Acarologia is proudly non-profit, with no page charges and free open access

Please help us maintain this system by encouraging your institutes to subscribe to the print version of the journal and by sending us your high quality research on the Acari.

Subscriptions: Year 2019 (Volume 59): 450 €
http://www1.montpellier.inra.fr/CBGP/acarologia/subscribe.php
Previous volumes (2010-2017): 250 € / year (4 issues)
Acarologia, CBGP, CS 30016, 34988 MONTFERRIER-sur-LEZ Cedex, France

The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under the reference ID 1500-024 through the « Investissements d’avenir » programme (Labex Agro: ANR-10-LABX-0001-01)

Acarologia is under free license and distributed under the terms of the Creative Commons-BY-NC-ND which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original author and source are credited.
ONTogeny AND MOrPhology
IN SCHWIEBEA ELONGATA BANKS, 1906 (ACARI: ACARIDAE)

by Kimiko OKABE *, Barry M. OCONNOR ** and Kazuyoshi KUROSA ***

SUMMARY: The postembryonic ontogeny of the thelytokous acarid mite, Schweibea elongata Banks, 1906, is described from specimens collected and reared from a swimming pool in Japan and preserved material from an eel hatchery in Canada. The male, heteromorphic deutonymph and homeomorphic immature stages are described for the first time. Variation is described in the form of the prodorsal sclerite, presence/absence of idiosomal setae c1 and d1, and in the form of the empodial claws of the female. Males and deutonymphs strongly resemble those of S. zingiberi Manson, 1972, but S. elongata males constantly retained dorsal seta d1. The deutonymphs of both S. elongata and S. zingiberi were identical morphologically.

INTRODUCTION

Study of the systematics and phylogeny of astigmatid mites is both enhanced and hampered by their dimorphic life-cycle. In the Astigmata, the deutonymphal instar (termed hypopus in older literature) has a completely different morphology than the feeding stages. In many cases, species with morphologically similar adults have strikingly different deutonymphs, and vice versa. While providing a second set of morphological characters for analysis, this dimorphism can only be fully utilized in phylogeny reconstruction if both sets of characters are known for many taxa. In the family Acaridae, fewer than half of the 82 currently recognized genera have at least one species known from both adult and deutonymphal stages. In addition to characters derived from morphology alone, patterns of ontogenetic change have proven useful as characters in phylogenetic analysis in the Acari (KLOMPEN & OCONNOR, 1989), however, an even smaller proportion of species in the family Acaridae have had their complete ontogenies described. These difficulties are particularly true in the large genus Schweibea. Of the approximately 80

* Forestry and Forest Research Institute, Kukizaki, Ibaraki 305-8687, Japan.
** Museum of Zoology and Department of Biology, The University of Michigan, Ann Arbor, Michigan 48109-1079, USA.
*** 5-21-15 Nishi-Ikebukuro, Tokyo 171-0021, Japan.
described species of *Schwiebea*, only seven are known from both the adult and heteromorphic deutonymphal stages (Woodring, 1966; Manson, 1972; Klimov, 1998; Wurst & Frank, 1998), and one (*S. nesbitti* Türk and Türk, 1957) has been described from all ontogenetic stages including the deutonymph (Wurst & Frank, 1998). Among species currently assigned to *Schwiebea*, adult morphology is relatively conservative, while at least two distinctive deutonymphal morphologies are known (Klimov, 1998).

Correlation of adults and deutonymphs in astigmatid mites is difficult because adults and homeomorphic immature stages are typically confined to discrete habitat patches, while the deutonymphs attach to insects or vertebrates for phoretic dispersal (Houck & O'Connor, 1991). While deutonymphs can occasionally be found in naturally occurring colonies, correlation of life-stages with absolute certainty is best accomplished through laboratory rearing. Rearing also frees populations from natural selective pressures and often allows a greater range of genetic variation to be expressed phenotypically.

In the present study, we describe the full ontogeny of *Schwiebea elongata* (Banks, 1906). We have previously demonstrated that this species reproduces by thelytokus parthenogenesis (Okabe & O Connor, in press), and in natural populations males were not observed. In our laboratory rearing, however, both deutonymphs and presumably spanandric males were obtained, allowing us to describe all developmental stages of this species.

**Materials and methods**

**Live individuals of S. elongata** were collected in an indoor swimming pool in Toride city, Ibaraki Prefecture, Japan. Another large series of ethanol preserved specimens representing females and homeomorphic immature stages was obtained from a tank in an eel hatchery in Charlottetown, Prince Edward Island Province, Canada. Mites from the Japanese population were originally reared in water with dry yeast, then transferred to mycelia of *Botrytis cinerea* (c285, preserved in Forest Pathology Laboratory, Kyushu Research Center, Forestry and Forest Products Research Institute, Japan) raised on PDA (potato dextrose agar) medium. We periodically transferred one randomly selected female from the mite colony to new media and maintained the re-established population over generations. Because relatively few males were produced in the colony, we selected females producing relatively more male offspring and established a new colony from these, then used males from this strain for analysis (Okabe and O'Connor, unpublished). We collected at least twenty individuals of each stage: female, male, tritonymph, deutonymph, protonymph and larva, randomly from the colony and transferred them to a mixture of Lactophenol and Nesbitt's fluid. After clearing them in the fluid, we mounted them in Hoyer's medium. Similar series of specimens were prepared from the preserved Canadian material.

Specimens were compared with the lectotype female and a paralectotype tritonymph from the type series of *S. elongata*, and with female, male and deutonymphal paratypes of the closely related, possibly sexual species, *S. zingiberi* all specimens in the U.S. National Museum of Natural History. We measured body length and width, dorsal setae, tarsi and legs of 20 individuals of each stage under a microscope with phase contrast optics. Voucher specimens from our study are deposited in the Japanese National Science Museum, Tokyo, the U.S. National Museum of Natural History, Washington, the University of Michigan Museum of Zoology, Ann Arbor, and the Canadian National Collection of Insects, Ottawa. In the following description, we follow Griffiths et. al (1990) for chaetotaxy of idiosomal setae and Grandjean (1939) for leg setae. All measurements are summarized in Table 1 and are given in micrometers.

**Description**

**Larva** (Figs. 1–8). Gnathosoma with relatively thin, chelate chelicerae; palpi with ventro-apical solenidion, two dorsal and one ventral filiform setae; subcapitulum with filiform ventral setae and spine-like palpal supracoxal setae.

Idiosoma (Fig. 1) with propodosomal dorsum with rectangular prodorsal sclerite, posterior edge indistinct to slightly indented; internal vertical (vi) and
TABLE I: Average size of each character in each stage of the mite.

Each size is represented with mean ± SD. The sample number of each was 20 except cl in tritonymph and protonymph and d1 in female.
a: Individuals which did not have cl were excluded from the data. The sample numbers for averages of the tritonymph and the protonymph were six and four, respectively.
b: Individuals which did not have d1 were excluded from the data. The sample number of it was 15 in female and 19 in male.
c: Individuals missing cl were excluded from the data. The sample number of it was 19 in male.

Legs (Figs. 3–8). Legs robust with relatively short segments. Setation: trochanters glabrous; femora I–II with filiform seta vF; genua I–II with short, spine-like setae mG and cG, genu III with filiform seta nG; tibiae I–II with anterior ventral setae hT thin spines, posterior ventral setae gT thicker spines, tibia III with seta kT a thin spine; tarsi I–II with proximal dorsal seta ba a thick spine adjacent to solenidion ø1, apical dorsal setae d and f and posterior lateral seta ra elongate, very finely foliate apically, apical seta e and ventral apical setae p, q, u, v, and s relatively thick spines; tarsus III generally similar but ba and la absent, setae r setiform, and w spine-like. Solenidia: genu I with 2 solenidia sigma, approximately equal in length, genua II–III with one solenidium sigma each; tibiae I–III each with elongate solenidium phi; tarsi I–II with one solenidium omega;
famulus seta on tarsus I small and bulbous. Pretarsi with robust empodial claw, without distinct membranous ambulacrum; condylophores well developed in tarsal apices.

Protonymph (Figs. 9–8). Generally similar to larva with the following changes. Prodorsal shield with distinct posterior indentation. Hysterosomal setae c1 variably present in both populations; posterior hysterosomal setae h3 added in paraproctal region displacing h2 to more dorsal position, paraproctal setae ps3 added lateral to anus in anterior quarter. Ventral idiosoma (Fig. 10) with coxal apodemes as in larva, anterior apodeme IV added, directed antero-medially. Genital primordia added with one pair of bulbous genital papillae, and genital setae (g) on genital valves.

Legs (Figs. 11–18). legs I–III as in larva but solenidion omega-2 added posterior proximo-dorsally on tarsus I. Leg IV added with slightly flattened filiform dorsoapical seta d, proximal ventral spine-like setae r and w, and ventroapical spine-like setae p, q, u and v.

Deutonymph (Figs. 19–28). Morphology strongly divergent from protonymph. Gnathosoma reduced, chelicerae absent, subcapitulum elongate bearing distinct palpal remnants at apex, palpal remnants bearing elongate apical solenidia and dorsal palpal setae; subcapitular remnant bearing spine-like palpal supracoxal setae mid dorsally.

Dorsal idiosoma (Fig. 19) well sclerotized, divided into propodosomal and hysterosomal sclerites by sejugal furrow. Both sclerites with distinct pattern of small punctations over entire sclerite. Propodosomal
sclerite very short and broad, with small, spinelike setae vi at apex, short, filiform to spinelike internal and external scapular setae (si, se) in transverse row; supracoxal seta of leg I elongate, originating on underside of overhanging sclerite above base of leg I. Hysterosomal sclerite with setae c1, c2, cp, d1, d2, e1, e2, f2, h1, h2, h3 all filiform to spinelike, h2 and h3 ventroterminal in position (f2 added in this stage). Opisthonthal gland openings anterior lateral between setae c3 and d2. Ventral idiosoma (Fig. 20) with anterior coxal apodemes I fused to form long, thin sternum not reaching apices of anterior apodemes III; anterior apodemes II thin, extending approximately as far posterior medially as apodemes I; posterior apodemes II very weakly developed, extending medially along apodemes III forming edges of trans-ventral groove; posterior apodemes III extending medially, with thin extenuation posteriorly fused to anterior apodemes IV on either side; anterior apodemes IV directly obliquely; posterior median apodeme extending from apices of anterior apodeme IV to area just anterior to genital primordia. Coxal setae 3a and 4a added; setae 1a, 3b and 4a conoidal, 3a filiform. Second pair of genital papillae added, papillae more elongate and thinner than in proto-nymph; genital setae filiform. Posterior attachment
organ well developed with conoidal setae ps1 and ps2 added, arranged posterior to and lateral to median suckers (derived from ad 1 + 2), ps3 reduced to alveolar vestige; median suckers with alveolar vestiges not contiguous; anterior suckers (derived from ad3) slightly wider in diameter than conoidal setae; anterior and posterior lateral and posterior median cuticular suckers well developed, all about as wide as conoidal setae.

Legs (Figs. 21–28). Legs relatively long, with typical deutonymphal modifications. Setation: trochanters I–III with filiform setae vR I–II and sR III added; femora I–II with setae vF filiform, femur IV with short, filiform seta wF added; genua I–II with setae mG and cG spinelike, genu III with nG filiform to slightly spinelike; tibiae I–II with gT and hT strong spines, gT distinctly thicker, tibiae III with kT a thin spine as long as the segment, tibia IV with kT added, a shorter thin spine; tarsus I with ba and s absent, wa a thin spine, ra, la, p, q and f thinly foliate, seta d filiform, seta e elongate, spoon-like apically, tarsus II similar to tarsus I but thinly spinelike ba present and e thinly foliate, tarsus III with d filiform, positioned proximo-dorsally, e, f, p, q foliate, positioned apically, s foliate, positioned subapico-ventrally, w and r foliate, proximo-ventral; tarsus IV with s, e and f
added, form and position of setae similar to tarsus III but with a long tapering spine and a shorter filiform to narrowly spikelike seta. Solenidia and famulus: Genua I–II with one apical sigma solenidion each, sigma III absent; tibiae I–IV with well-developed phi solenidia; tarsus I with solenidion omega 3 added on proximal anterior side slightly apical to $\omega_1$, $\omega_1$ with bulbous tip, $\omega_2$ short, proximal to $\omega_1$ on posterior side, tarsus II with omega similar in shape and position to $\omega_1$ of tarsus I; famulus eta of tarsus I short, spine-like, positioned between solenidia $\omega_1$ and $\omega_3$. All pretarsi similar, consisting of hooked empodial
claw arising from tarsal apex, condylophores poorly visible in tarsal apex, membranous ambulacrum lacking.

TRITONYMPH (Figs. 29–38). Morphology generally similar to protonymph with the following modifications. Ventral idiosomal (Fig. 30) setae 3a and 4a, added in deutonymph, appear respectively anterior to and lateral to genital primordia; genital papillae, with second pair added in deutonymph, bulbous as in protonymph. Hysterosomal setae c1 present in some individuals, c2, c3, f2, ps1, ps2 regressed as in protonymph. Legs (Figs. 31–38) similar to protonymph with deutonymphal additions of solenidion omega 3 on tarsus I apical in position, e, f, and s of tarsus IV similar in form and position to homologues on tarsus III, tibia IV with KT and solenidion phi and femur IV with wF added in deutonymph.

FEMALE (Figs. 39–49). Morphology generally similar to tritonymph with the following changes. Hysterosomal dorsum (Fig. 39) with seta c1 always absent, seta d1 variably present or absent. Ovipore functional, with folded internal pseudo-ovipositor, setae g on genital valves, 3a adjacent to valves near anterior end. Copulatory opening terminal, at end of short papilla; spermathecal duct relatively short, leading to rounded spermatheca with characteristic pattern of cells, number of cells varied from 4–20 with one individual with cells completely indistinct. Legs (Figs. 41–49) similar to tritonymph but some individuals with one or more empodial claws distally bifurcate.

MALE (Figs. 50–59). All observed males of "heteromorph" type, having enlarged legs III. Morphology generally similar to tritonymph with the following changes. Prodorsal sclerite with posterior
indentation not as deep as in female or immature stages. Hysterosomal seta c1 always absent, seta d1 present in 19 of 20 individuals. Posterior hysterosoma with ovoid sclerite extending anteriorly to level of setae e2, extending posterovertrally around para­anal suckers. Posterior ventral hysterosoma with setae ps1, ps2 added, on ventral projection of poste­rior sclerite, ps3 on anterior edge of para-anal sucker. Ventral idiosoma (Fig. 51) with coxal apodemes thic­ker than in tritonymph, particularly anterior apo­deme III. Genital opening between coxal fields IV; aedeagus small, with triangular supporting apode­mes; setae g on anterior edge of genital valves, setae 3a between medial termini of apodemes IV, setae 4a flanking genital opening.

Legs (Figs. 52–59) I–II similar to tritonymph in form and setation. Leg III enlarged, tarsus short, with very thick empodial claw; setation as in trito­
nymph but both r and w of tarsus setiform. Leg IV similar to tritonymph but setae d and e of tarsus modified into suckers positioned in apical half of segment.

RESULTS

Examination of series of specimens representing all life stages in *S. elongata* allowed us to document intraspecific variation in this species as well as describe ontogenetic changes. Ontogenetic changes in *S. elongata* represent a combination of ancestral changes observed in many groups of sarcoptiform mites and more derived changes seen only in closely related taxa. Examples of transformations presumed ancestral in the Astigmata include the pattern of addition of leg setae and solenidia, protonymphal addition of idiosomal seta h3 and ps3, addition pattern of genital papillae, coxal and genital setae. Regression of setae si, c2, c3 and f2 in non-deutonymphal instars is shared among genera related to *Schwiebea* such as *Histiogaster* Berlese, 1883, *Naiadacarus* Fashing, 1974, and *Thyreophagus* Rondani, 1874.

Certain morphological characters were observed to vary among individuals as well as among ontoge-
FIGS. 31–38: Schwiebea elongata triotonymph. 31.-Leg I, dorsal. 32.-Tarsus I, ventral. 33.-Leg II, dorsal. 34.-Tarsus II, ventral. 35.-Leg III, dorsal. 36.-Tarsus III, ventral. 37.-Leg IV, dorsal. 38.-Tarsus IV, ventral.
netic stages in *S. elongata*. The shape of the prodorsal sclerite varied as to whether a posterior indentation was visible or not and the depth to which the sclerite was indented when visible. The posterior edge of the sclerite was often impossible to discern in poorly sclerotized individuals as well as those which had been cleared longer.

Within the Japanese population, 34% of 70 females examined showed the bifurcated empodial claws as shown in Figure 49. Some had one or more bifurcate claws only on one side but others expressed the condition on both sides. Although we examined female specimens fixed before and after laying eggs (40 and 30, respectively), there was no significant difference in occurrence of bifurcate claws between them ($\chi^2$ test, $p>0.05$), indicating that this condition does not result during the sclerotization process following the molt. We did not observe bifurcate claws in males or any immature stages, nor did we observe them in any females from the Canadian population.

Vestiges of the alveoli of dorsal setae si, c2 and c3 (and c1 when setae were absent) were visible in almost all the specimens of males, tritonymphs, protonymphs and larvae. Most of the tritonymphs and protonymphs bore a tiny black dot in the alveolus of c1. When the setae were not measurable under magnification of 1,000 times, we regarded the seta as absent. Setae c1 showed a variable presence in all ontogenetic stages except the adult female where it was invariably absent. All larvae examined from the reared Japanese population lacked the seta, however it was present in some larvae from the Canadian population (table 2). Seta d1 also showed variation although mostly in the adult female. The seta was present in all juveniles and all but one adult male. However, only 5 of 80 examined females in the Japanese population expressed these setae.
Figs. 41–49: *Schwiebea elongata* female. 41.-Leg I, dorsal. 42.-Tarsus I, ventral. 43.-Leg II, dorsal. 44.-Tarsus II, ventral. 45.-Leg III, dorsal. 46.-Tarsus III, ventral. 47.-Leg IV, dorsal. 48.-Tarsus IV, ventral. 49.-bifurcated empodial claw from 2 different individuals (a and b).
Table 2: The percentage of dorsal seta cl present in juveniles of the Japanese and Canadian mites (z-test, *, p<0.05, **: p<0.01).

<table>
<thead>
<tr>
<th></th>
<th>Japanese</th>
<th>Canadian</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of Tritonymphs</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>cl present</td>
<td>30%</td>
<td>35%</td>
</tr>
<tr>
<td>No. of Protonymphs</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>cl present</td>
<td>20%</td>
<td>40%</td>
</tr>
<tr>
<td>No. of Larvae</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>cl present</td>
<td>0</td>
<td>25%**</td>
</tr>
</tbody>
</table>

**DISCUSSION**

*Schwiebea elongata* was described by BANKS (1906) (as *Rhizoglyphus elongatus*) from female mites collected from clover roots thought to have originated in Missouri, USA. Following redescription of this species and transfer to the genus *Schwiebea* (MANSON, 1972), FAIN and FAUVEL (1988) included it in the “barbei” group of species. Most of the species in this group have been described from small series of adult females, and we suspect that many may be parthenogenetic like *S. elongata*. Our observations on ontogenetic transformations and intra-population variability call into question many of the characters previously used to separate species in this group. Notably, the indented prodorsal sclerite, presence/absence of setae cl and d1 (d1 and d2 of previous authors), number of cells in the female spermatheca, and general size characteristics, were all found to vary within a population reared from a single female foundress. In the key to females of *Schwiebea* given by FAIN (1982), *S. elongata* is characterized by a non-indented prodorsal sclerite and absence of setae d1 (d2 of FAIN). In the lectotype female of *S. elongata*, it is impossible to see the posterior border of the prodorsal sclerite due to weak sclerotization or over clearing. MANSON (1972) illustrated this specimen with a complete posterior border, but there is a fold in the cuticle between the scapular setae that appears as the posterior edge of the sclerite in Manson’s figure. In a paralectotype tritonymph we examined, the prodorsal sclerite is clearly indented as we observed in the new material described above. WURST and FRANK (1988) described the homeomorphic immature stages of *S. talpa* Oudemans, 1924 as having an indented prodorsal sclerite, while the sclerite is not indented in adults. In *S. nesbitti*, the same authors describe the homeomorphic juvenile stages with non-indented sclerites while the strongly sclerotized adults lack a distinct prodorsal sclerite.

The lectotype female of *S. elongata* does lack setae d1, as does the majority of females examined in our material, however, the seta is present in some individuals of all ontogenetic stages in our material. It should be noted that the seta indicated as d1 in the redescriptions of *S. talpa* and *S. nesbitti* by WURST and FRANK (1998) is actually e1; both of those species apparently lack d1 throughout ontogeny. Similarly, the seta indicated as e1 by those authors is h1, and h1 is h2.

The amount of variation in size, shape and presence/absence of setae in *S. elongata* appears unusual. We suspect that two factors may be involved. First, the species is parthenogenetic, so spontaneous mutations which may occur will not be masked by recombination. A possible example of this is the bifurcate empodial claws observed in many females of the Japanese population, but not seen in any individuals of the Canadian population. This mutation has not been previously documented in astigmatid mites.

Release from selective pressures in the laboratory colony may account for some of the other variation we observed, notably in the expression of idiosomal setae. Laboratory reared mites were provided unlimited food and a predator-free environment, and new colonies were begun using randomly selected female foundresses. It is interesting to note that although the number of generations passed were the same in both females and males after the selection, males did not show variation in phenotypic traits like the female. Although the species reproduced normally in the complete absence of males, the male genitalia are normally developed, although we are unsure if they were functional. The male genital morphology of *S. elongata* is similar to that of *S. zingiberi*, the female of which is morphologically very similar to *S. elongata* differing only in spermathecal form. There are no observations on the mating system in *S. zingiberi*, although MANSON (1972) described both males and females.

A full taxonomic treatment of the species in the “barbei” group will be presented elsewhere, but we
note here the utility of laboratory reared populations in helping elucidate the degree of potential phenotypic variation in these mites.

ACKNOWLEDGEMENTS

We thank Mr Robert SMILEY, USDA Systematic Entomology Laboratory, Beltsville, for the loan of the type specimens of Schwiebea elongata and S. zingiberi. We thank Dr Kazumi TAGAMI, Tsukuba University, Japan, for the original colony of the Japanese population of S. elongata, and Dr J. DAVIDSON, Fisheries Canada, Charlottetown, P.E.I., for the Canadian material, and the Forest Pathology laboratory, Kyushu Research Center, Forestry and Forest Products Research Institute, Kumamoto, for the stock culture of Botrytis cinerea. This research was sponsored in part by grants from the Japanese Science and Technology Agency to K. OKABE, and the U.S. National Science Foundation to B. M. OCONNOR (DEB-9521744).
REFERENCES


