usual (Weigmann & Wunderle, 1990). *Topobates carpathicus* Weigmann et Miko has 12 pairs of notogastral setae in the adults (dm and dp present), but some individuals show an additional vestigial pair of da -setae.

All these examples of abnormal additional notogastral setae in adult Scheloribatidae beg for a unifying explanation. The existence of 15 pairs of notogastral setae in the juveniles indicate that genes for these setae are present. It seems most probable that the additional setae of the unideficient pattern of the nymphs are repressed morphogenetically in the adult phenotype, yet there is a latent potential to develop these setae in the adult instar! One consequence of this hypothesis is that additional notogastral setae of the adults are atavistic reminiscences of ancestral characters, in abnormal (often asymmetric) cases as well as in *Topobates* and other genera of the *Schelorbates* complex. There are no convincing apomorphies to define distinct genera in a suffi-