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THE 20TH ANNIVERSARY OF A MODEL MITE: A REVIEW OF CURRENT KNOWLEDGE ABOUT *ARCHEGOZETES LONGISETOSUS* (ACARI, ORIBATIDA)

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ABSTRACT — With about 10,000 described species and densities reaching 400,000 ind/m^2, the Oribatida (without Astigmata) represent the most prevalent group of soil mites. However, with the exception of their taxonomy, many aspects of the biology of oribatid mites have been poorly studied. This might be explained in part by the previous lack of a model species. However, in the last 20 years, more and more non-taxonomic studies regarding development, genetics, morphology, chemical ecology and ecotoxicology have become available, with a significant number focused on the trhypochthoniid oribatid mite *Archegozetes longisetosus*. A well-defined laboratory strain of this pantropical parthenogenetic species was established in 1993 by one of us (RAN), and has since spread through numerous laboratories worldwide. In this review, we summarize the scientific achievements this lineage has enabled while becoming a model system for general zoology, ecology and evolution.

KEYWORDS — model organism; Chelicerata; Acari; Oribatida

WHAT MAKES A MODEL ORGANISM ?

Several major leaps in understanding life on earth can be attributed to the adoption of model organisms. Species like the rockcress *Arabidopsis thaliana* (L.) Heynh 1842, the fruit fly *Drosophila melanogaster* Meigen 1830, the zebrafish *Danio rerio* (Hamilton, 1822) and the rat *Rattus norvegicus* (Berkenhout, 1769) provided starting points for examining the complexity of life in detail. Comparisons of individual studies with results from model species have yielded insights into phylogeny, physiology, genetics, evolution and several other fields of life sciences. However, research fostered by the establishment of model organisms also demonstrated the difficulties of generalizing results, especially when the model organism was only distantly related to the taxa to which researchers wished to apply the results. Expanding the number of model taxa covering traditionally recognized major metazoan clades could help solve this problem.

The Chelicerata represent a major subgroup of the Arthropoda and have a long evolutionary history, dating at least to the Ordovician era (Weygoldt, 1998). Despite its diversity, only a few species of

chelicerates have been investigated thoroughly: e.g. the horseshoe crab *Limulus polyphemus* L., the spider *Cupiennius salei* (Keyserling 1877), the ticks *Ixodes ricinus* (Linnaeus, 1758) and *I. scapularis* Ray, 1821, or the spider mite *Tetranychus urticae* Koch 1836. Since the phylogeny of Chelicerata is still controversial, further chelicerate model species are needed for comparative analyses. This is particularly true of the highly diverse Acari, which are found in almost any habitat from subarctic glacial springs to tropical rainforests, and have become increasingly recognized as important model systems (Walter and Proctor, 2010). While Acari is a traditionally recognized taxon consisting of Actinotrichida (= Acariformes) and Anactinotrichida (= Parasitiformes+Opilioacarida), doubt has repeatedly been cast concerning whether these two groups really form a monophyletic clade or whether 'Acari' is diphyletic and therefore an artificial systematic entity (Dabert *et al.* 2010 and references therein). Within the Actinotrichida, the Sarcoptiformes are considered to comprise Astigmata and Oribatida, although the phylogenetic relationship between these two taxa remains controversial. Some authors propose the origin of Astigmata to be nested within Oribatida, rendering the traditional concept of 'Oribatida' paraphyletic (Norton 1994, 1998; Dabert *et al.*, 2010). When following the arguments of Norton (1994), one candidate as sister-group of Astigmata is the oribatid family Trhypochthoniidae, which consists of about 65 obligatorily parthenogenetic species (Maraun *et al.*, 2004; Heethoff *et al.*, 2011a). Hence, thorough knowledge of a model species in this family will help us to understand: (i) the evolutionary origin of the Astigmata, (ii) the phylogenetic relationship of Anactinotrichida and Actinotrichida and (iii) their position within the Chelicerata.

One member of Trhypochthoniidae, *Archegozetes longisetosus* Aoki, 1965 (Fig. 1), has already been referred to as a model mite (Thomas, 2000; Heethoff *et al.*, 2007a; Barnett and Thomas, 2011) and is the oribatid mite most studied under laboratory conditions (Smrž and Norton, 2004; Heethoff and Cloetens, 2008). Since *A. longisetosus* meets the requirements stated for model organisms (e.g. rapid development, easy rearing under laboratory conditions; see Thomas, 2000 and Grbic *et al.*, 2007), a laboratory strain was named *Archegozetes longisetosus* **ran** (Heethoff *et al.*, 2007a) in reference to its founder (**R**. **A**. **N**orton). The parthenogenetic lineage was raised from one single gravid female taken from a population sampled in 1993 from coconut debris in Puerto Rico (Smrž and Norton, 2004) and since then its offspring have been spread through numerous laboratories worldwide. In this review, we summarize the more than 70 existing scientific papers dealing with taxonomy, ecology, phylogeny, morphology and development of *A. longisetosus,* many of which were based on this strain.

Taxonomy and distribution

The genus *Archegozetes* was proposed by Grandjean (1931) with the Sumatran species *Epilohmannia magna* Sellnick, 1925 as type by original designation. It was proposed without a diagnosis or reference to a family, and its first classification appears to be that of Vitzthum (1942) who included it in Epilohmanniidae. This assignment was made apparently with the same level of doubt with which Sellnick (1925) assigned the type species (accompanied by a question-mark) to the genus *Epilohmannia*. In his seminal paper on oribatid mite classification, Grandjean (1954) included *Archegozetes* in Trhypochthoniidae Willmann 1931, though also with unexplained doubt, and it has remained there. Beck's (1967) analysis of this family placement is the most complete. Trhypochthoniidae currently comprises 65 species in nine genera in the middle-derivative oribatid mite hyporder Nothrina, of the infraorder Desmonomata (Subías, 2004; Norton and Behan-Pelletier, 2009; Schatz *et al.*, 2011).

Only seven species-group names have been proposed, but despite this low diversity there has been much confusion in the literature. *Archegozetes longisetosus*, originally collected in Thailand, was the second species proposed, and Aoki (1965) provided a table of character states that seemed to clearly distinguish it from *A. magnus*. Most of these related to relative length and shape of various setae, but also leg setal counts, solenidial shape and cuticular structure were included. Beck's (1967)

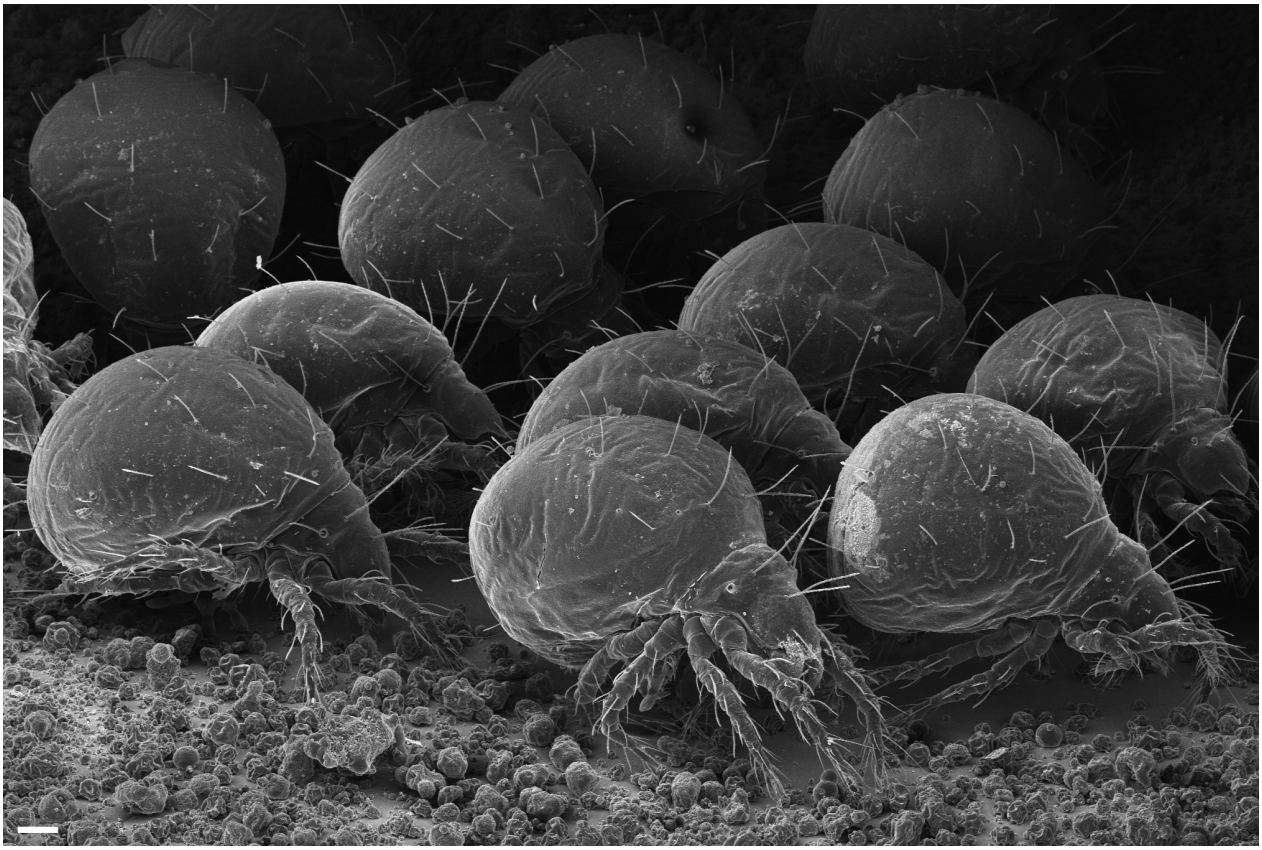

FIGURE 1: SEM-micrograph of a group of adult *Archegozetes longisetosus* on unicellular alga (*Chlorella*). Scale bar: 100 μm.

thorough study of Brazilian and Thai specimens of *A. longisetosus* concluded that it was indeed distinct from *A. magnus,* but distinguishable only by the longer and more barbed notogastral setae, plus a differently shaped supracoxal seta (a minute character that is rarely described in the literature); he considered the other differences cited by Aoki (1965) too variable to distinguish the two species.

The concept of *A. magnus* used by both Aoki (1965) and Beck (1967) was clearly based on van der Hammen's (1955a, b) detailed redescription, which was based on specimens from New Guinea. However, Sellnick's (1925) figure shows clearly that the Sumatran population had setae with length intermediate between that studied by Aoki (*A. longisetosus*) and that studied by van der Hammen (purportedly *A. magnus*). As setal length has been a primary distinguishing trait among species in the genus, and as van der Hammen's work is usually accepted as representing *A. magnus*, this was probably the first point of confusion regarding species concepts in *Archegozetes*.

Since that time, three other species have been proposed: *A. tuberculatus* Sarkar, 1985 from India and two species from Mexico, *viz. A. veracruzensis* Palacios-Vargas and Iglesias, 1997 and *A. chamelensis* Palacios-Vargas and Iglesias, 1997. Two subspecies of *A. magnus* were also proposed: *A. magnus indicus* Bhaduri and Raychaudhuri, 1968, from India, and *A. magnus mediosetosus* Mahunka, 1978 from the Seychelles. A series of taxonomic actions have affected these names and species concepts: (1) Mahunka (1978) treated *A. longisetosus* as a subspecies of *A. magnus*; (2) *Archegozetes magnus indicus* was noted to be a junior synonym of *A. longisetosus* by Sarkar (1985, citing an unpublished 1971 thesis by A. K. Bhaduri); (3) *Archegozetes chamelensis* was found to have been described from a

tritonymph and considered a synonym of *A. longisetosus* (Estrada-Venegas *et al.*, 1999); (4) *Archegozetes tuberculatus* has been considered a junior synonym of *A. magnus* (Subías, 2004); (5) *Archegozetes magnus mediosetosus* has been considered a junior synonym of *A. magnus* by Badejo *et al.* (2002). Adding to this confusion, the latter authors considered *A. veracruzensis* to be a junior synonym of *A. magnus* in their text, but of *A. longisetosus* (considered a morphotype they did not study directly) in their abstract. In essence, Badejo *et al.* challenged anyone to provide good evidence that all *Archegozetes* are not conspecific.

The resolution of such controversies requires more types of information than are currently available for the nominal species of *Archegozetes*, populations of which all are probably clonal in nature. The integration of molecular and morphometric approaches, applied in a modern context of species concepts, will be essential (see below). At this point, it seems most reasonable to follow the moderate approach of Subías (2004; see also Beck, 1967) in recognizing *Archegozetes longisetosus* as being distinct from *A. magnus* (and its subspecies *A. magnus mediosetosus*). The current advantages are that (1) with its long notogastral setae, which seem quite consistent within and among populations, *A. longisetosus* is the most recognizable of all described morphotypes, and (2) during periods of taxonomic uncertainty, maintaining a more finely split taxonomy is preferable to premature lumping, which would result in the loss of information, should opinions change.

Collectively, *Archegozetes* is found throughout the tropical regions of the world, on both continents and islands, and also extends into subtropical latitudes. We will not list locations in detail, but *Archegozetes longisetosus* is widely distributed across the Oriental, Australian and Neotropical regions; we know of no reports from the Ethiopian region, though *A. magnus* occurs there (Subías *et al.*, 2012). As many *Archegozetes* records are from oceanic islands, in coastal regions of continents, or near major freshwater bodies, Badejo *et al.* (2002) suggested that water-borne movement might be important for dispersal in these parthenogenetic, colonizing mites (see below), but they are by no means restricted to such locations.

PHYLOGENY

Data relating to the phylogenetic relationships of *A. longisetosus* or its family Trhypochthoniidae have come from both traditional and molecular studies. Knülle (1957) used morphological data to perform the first phylogenetic analyses (*sensu* Hennig, 1950) of oribatid mites and he grouped Malaconothridae and Trhypochthoniidae (including his Trhypochthoniellidae) as Trhypochthonioidea (now Malaconothroiodea), although he did not study *Archegozetes* per se. Haumann (1991) broadened the taxonomic range of this 'cladistic' work and considered this superfamily to be the sister-group of Holosomata ('Nothroidea', Nanhermanniidae, Hermanniidae and Circumdehiscentiae (= Brachypylina)); in other words, he viewed them as the earliest derivative of what authors have referred to as 'Desmonomata', in its restricted sense. By contrast, Norton (1994, 2007) viewed Trhypochthoniidae and Malaconothridae as being rather derived mites, with an evolutionary history of paedomorphosis that continued most strongly in their hypothesized relatives, the Astigmata.

The first relevant molecular phylogeny (based on the nuclear ribosomal D3-region) including Trhypochthonioidea was published by Maraun *et al.* (2004). Three trhypochthoniid species/genera were represented: *A. longisetosus*, *Trhypochthonius tectorum* (Berlese, 1896) and *Mucronothrus nasalis* (Willmann, 1929). Trhypochthoniidae appeared to be paraphyletic in this study, with *T. tectorum* and *M. nasalis* being sister groups, but with *A. longisetosus* grouping equivocally with a wide range of different taxa – depending on the kind of phylogenetic analyses applied. Laumann *et al.* (2007) demonstrated that the D3-region is probably already highly saturated in oribatid mites at this level of relatedness, and hence might generate misleading results. Using the much more conserved 18S rDNA gene, Domes *et al.* (2007) and Maraun *et al.* (2009) confirmed that *A. longisetosus*, *T. tectorum*, *T. americanus* (Ewing, 1908) and *Mainothrus badius* (Berlese,

1905) form a well-supported cluster, indicating that Trhypochthoniidae is indeed monophyletic.

Since all known members of Trhypochthoniidae are parthenogenetic, one is confronted with the methodological, technical and philosophical problem of species delimitation and delineation. Hence, cryptic diversity (*i.e.* a hidden number of additional species validated by one species concept, but not by another) can be expected in such parthenogenetic clusters and this has been demonstrated for other oribatid mite genera: *Platynothrus* (Heethoff *et al.*, 2007b) and *Tectocepheus* (Laumann *et al.*, 2007). Heethoff *et al.* (2011a) proposed an integrative taxonomical framework including morphological, molecular and chemical data for a reproducible delineation of parthenogenetic *Trhypochthonius* lineages. Using such a framework, future studies might provide more reliable species concepts within *Archegozetes*, as well as in other Trhypochthoniidae and indeed all other parthenogenetic oribatid mites.

Life history and development

Life history and development of a parthenogenetic organism can be seen in part as circular processes since no 'new' genetic material is incorporated in the next generation. We briefly summarize the development of *A. longisetosus* here by reviewing development and morphology of the post-embryonic free-living instars (larva, proto-, deuto-, tritonymph, adult) and life history, development of the germline, mechanism of parthenogenesis, structure of the adult ovary, cleavage patterns and embryonic development.

Almost 30 years ago, Aeschliman and Hess (1984) answered the question 'What do we know about the embryology of acarines today?' with 'Nothing really new during the past 25 years'. This remained mostly unchanged for another 15-20 years (Walzl, 2004) and embryology is still one of the least studied fields in acarology (Laumann *et al.*, 2010a). The first application of 'modern' techniques to unravel developmental processes in oribatid mites using gene expression studies of homeobox genes was performed with *A. longisetosus*. It showed that, in contrast to common opinion, chelicerates retain their deutocerebral segment, which renders the chelicerae homologous to the first instead of the second antennae / intercalary segment of Mandibulata (Telford and Thomas 1998a). Following this first expression study, further studies in a developmental genetic context have examined expression patterns of *zen* (Telford and Thomas, 1998b), *distal-less* (Thomas and Telford, 1999), *engrailed* and *hedgehog* (Barnett and Thomas, 2012), further limb gap gene expression patterns (Barnett and Thomas, 2013a) and *Ultrabithorax* and *Abdominal-B* (Barnett and Thomas, 2013b). *Dachshund* expression, for example, provided evidence that *A. longisetosus* has a three- rather than a two-segmented chelicera (Barnett and Thomas, 2013a; see also Alberti *et al.*, 2011 for morphological evidence of the cheliceral trochanter in *A. longisetosus*). As of July 2013, GeneBank (NCBI) provides the sequences of 16 different developmental genes for *A. longisetosus*, and RNA interference (RNAi) protocols will soon be developed (Barnett and Schmidt-Ott, 2013). These will provide further opportunities to understand the developmental genetics of mites.

A number of laboratory studies dealt with life history traits of this species (Haq, 1978; Haq and Adolph, 1981; Honciuc, 1996; Seniczak, 1998; Estrada-Venegas *et al.*, 1999; Heethoff *et al.*, 2007a). Observed life cycles ranged from 28 to 88 days, with each juvenile instar occupying 10 to 12 days under typical culture conditions. Eggs are laid in clutch sizes of 2 – 42, at an average of 1.3 eggs/day (Heethoff *et al.*, 2007) and with the total number of offspring produced by individual females ranging from 31 to 238. Seniczak (1998) showed that food significantly influences fecundity and development, with unicellular algae (*Protococcus* sp.) leading to higher reproduction than lichens (*Cladonia* sp.) or tree bark (*Prunus padus*). Furthermore, fecundity seems to be density-dependent with lower densities leading to higher reproductive output and larger offspring (Seniczak, 2006). Regardless of culture density, *A. longisetosus* commonly builds large aggregations of up to several hundred individuals of mixed instars (Fig. 2), in which they spend the quiescent period prior to molting (Haq, 1982).

Population densities of *A. longisetosus* in India

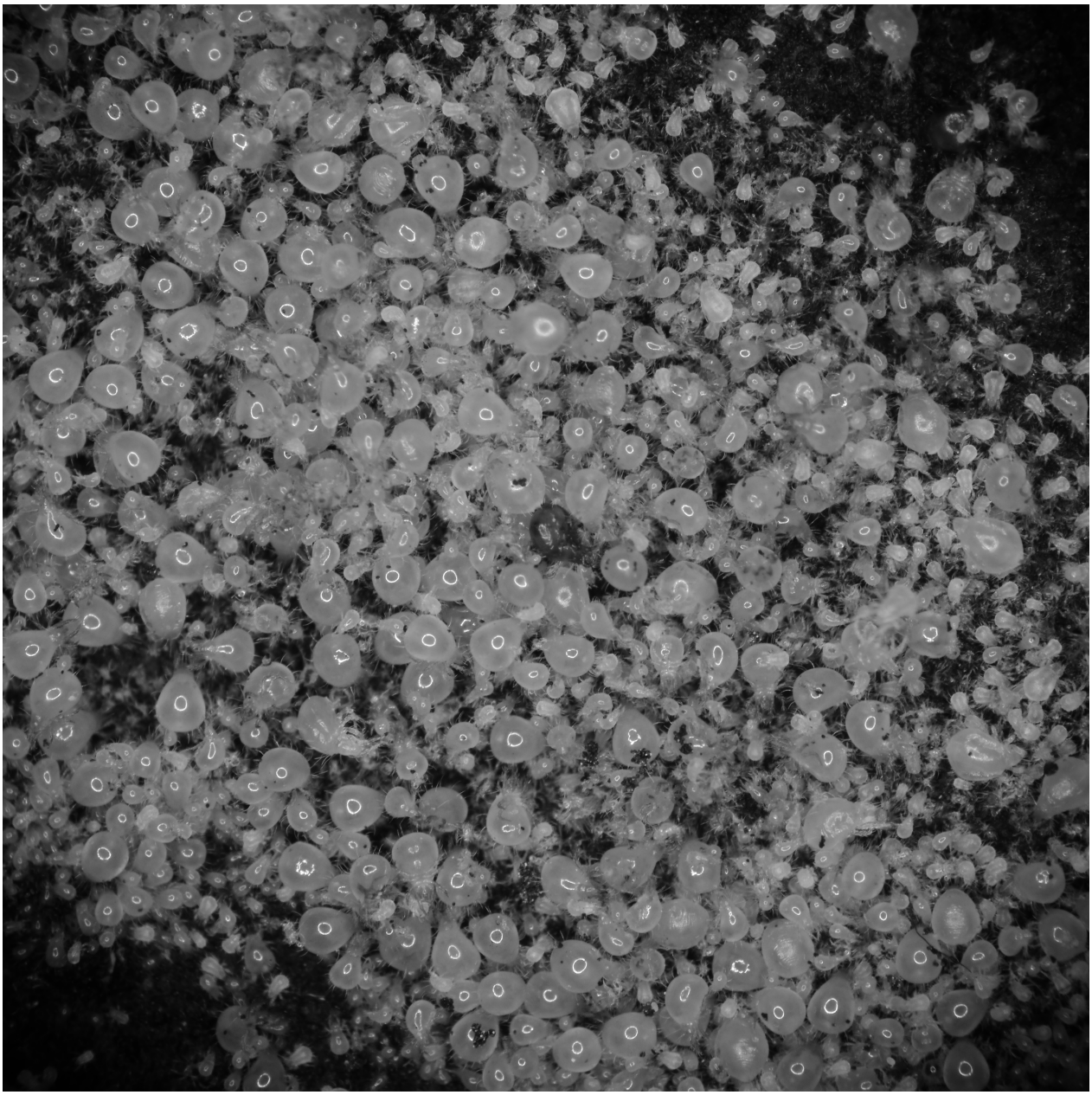

FIGURE 2: Molting aggregation of individuals from all active instars (larvae, proto-, deuto-, tritonymphs and adults) of *Archegozetes longisetosus* ran in a laboratory culture.

were shown to depend on vegetational conditions, with highest relative abundances found in grasslands and paddy fields, intermediate abundances in banana plantations and lowest relative abundance in an *Acacia auriculiformes* forest (Bhattacharya *et al.*, 1981). Frequencies were also strongly influenced by human activities such as agriculture, and can drop about 15-fold from 30 % in newly established to 2 % in permanent rice fields, with an analogous drop in abundance (Bhattacharya *et al.* 1980). On the other hand, *A. longisetosus* seems to be a good colonizing species: after burning of fields in Brazil they were the most abundant oribatid mite species in refugial (unburned) areas after 40 – 60 days and reached highest abundances also in the burned areas after 10 – 12 months (de Oliveira and Franklin, 1993). During sampling for *A. magnus* and *A. longisetosus* in the Caribbean region, it was clear that they occurred primarily in disturbed habitats, such as raked piles of organic trash, litter under roadside bushes and similar substrates, and were rather rare in natural forest soils (R.A.N., unpublished). The apparently good colonizing abilities of *Archegozetes* might in part be explained by passive abiotic dispersal combined with parthenogenesis, but perhaps also by active or passive phoresy on other arthropods (e.g. harvestmen; Townsend *et al.*, 2008) or vertebrates (e.g. amphibians; Beaty *et al.*, 2013). While current reports of phoresy relate to *A. magnus* (sensu van der Hammen, 1955a), *A. longisetosus* can generate very high holding forces (1200 times their body weight) with their legs and claws (Heethoff and Koerner, 2007) and hence this species seems physically able to cling to larger animals for transport purposes.

The external morphological development of the free-living instars of *Archegozetes* was first described by Hammen (1955b) for *A. magnus* (as *A. magna*, in his sense) and by Seniczak and Seniczak (2009) for *A. longisetosus*. Using scanning electron microscopy (SEM), Thomas and Telford (1999) and Heethoff *et al.* (2007a) provided the first micrographs of *A. longisetosus* embryos, prelarvae and larvae. As is the rule in Acari, the larva is hexapod and the fourth pair of walking legs first develops at the molt to the protonymph. However, the bud of the fourth pair of legs is already visible in mid-stage embryos preceding the regressive prelarva and hind-leg development seems to be linked to opisthosomal segmentation (Barnett and Thomas, 2012).

Ecotoxicology

Its relatively high reproductive output and defined series of molts makes *Archegozetes longisetosus* a suitable candidate species for ecotoxicological studies that analyze influences of environmental pollution on development, fecundity and survival. Since the first ecotoxicological studies investigating the influence of copper (Seniczak *et al.* 1996, 1997, 1999a), *A. longisetosus* has been used as a model for studying the influence of lead (Senizcak and Seniczak, 1998; Senizcak *et al.*, 1999a, b; Köhler *et al.*, 2005), cadmium (Senizcak and Seniczak, 2002; Senizcak *et al.*, 2006, 2009) and zinc (Senizcak *et al.*, 2005) on development and life history parameters. It was generally shown that high concentrations of heavy metals decrease fecundity and induce developmental malformations, most visibly those of the fourth pair of walking legs during the development from larva to protonymph (Köhler *et al.*, 2005). In a study of insecticide residue toxicity to nontarget microarthropods in Indian soils, Pramanik *et al.* (1998) found *A. longisetosus* to be the most sensitive of the three tested oribatid species, and the second-most sensitive of all six microarthropod species tested.

Parthenogenesis

Parthenogenesis (more precisely in this case: thelytoky) is widespread in oribatid mites and has been demonstrated for *A. longisetosus* by rearing and by the absence or extreme rarity of males in field populations and culture (Palmer and Norton, 1990, 1991). The cytological mechanism involved is still not completely understood (Heethoff *et al.*, 2009). Based on theoretical considerations and a small amount of allozyme data, Wrensch *et al.* (1994) proposed an automictic mechanism with inverted meiosis and terminal fusion of second-division nuclei. One prerequisite for this mechanism is that chromosomes are holokinetic, and Heethoff *et al.*

(2006) have shown that this is true of *Archegozetes*, which is diploid with 2n = 18. Following meiosis I, the first polar body seems to degenerate, and meiosis II seems incomplete (Laumann *et al.*, 2008). With a 'normal' meiotic sequence (first reductional, then equational) all offspring would inevitably be homozygous. Palmer and Norton (1992) instead found that some allozyme loci of *A. longisetosus* were heterozygous and do not recombine. Hence, all experimental evidence – holokinetic chromosomes, degeneration of the first polar body, heterozygosity and absence of recombination – are in perfect accordance with the hypothesis of Wrensch *et al.* (1994).

Germline

The development of gametes (oocytes) and the linked development of reproductive organs have been studied in *A. longisetosus*. The ovary develops from an unpaired ventral mass of mesodermal tissue in the larva and grows continuously. In the deutonymph, the ovary increases and contains a growing number of germcells, indicating proliferation of oogonia at this stage (Bergmann and Heethoff, 2012b). The oviducts start to develop in the protonymphal instar as lateral extensions from somatic precursors (Bergmann *et al.*, 2008; Bergmann and Heethoff, 2012b). Oviducts are discernible as tubular structures connecting the ovary with the unpaired genital duct during the deutonymph/tritonymph transition. Differing from the general model of chelicerate oviductal growth (Goodrich, 1945; Anderson, 1973), developmental data so far suggests retrograde growth and a secondary contact with the ovary (Bergmann and Heethoff 2012b). Secondary contact of ovary and oviducts was previously described for an oribatid mite from the infraorder Brachypylina, *Xenillus tegeocranus* (Hermann, 1804) (Warren, 1947). In this study, oviducts were described as ectodermal structures originating from the invagination of the genital porus. The interpretation of oviducts being ectodermal tissue might be due to their apparent retrograde elongation (Figure 3, right column). The oviducts of *A. longisetosus* were interpreted as mesodermal due to the fact that they never exhibit a cuticular lining, whereas the vagina does. They furthermore originate from a tissue that is separated from the ventral body wall by an epithelial layer identified as the epidermis in early nymphal instars (Bergmann and Heethoff 2012b). In the adult the ovary develops two protrusions in which oocytes move towards the oviducts (Bergmann *et al.*, 2008). Here, meiosis continues until the diploid oocyte is restored by terminal fusion (Laumann *et al.*, 2008), and vitellogenesis takes place (Bergmann *et al.*, 2010). The very different development and function of the central unpaired part of the ovary and the paired protrusions toward the oviducts led Bergmann *et al.* (2008) to a new nomenclature for these structures: the central part was termed 'rhodoid' and the lateral protrusions 'meroi' (singular: 'meros'). These terms were chosen because the anatomical subdivisions of the adult ovary do not fit the traditional definitions of germarium and vitellarium as ovarian subdivisions: premeiotic mitoses cease no later than in early tritonymphal instar in the rhodoid, and vitellogenesis starts after oocytes enter the distal part of the meroi after metaphase I. The trophic type of the ovary was described as panoistic (Bergmann *et al.* 2010). Anatomically, the meroi can be understood as a derivation of the centrifugally developing oocytes typical for the chelicerate type of arthropod ovaries (Makioka, 1988).

When the zygote (*i.e.* diploid one-cell stage) passes from the ovarial meros into the oviduct via the oviductal bulb, the egg-shell immediately compacts and becomes impermeable. Because this interrupts the direct connection to the mother, Bergmann and Heethoff (2012a) defined the generational border to occur at this ovary/oviduct-transition and described the oviducts as functional brood chambers. Cleavage is then initiated in the proximal part of the oviducts (Laumann *et al.*, 2010a).

Cleavage

Traditionally, cleavage patterns of Acari were described as being superficial, sometimes preceded by a holoblastic phase (Laumann *et al.*, 2010a and references therein). In *A. longisetosus*, early cleavages are holoblastic and blastomeres give rise to yolk-free micromeres and macromeres containing all the

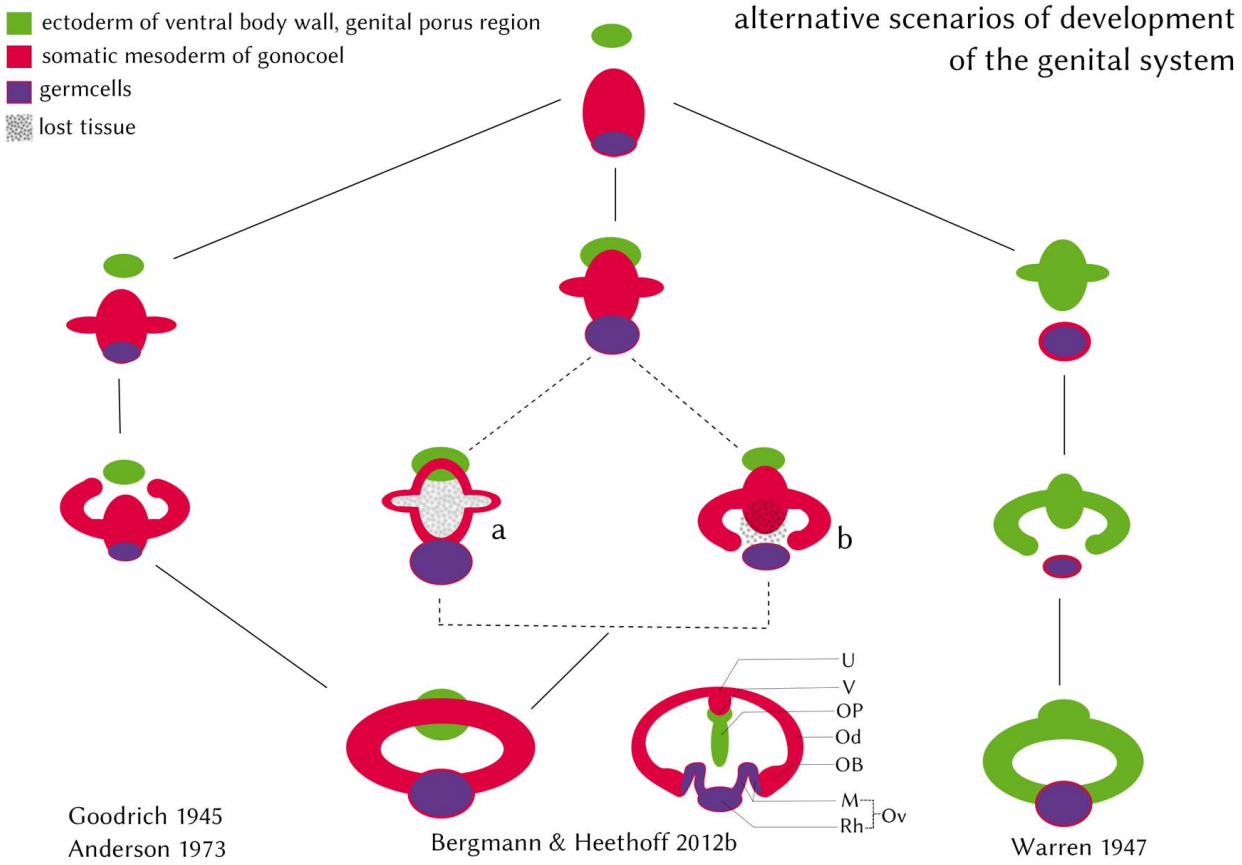

FIGURE 3: Schematic representation of different scenarios of genital system ontogenesis in *Archegozetes longisetosus*. Dorsal view, ontogenetic series top to bottom. Left column shows oviducts as anterograde developing coelomoducts following the 'classical' view of Goodrich (1945) and Anderson (1973). Right column shows an alternative description by Warren (1945), interpreting the oviducts as retrograde developing ectodermal invaginations. Middle column shows two scenarios derived from the information obtained in studies of *A. longisetosus* (Bergmann *et al.* 2008, Bergmann and Heethoff 2012b). It is unclear whether the oviducts derive from a fold at the rim of the gonocoel with a primary contact site at the ovary (a) or are retrograde developing tubular extensions with a secondary contact site at the ovary (b), and whether their lumen is primary (coelomic cavity) or secondary.
Abbreviations: M: meros; OB: oviductal bulb; Od: oviduct; OP: ovipositor; Ov: ovary; Rh: rhodoid; U: uterus; V: vagina.

yolk. Micromeres do not form a superficial preblastoderm layer. Instead, they form an external, monocellular layer that covers the whole surface of the embryo. Laumann *et al.* (2010b) reviewed available studies on acarine embryology and concluded that most studies reporting superficial cleavage probably suffered from methodological (fixation and microscopy) shortcomings – hence, their results remain questionable. Holoblastic and total cleavage seems to be the general pattern, at least for actinotrichid mites (Laumann *et al.*, 2010a, b).

Feeding Biology

Chelicerates ingest food in two fundamentally different ways: as fluids or as solid particles. Most predaceous terrestrial arachnids are fluid feeders with or without external pre-digestion. The plesiomorphic feeding mode of chelicerates, however, is presumably particle feeding, as can be found in the extant marine chelicerate classes Xiphosura and Pycnogonida. Within terrestrial Arachnida, particle feeding is restricted to some Opiliones (Acosta and Machado, 2007) and several groups of Acari (Heethoff and Norton, 2009a), including oribatid mites. *Archegozetes longisetosus* is one of the best-known arachnids regarding food processing, from the standpoint of both structure and function. The gross organization of the digestive system was shown by Heethoff *et al.* (2008; see also Betz *et al.*, 2007) in the form of a virtual passage through the tract using synchrotron-X-ray-tomography. The fine structure and functional morphology of the gnathososma of *A. longisetosus* have been studied in great detail by Alberti *et al.* (2004, 2011). Heethoff and Norton (2009b) established a biomechanical model of the chelicera, which was subsequently used to study trophic positions of other oribatid mites (Perdomo *et al.*, 2012). Alberti *et al.* (2003) provided a detailed study on the fine structure of the digestive system and fat body of *A. longisetosus*, and Heethoff and Norton (2009a) analyzed the functional morphological basis of defecation.

At the cellular level, Smrž (2006) reported free cells (haemocytes) 'between the internal organs in the mesenchymal tissue in the opisthosoma', and noted that they were associated with (and sometimes connected to) the alimentary system. Alberti *et al.* (2003) described these cells as 'fat-body cells', being connected to the midgut by small finger-like processes. Both Alberti *et al.* (2003) and Smrž (2006) suggested that the morphology of these cells indicates they are associated with food processing. Smrž and Norton (2004) and Smrž (2009) have also shown that food type influences the shape of food boluses, caecal cell-appearance, the presence of internal bacteria and enzyme (chitinase) activity in *A. longisetosus*. Rémen *et al.* (2010) fed *A. longisetosus* with the mycorrhizal fungus *Laccaria laccata* (Cooke) and were able to molecularly detect the fungus in the gut of five pooled mites. Heidemann *et al.* (2011) have shown that *A. longisetosus*, along with other oribatid mite species, feed also on living and dead nematodes (*i.e.* they can act as predators and scavengers).

The natural feeding strategies of oribatid mites remain poorly understood (Schneider *et al.*, 2004) and, since it accepts a wide range of food, *A. longisetosus* can be a valuable model for establishing different molecular food detection techniques that can be applied to field-sampled oribatid mites of this and many other species.

Defense

While it is still not clear what most oribatid mites feed upon, their significance as a resource in soil food webs is even less understood (Heethoff *et al.*, 2009). A small variety of predators (e.g. scydmaenid beetles, ants) feed on oribatid mites (references in Peschel *et al.*, 2006; Heethoff *et al.*, 2011b; Jaloszynski and Olszanowski, 2013), but regulation of oribatid mite density by top-down control seems unlikely, at least for the larger and more sclerotized groups (Schneider and Maraun, 2009). Peschel *et al.* (2006) performed the first statistically supported feeding experiments with oribatid mites as prey and concluded that adult oribatid mites may live in 'enemy-free' space. Several morphological traits of oribatid mites can be interpreted as adaptations to predator defense: sclerotized or mineralized cuticle, protective setae, hard roof- or wing-like projections (tecta), jumping capabilities, specialized body

forms, or some combination of these (Norton, 2007). In one specialized form, ptychoidy, animals can retract their legs into a secondary body cavity and encapsulate by retracting the prodorsum (Schmelzle *et al.*, 2009). Ptychoidy evolved at least three times independently and in each case is associated with cuticular mineralization (Pachl *et al.*, 2012), which helps make the resulting spheroid unbreachable by most small predators.

In addition to morphological traits for predator defense, most oribatid mites (the glandulate Oribatida including Astigmata; Sakata and Norton, 2001) possess a pair of opisthonotal exocrine glands (= oil glands). These glands may produce complex blends of aromatics, hydrocarbons, terpenes and alkaloids in species-specific combinations (Raspotnig *et al.*, 2011 and references therein). *Archegozetes longisetosus* was among the earliest oribatid mite species for which oil gland secretions were chemically characterized (Sakata and Norton, 2003; Raspotnig and Föttinger, 2008; Heethoff and Raspotnig, 2011), and they consist of eleven compounds: 2,6-HMBD (= 2-hydroxy-6-methyl-benzaldehyde), neral, geranial, neryl formate, γ-acaridial (= 3-hydroxybenzene-1,2-dicarbaldehyde), tridecane, pentadecene, pentadecane, heptadecadiene, heptadecene and heptadecane (Heethoff and Raspotnig, 2011). The main solvent of the secretions is pentadecane (Heethoff, 2012).

Archegozetes longisetosus is a valuable model system to investigate chemical ecology and the evolution of oil gland secretions for several reasons. First, it produces the full set of the so-called 'Astigmata compounds', which constitutes evidence that Astigmata evolved from within Oribatida (Sakata and Norton, 2001). Further, individuals can be 'chemically disarmed' by hexane treatment (Heethoff and Raspotnig, 2012a); evaporation dynamics of secretions have been investigated (Heethoff and Raspotnig 2012b); the regeneration dynamics are known (Heethoff, 2012); and it has been shown that *A. longisetosus* is significantly protected from predation by chemical rather than morphological defense (Heethoff *et al.*, 2011b; Heethoff and Raspotnig, 2012c). Hence, this species is an ideal candidate to investigate density-dependent dynamics of different generalist predator-prey-interactions with respect to chemical defense.

Conclusions

Acari are the most speciose and ecologically diverse group of chelicerates (Walter and Proctor, 2010; Zhang, 2011). With this review, we hope to convince readers that there are many highly interesting questions of general biological importance that can be addressed using mites as models — and we believe that *Archegozetes longisetosus* ran is a highly suitable candidate for such a model. Please contact the corresponding author if you want to start your own culture — he will be happy to provide some specimens and a rearing protocol.

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