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Adding to the Reproductive Biology of the Parthenogenetic Oribatid Mite, *Archegozetes longisetosus* (Acari, Oribatida, Trhypochthoniidae)

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Abstract: The oribatid mite, *Archegozetes longisetosus*, serves as a chelicerate model organism due to its relatively short life cycle and ease of laboratory culturing. It is a parthenogenetic species and all cultures recently used in different laboratories are descendants of a single female collected in 1993. While aspects of its developmental and functional biology have been published, knowledge of its reproductive rate and reproductive system is meager, and data on its life history are contradictory. Herein, we present the gross morphology of the reproductive system as obtained by SEM techniques and X-ray synchrotron microtomography, a new tool for studying mite anatomy. We investigated its reproductive rate by isolating 48 females from cultures and observing reproduction and development at 23 °C. Females repeatedly laid eggs in clutches containing 2-30 eggs. Within 51 days, each female produced, on average, 55 offspring with a maximum of 147. The reproductive rate averaged 1.3 eggs/day.

Key Words: *Archegozetes longisetosus* ran, Oribatida, reproduction, parthenogenesis, reproductive system, development, X-ray synchrotron microtomography, life history

Introduction

Oribatid mites (Acari, Oribatida) are a speciose group of mainly soil-living chelicerate micro-arthropods, with about 10,000 described species (Schatz, 2002). They are important decomposers in forest ecosystems, fallows, fields, and meadows, with densities up to 500,000 individuals per square meter in acidic soils of northern boreal forests (Maraun and Scheu, 2000). Parthenogenesis is 10 times more common in oribatid mites than in other metazoan taxa (Norton et al., 1993), and some of the parthenogenetic lineages probably have existed for a hundred million years (Heethoff et al., 2007) and evolved general purpose genotypes allowing them to exist under a wide range of ecological conditions (Heethoff et al., 2000).

Reproduction and development of oribatid mites

Regarding reproductive potential and diversity of ontogeny, mites are without peer among the chelicerates. Mites begin their lives as eggs, laid singly or en masse, with the egg shapes showing a wide range of different morphologies (Walter and Proctor, 1999). Oviposition in oribatid mites is accomplished with an extrusible ovipositor, which can be as long as the female body when extruded and is retracted by direct muscular action (Grandjean, 1956). Reproductive strategies range from iteroparity (repeated production of a few eggs) to semelparity (single production of many eggs). Usually, eggs are laid in crevices at an early developmental stage (embryo or prelarva), but larviparity also may occur (Walter and Proctor, 1999). The assumed ancestral developmental series of Acari is retained in oribatid mites: embryological development terminates in a regressive prelarva; this first instar is succeeded by the larva, protonymph, deuteronymph, tritonymph, and adult. In most mites the first active instar is the hexapod larva; the prelarva is inactive (calyptostase) and remains inside the egg shell in most acariform mites, although exceptions are known (Otto, 1997).

Oribatid mites tend to have low reproductive outputs and long developmental periods of 50 weeks or more are common for species of temperate zones (Norton, 1994;

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Walter and Proctor, 1999). The time for development might be reduced in tropical species like the parthenogenetic *Archegozetes longisetosus* (Haq, 1978).

The morphology of the female reproductive system in the Acari also spans a wide range (Evans, 1992). According to the group, the ovary can be unpaired, paired, or divided into germinal and nutritive regions (Evans, 1992; Alberti and Coons, 1999). Oribatid mites usually have an unpaired ovary from which 2 oviducts originate and proceed through the opisthosoma until they fuse again at the vagina. The genital tract continues as an ovipositor, a long cuticular tube, which, when not in use, is invaginated and folded inside the body. The tip of the ovipositor has 3 eugenital lobes, 2 anterolateral, and 1 posterior lobe. The mechanism behind oviposition is poorly understood. It has been assumed that hemolymph pressure extends the ovipositor and that muscles attached to its wall retract it (Michael, 1884; Grandjean, 1956). Wallwork (1977) suggested further that muscles inserted on the pleated wall are responsible for oviposition, although no mechanism was explained.

Archegozetes longisetosus

Archegozetes longisetosus is an oribatid mite having good potential as a model organism. The species is parthenogenetic (Palmer and Norton, 1990, 1992), has a pan-tropical distribution (Palmer and Norton, 1991), is relatively large (approximately 800-1100 µm; Seniczak, 1998), has a short generation time in the laboratory, and has a high fecundity. Since all instars have a translucent cuticle, food boluses, fecal pellets, and eggs are easily visible, recent feeding activity and reproductive states can be determined in living individuals. This makes it one of the most studied species of oribatid mites under laboratory conditions (Smrz and Norton, 2004). The species shows patterns in segmental development that are similar to those of other chelicerates (Telford and Thomas, 1998a, 1998b) and the embryonic development of the appendages has been investigated (Thomas and Telford, 1999). *A. longisetosus* has also been a subject of heavy-metal toxicology (Senizcak et al., 1997, 1998, 1999; Seniczak and Seniczak, 2002; Köhler et al., 2005), gland chemistry (Sakata and Norton, 2003), aggregation and molting (Haq, 1982), ultrastructural analysis of the digestive system and the gnathosoma (Alberti et al., 2003, 2004), and food selection and internal food processing (Smrz and Norton, 2004). Cytological studies (Heethoff et al., 2006) and molecular sequences are also available (Telford and Thomas, 1998a, 1998b; Thomas and Telford, 1999; Maraun et al., 2003).

Despite increasing knowledge of different areas of its biology, little is known about the reproduction of *A. longisetosus*. The morphology of its reproductive system remains uninvestigated. While some studies have addressed aspects of the life history (Haq, 1978; Haq and Adolph, 1981; Honciuc, 1996; Senizcak et al., 1997, 1998, 1999; Estrada-Venegas et al., 1999), their results are often contradictory regarding food preferences and developmental parameters.

Materials and Methods

Specimens of *A. longisetosus* (Figure 1) used in this study were derived from a culture initiated by R. A. Norton in 1993 from a single female collected from decomposing coconut debris at Luquillo, Puerto Rico. We started our own culture in November 2004 with about 200 specimens from Norton's culture. Our mites are cultured on a plaster-of-Paris/charcoal substrate (9:1) in plastic jars, in constant dark at 23 °C. Bark from different trees with unicellular algae (mainly *Protococcus*) growing on them is provided as food and replaced each week. Cultures are watered with some drops of fresh water whenever necessary to keep air humidity at about 90%.

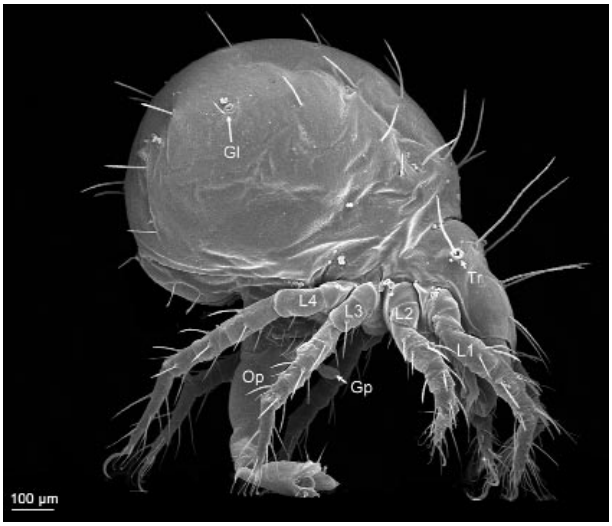

Figure 1. Lateral view of an adult *A. longisetosus*. The trichobothrium (Tr) on the prodorsum is a typical mechanoreceptor present in nearly all oribatid mites. Also visible is the opening of the opisthosomal gland (Gl), the extruded ovipositor (Op), and 1 of the 6 genital papillae (Gp). L1-L4: walking legs.

Scanning electron microscopy

For scanning electron microscopy (SEM), specimens were prepared as follows: fresh specimens were taken from the culture, cleaned with a fine brush, and placed in 70% ethanol for 12 h followed by 8 h in 95% ethanol, 8 h in 100% ethanol, and another 2 h in fresh 100% ethanol. This kind of fixation usually ensures that the ovipositor is extruded out of the body in adult specimens (Figure 1). Samples were critical point dried in CO_2 and sputter-coated with a 20-nm thick layer of a gold-palladium mixture. Micrographs were produced on a Cambridge Stereoscan 250 Mk2 scanning electron microscope at 20 keV.

X-ray synchrotron microtomography

Fresh adult specimens were taken from the culture, cleaned with a fine brush and placed in glutaraldehyde for 60 h. Specimens were dehydrated in a graded ethanol series of 70%, 75%, 80%, 85%, 90%, 95%, and 100% with 3 changes at each concentration, and 10 min between changes. Finally, samples were placed in fresh 100% ethanol overnight and critical point dried in CO_2. X-ray synchrotron microtomography was conducted at the European Synchrotron Radiation Facility (ESRF, Grenoble, France) at beamline ID19. The technique is explained in detail on the ESRF website (http://www.esrf.fr/). A mixture of phase contrast and absorption techniques was used at 20.5 keV. Scans were performed at a resolution of 0.7 µm. Image analyses of the voxel data were made with VGStudio Max 1.2.1 software (Volume Graphics, 2005).

Reproductive rate

To determine the individual reproductive rate of *A. longisetosus*, 48 adult females of unknown age with visible eggs in their oviducts were taken from our culture and separated individually in tissue culture plates with 24 wells. Each well had a diameter of 16 mm and a height of 17 mm. The bottoms of the wells were filled with a 6-mm deep plaster-of-Paris/charcoal mix (9:1). Bark of different trees with algae (mainly *Protococcus*) and some lichens growing on them was provided as food and replaced when necessary (every 3-4 days), air humidity was kept at about 90%. Eggs and later offspring were counted every day and the developmental stages were discriminated (except on days 11, 17, 24, 31, 37, and 46). If an adult died, all offspring were placed in 70% ethanol and counted. Offspring were removed from the wells when molting into the adult stage to avoid the presence of multiple reproductive females in each well. After 51 days the large number of specimens in the wells precluded our distinguishing instars, and so only the number of offspring from each female was recorded.

Results

The reproductive system of *Archegozetes longisetosus*

The ovary is unpaired and located posterior to the ovipositor (Figures 2 and 3). Two oviducts originate from the ovary; they pass through the body in a loop and join at an anterior position to enter the vagina (Figure 4). Eggs are produced in the ovary and consecutively grow as they progressively move toward the vagina. The young eggs at the beginning of the oviduct are closely packed and cuboid; during vitellogenesis and growth they gradually become egg-shaped.

The ovipositor is folded inside the body when not in use (Figure 2). When extruded, it reaches a length of about 600 µm, which is two-thirds of the length of the female (Figure 1). The outer surface of the ovipositor is highly corrugated.

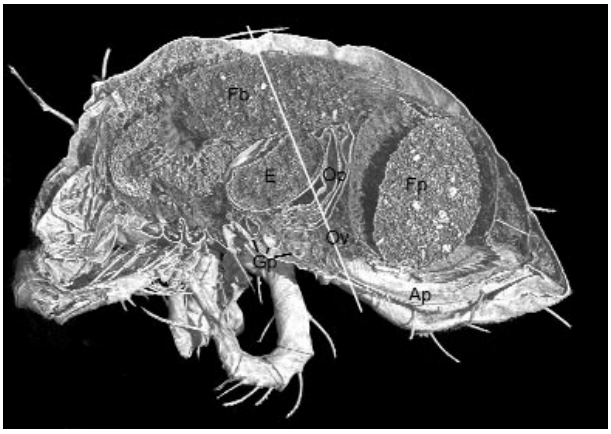

Figure 2. Longitudinal virtual cross section through an adult *A. longisetosus*, as obtained by X-ray synchrotron microtomography. The ovipositor (Op) is retracted inside the body and folded at the circular fold (cf). One egg (E) is visible, located in the vagina. The ovary (Ov) is located at a posteroventral position to the Op. The oviducts are not visible due to their more lateral position in the animal (see Figure 4). Ap: anal plate; Gp: genital papillae; Fp: fecal pellet; Fb: food bolus. The white line indicates the section shown in Figure 3.

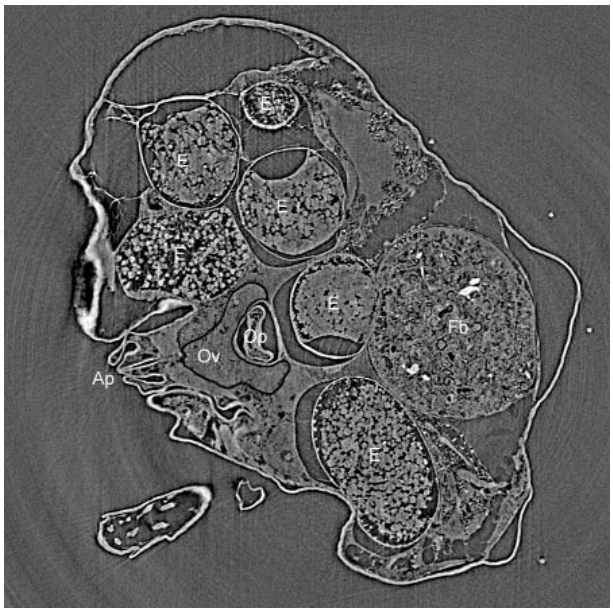

Figure 3. Axial cross-section as obtained by X-ray synchrotron microtomography (for orientation see Figure 2). Several eggs (E) and the horseshoe-shaped ovary (Ov) are visible. The ovary was manually outlined. Fb: food bolus; Ap: anal plate.

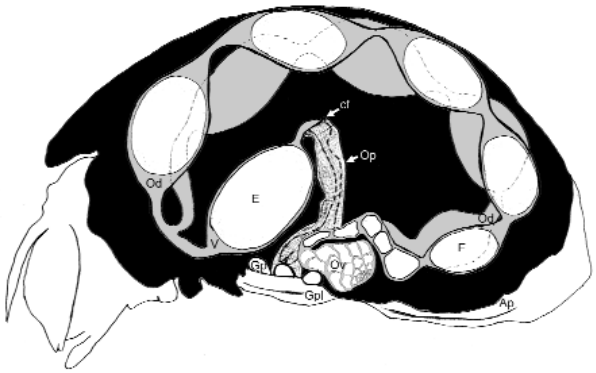

Figure 4. Schematic overview of the reproductive system of *A. longisetosus* drawn from observations made by X-ray synchrotron microtomography. The unpaired ovary (Ov) is located posteroventral to the ovipositor (Op). Two oviducts (Od) originate from the ovary and pass as 2 loops through the animal. They merge at an anterior position of the Op in the vagina (V). During oviposition, the genital plate (Gpl) opens and the ovipositor is extruded by increased hemolymph pressure. cf: circular fold of the ovipositor.

Reproduction and development

Eggs have a plain surface, an ellipsoid appearance, and an average length of 200 µm and width of 120 µm when being laid (Figure 5). We counted 10 eggs in a gravid female by synchrotron microtomography, but observed up to 30 eggs by dissecting and recorded clutches of this size in our experiment. After oviposition, eggs develop into a moderately regressive prelarva (Figure 6) inside the egg chorion; appendages are represented by partially segmented vestiges, but all setae are missing. The active larva (Figure 7) hatches through both the prelarval cuticle and egg chorion and then quickly begins feeding. While the stomodeum is still clearly visible in the prelarva, it becomes hidden within the gnathosoma during development into the larva. As is typical of mites, the larva lacks the fourth pair of walking legs and no genital vestibule is developed. The development of the larva into the consecutive instars (protonymph, deuteronymph, tritonymph, and adult) is accomplished during respective periods of quiescence, which last 2-3 days during the molting process. The nymphal stages differ in several aspects. The most visible is the setal configuration of the genital plate. The genital plate is absent in the larva. It

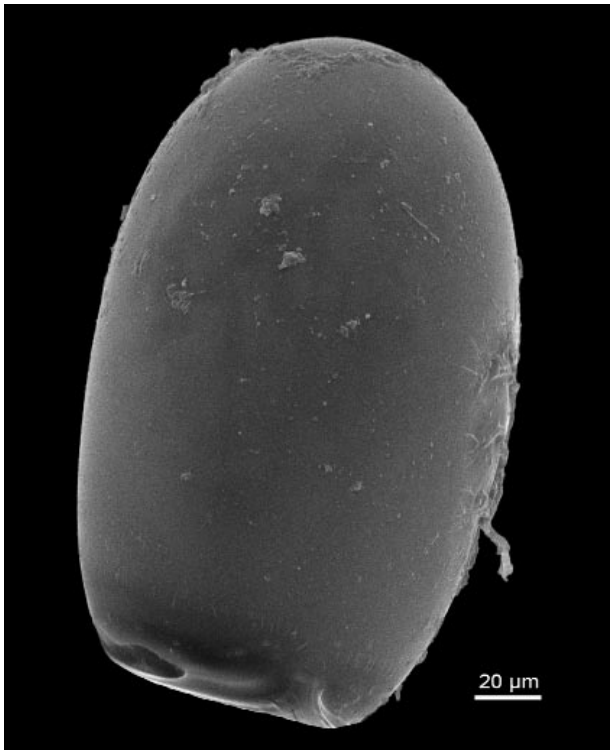

Figure 5. An egg of *A. longisetosus*.

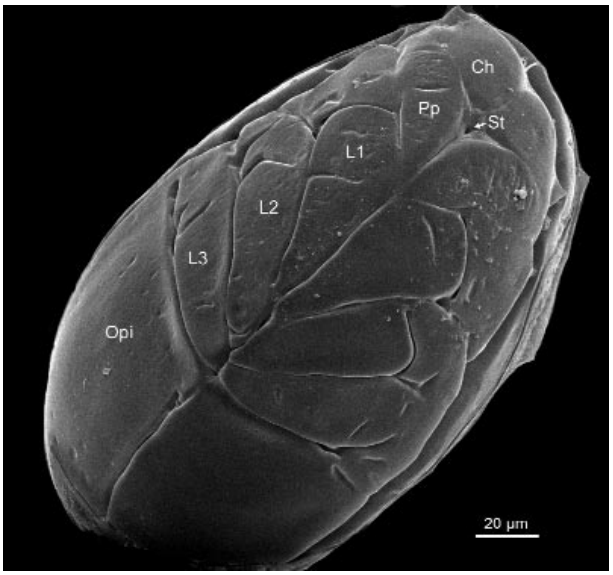

Figure 6. Regressive prelarva of *A. longisetosus*. The eggshell was removed. The prelarva hatches inside the eggshell into the larva. Vestiges of the appendages are visible, except for those of the fourth pair of walking legs. Visible is the stomodeum (St), the mouth opening, which becomes hidden in the gnathosoma in later development. Opi: opisthosoma; Pp: pedipalps; Ch: chelicera; L1-L3: walking legs.

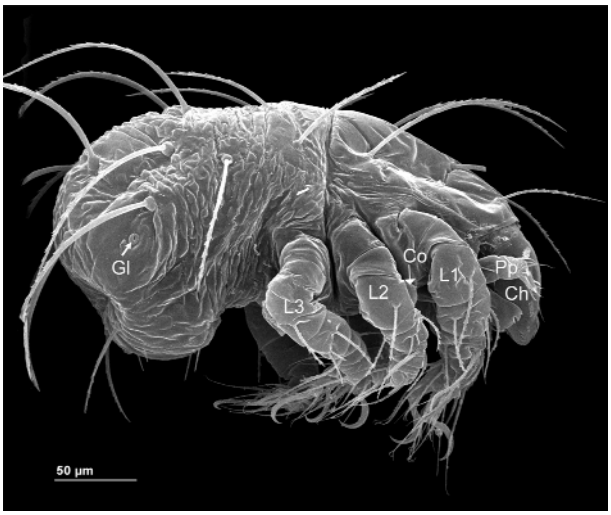

Figure 7. Lateral view of a larva of *A. longisetosus*. The fourth pair of walking legs is not yet developed. Gl: opisthosomal gland; Pp: pedipalps; Co: Claparède organs; Ch: chelicera; L1-L3: walking legs.

contains 1 pair of setae in the protonymph, 4 pairs in the deuteronymph, and 6 pairs in the tritonymph.

Seven of the 48 separated females died before laying eggs. Data concerning oviposition and hatching time was thus collected from 41 individuals, of which 22 survived the 51-day period in which all developmental stages of the offspring were determined separately; from these 22 mites data on the time course of reproduction and development were recorded (Figure 8). The first instance of oviposition was on day 8 after separation from the main culture and the last was on day 32. Clutch size ranged between 2 and 30 eggs, but most clutches had 12-15 or 19-20 eggs. Females laid either a number of smaller clutches within a few days, or a single large clutch. Generally, females used hidden spots for laying eggs, like crevices in the bark provided as food or cavities in the plaster-of-Paris. Laying of the whole clutch is a rather time-consuming process that can take several hours.

The estimation of hatching times yields a distribution that shows rather strong accumulations around 0-3, 6-11, and 12-17 days. Soon after hatching, the young

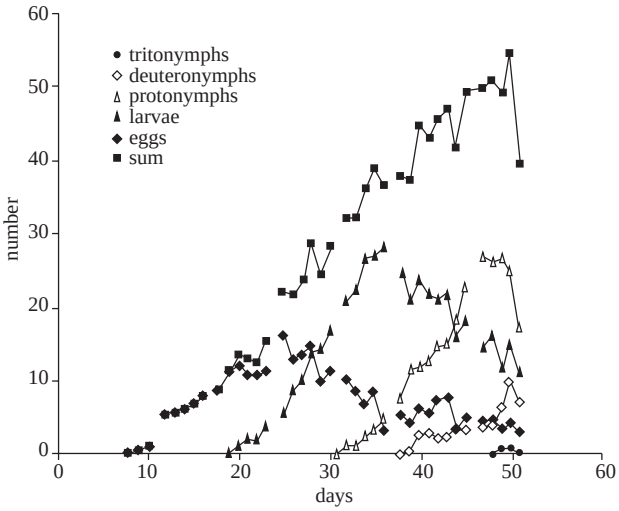

Figure 8. Developmental time-curve of 22 females and their offspring in a period of 51 days (averaged values). First eggs were laid at day 8, the first larvae occurred on day 19, and on day 31 the first protonymphs occurred. First molting into deuteronymphs occurred on day 38 and into tritonymphs on day 48. The iteroparous behavior can be seen by several local maxima of the egg-curve; however, the following developmental stages show a bell-like distribution suggesting some kind of synchronization. The sum shows a quasi-linear growth. Missing lines indicate missing data.

larvae are quite mobile and actively feed. As in all following instars their opisthosoma at first has a wrinkled appearance (Figure 7) and then rapidly increases in volume, developing a smooth, shiny surface.

All stages, except the adult, are very pale whitish with a more or less transparent integument that allows viewing of inner organs, notably the midgut, ventriculus, ceca, and opisthosomal glands. The immediate surroundings of the opisthosomal glands in all instars appear as a pair of dark brown spots situated dorsolaterally in the opisthosoma. This coloration develops some time after ecdysis, when the glands are visibly filled.

The adult ecloses with a light brown cuticle that turns amber within a few days. Since it is lightly sclerotized, the integument does not show the transition in texture of the larval and nymphal stages, but instead has a more or less granulated surface. In general, the data suggest that from the hatching of the egg, the following stages of larva, protonymph, deuteronymph, tritonymph, and adult follow each other at intervals of roughly 10-12 days. Five of the adult females survived long enough for their oldest offspring to molt to the adult stage. In these cases, the total time of development took 35 to 62 days, with an average of 48.5 days.

In this experiment the average number of progeny within the period of 51 days was 55 per female, the maximum number being 147. The average reproductive rate was 1.3 eggs/day.

Discussion and Conclusions

Morphology of the reproductive system

With its unpaired ovary, paired oviducts that pass loop-like through the body to join at the vagina, and the absence of a uterus, the gross morphology of the reproductive system of *A. longisetosus* resembles the ground pattern for oribatid mites (Michael, 1884; Alberti and Coons, 1999). The ovary is horseshoe-shaped and loosely embraces the ovipositor from a posterior direction (Figure 3). Michael (1884) stated that the ovary of oribatid mites underlies the ventriculus, which is situated anterior to the ovipositor; however, we found the ovary to be positioned more posteriorly. The ovipositor shares common features with that of other oribatids; eugenital lobes and their setae resemble those of other Desmonomata, the group that includes Trhypochthoniidae (Grandjean 1956). Although several cytological studies exist (Taberly, 1987; Witalinski, 1987; Heethoff et al., 2006), little is known about the ovary ultrastructure or the development of the reproductive system of oribatid mites.

Development

Eggs were laid at an early stage of development after the initiation of crenation. The shape of the eggs is very simple and there is no visible structure on the surface (Figure 5). This is common among oribatid mites, although different egg shapes occur in other taxa (Walter and Proctor, 1999). The eggs are white with a hard shell, which is different from those of some other oribatid mites in which eggs become dark brown and have a perforated surface (Michael, 1884).

Detailed information on the embryology of Acari is meager and mainly based on tick studies from the 1960s and 1970s (Evans, 1992). New information for astigmatic (Walzl et al., 2004) and oribatid (Lange and Tolstikov, 1999) mites has appeared, but most relevant is the study of *A. longisetosus* by Thomas and Telford (1999). Most embryological development, culminating in the prelarva, presumably occurs after oviposition.

The degree of regression of the prelarva is extensive; appendages are conspicuous but vestigial, and no setae exist. As such, it is similar to the prelarva of the confamilial species *Trhypochthoniellus setosus* (Lange and Tolstikov, 1999). Estrada-Venegas et al. (1999) reported that backward-directed opisthosomal setae exist, but this is an error, they were probably observing a pharate prelarva, with a developing larva inside. While regressive, the prelarva of *A. longisetosus* is only intermediate in the span of prelarval morphologies, which ranges from a well-formed, partly hatching, setose instar in *Palaeacarus* (Lange, 1960) to the egg-like apoderm that typifies the derived Brachypylina (Grandjean, 1962). Accordingly, Desmonomata are phylogenetically a middle derivative group of oribatid mites (Maraun et al., 2003 and cited references).

The shriveled appearance of the larva directly after hatching is normal for oribatid mites and changes after inflation and hardening, as previously shown by Thomas and Telford (1999).

Reproduction

Published information on food preferences of *A. longisetosus* is conflicting. While Haq and Adolph (1981) stated that *Protococcus* (green unicellular alga) was rejected by all instars, Honciuc (1996) and Senizcak (1998) showed that this alga is the preferred food, leading to the highest rate of reproduction and even to increased body size (Seniczak, 1998). Estrada-Venegas (1999) stated that food has no influence on development, but Smrz and Norton (2004) showed that different food resources may cause differential processing in the gut.

As mentioned above, the animals in our culture were fed with bark covered with green algae, of which *Protococcus* sp. contributed the major proportion. Other potential food sources provided with the same material were the bark itself, some fungi, and lichens. In contradiction to the results reported by Haq and Adolph (1981), mites were observed feeding almost entirely on the algae, abandoning pieces of bark cleared from their cover of algae, even if lichens remained. We never observed feeding on lichens or bark, nor could traces of feeding on these materials be found.

In published life-history studies (Haq, 1978; Haq and Adolph, 1981; Honciuc, 1996; Senizcak et al., 1997, 1998; 1999; Senizcak, 1998; Estrada-Venegas et al., 1999), the life-cycle ranged between 28 and 88 days. Eggs were laid in clutches containing 2-42 eggs, the larvae hatched 5-8 days after oviposition, and the number of offspring a single female produced during her life ranged between 31 and 238. The very rapid process of egg laying reported by Estrada-Venegas et al. (1999) in Mexican *A. longisetosus* could not be observed in our strain. This might have been due to a different genetic constitution of the Mexican strain or due to different laboratory conditions; however, the habit of placing the eggs in hidden places or into the substratum is in accordance with their observations. This leads to difficulties in finding all eggs for counting, while trying to cause the minimum disturbance in the culture well. Furthermore, this could render the hatching times of 0-3 days an artifact of counting errors and account for the discrepancy of egg versus larvae numbers in our counting. Therefore, our data on the time of hatching after oviposition have to be interpreted with some caution. If the observation of a 2-peaked distribution of hatching times (6-11 and 12-17 days) is not an error of an unknown source, a possible explanation could be that many eggs from large clutches were laid at a much less advanced state of development. This points to 2 possible strategies in egg laying behavior, both of which could be realized in *A. longisetosus,* given the observed distribution of hatching times: they could either lay a small number of highly developed, fast hatching eggs or a big clutch of less developed, slow hatching eggs.

The larvae are very active and clearly visible on the bark, which makes them less prone to counting errors than are eggs. The developmental time of all stages averaged 10-12 days, leading to a mean life cycle of 48.5 days. Published studies estimated a life-cycle-duration ranging between 32 (Senizcak et al., 1997) and 88 days (Estrada-Venegas et al., 1999). Our observations are in between and well in accordance with the data presented by Haq (1978) and Honciuc (1996). As mentioned above, the highest observed number of 147 does not represent the maximum offspring of one female during its entire lifetime, due to the fact that the females used in this study were already adults. Up to 321 offspring have been produced by a single female (Senizcak et al., 1999).

However, exact determination of the time course of development requires further studies under different laboratory conditions, starting with freshly molted females.

Comparing all results, it seems obvious that small differences in parameters like temperature, humidity, and diet can have a major influence on the reproductive biology of *A. longisetosus*. Genetic strains of this parthenogenetic species may also underlie variation, as well as mites used in published experiments coming from very different sources, i.e. India, Mexico, and Puerto Rico. To obtain comparable results, the standardization of rearing protocols seems desirable.

Conclusions

We presented the first observations on the gross morphology of the reproductive system of *A. longisetosus* and the first application of X-ray synchrotron microtomography for the observation of the internal anatomy of whole microarthropods. We predict that this technique will become an important tool for non-invasive investigations of internal structures of biological material.

A comparison of our life-history study of *A. longisetosus* with others suggests that even slight differences in laboratory conditions can have a substantial effect on the reproductive rate. A well-defined laboratory system for culturing of this parthenogenetic strain should be established to make the results from different laboratories more comparable. This is especially important as most lineages of *A. longisetosus* recently used in different studies derived from a single female, and allozyme studies (Palmer and Norton, 1992) suggest fidelity in genotype between mother and daughter.

It is common and helpful to have a specific name for a genetic lineage, which serves as a model organism and is held in different laboratories. This name may indicate a specific character that differentiates the strain from the wild-type or if there is no such character it may indicate the origin of the strain. No such name has been established for the lineage of *A. longisetosus* initiated in 1993 by R. A. Norton, and so we suggest naming it *Archegozetes longisetosus* ran, in reference to its originator.

Acknowledgments

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