Multivariate Analysis of Morphological Variation in Two Cryptic Species of *Sancassania* (Acari: Acaridae) from Costa Rica

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ABSTRACT Populations of *Sancassania* mites were collected in Costa Rica from scarabaeid and passalid beetles and cultured. The populations proved to be reproductively incompatible due to postzygotic isolation and show 1.4% difference in domains 2 and 3 of the 28S nuclear rDNA gene, indicating the populations represent distinct species. Because the mites were virtually indistinguishable morphologically, 61 morphological characters of 50 females and 101 characters of 60 deutonymphs of the two species were analyzed. Traditional univariate morphometrics could not separate them. Multivariate analyses of variance (principal component and discriminant function) were used to interpret morphological differences between the two species in relation to factors that influence their morphology in a laboratory and field setting. Principal component analyses were done on size and shape as well as shape variables alone. The discriminant function analysis was done on a reduced subset of shape variables. In both cases, the shape analyses resulted in complete separation of the two species and the characters contributing strongly to the discrimination were used in formal description of the two species, *Sancassania salasi* sp. nov. and *S. ochoai* sp. nov. Although deutonymphs of *S. salasi* taken from field-collected beetles show a significantly smaller magnitude of size variation, they show significant deviation in shape compared with cultured deutonymphs of the same species, a potential problem for correlation of specimens of other *Sancassania* species from culture and nature. Characters that provide the strongest contribution to these intraspecific shape changes are, therefore, taxonomically unreliable.

KEY WORDS multivariate analysis, discrimination, cryptic species, Acari, *Sancassania*

THE INFLUENCE OF HABITAT on morphology is particularly important for mites that are associated with different insect host species and/or use a variety of feeding substrates. The cosmopolitan genus *Sancassania* (=*Caloglyphus*) is among the most biologically diverse groups of mites. Its host associations include Coleoptera (mainly Scarabaeoidea), Hymenoptera, Orthoptera, Myriapoda, and terrestrial Crustacea. Species associated with synanthropic habitats are of agricultural, medical, and veterinary importance (Hughes 1976, Mullen and OConnor 2002). Despite differences in biology, the genus is morphologically conservative but notorious for its intraspecific variability. As a result of the lack of quantitative evaluation of characters and small sample sizes, prior *Sancassania* taxonomists have used characters to discriminate nominal species that are likely to be influenced by environmental factors. Seventy-five species and one subspecies have been described, but ≈79% of them are known from the original descriptions only.

We cultured two populations of *Sancassania*, associated with different coleopteran hosts in Costa Rica to determine their specific status and to quantify the degree to which morphological characters could discriminate between the two in relation to factors that influence their morphology in culture and nature. We used crossing experiments and 28S nuclear rDNA sequence data to determine that the populations were reproductively isolated and genetically distinct. Because traditional morphological comparison and univariate analyses could not correctly differentiate the two species on the basis of characters traditionally used to separate species of *Sancassania*, we used multivariate morphometrics to describe their variation and determine which components were most influenced by environmental factors.

In the taxonomic descriptions below, idiosomal chaetotaxy follows Griffiths et al. (1990). The leg chaeto- and solenidiotaxy follow Grandjean (1939). Distances of male tarsus IV follow Zachvatkin (1941). All measurements are in micrometers. Statistical data are presented as range, mean ± SE.

Materials and Methods

Material. Mite deutonymphs were collected from *Xyloryctes lobicollis* Bates (Coleoptera: Scarabaeidae) and *Passalus spiniger* Bates (Coleoptera: Passalidae) at two localities in Costa Rica in 1997. Host beetles will be deposited in the University of Michigan Museum of Zoology, bearing voucher labels reading: "Mites re-

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moved, B.M. OConnor #97-0430-029a" for *X. lobicollis* and "Mites removed, B.M. OConnor #97-0430-056" for *P. spiniger.* Cultures of both populations were started with a few deutonymphs on the fungus *Botryotinia fuckeliana* (de Bary) Whetzel (=*Botrytis cinerea* Pers.) (Helotiales: Sclerotiniaceae), following the method described by Okabe and OConnor (2001). Cultures were maintained in incubators at a temperature of ≈20°C and renewed every 1 to 2 mo with a few individuals. Specimens for study were cleared in Nesbitt's fluid and mounted in Hoyer's medium (OConnor and Houck 1991). Ten additional deutonymphs were taken from the pinned *X. lobicollis* preserved previously as a voucher and two other museum specimens of *X. lobicollis* (labeled "Mites removed, B.M. OConnor #97-0430-29b & c") from the same collection. No additional mites were found on the voucher of *P. spiniger.*

Type material of the new species is deposited in the following institutions: University of Michigan Museum of Zoology, Ann Arbor, MI (UMMZ); U.S. National Museum of Natural History, Washington, DC (mite collection housed in Beltsville, MD) (USNM); Instituto Nacional de Biodiversidad, San Jose, Costa Rica (mite collection housed at Estacion Biologica La Selva) (INBio); Zoological Institute, Russian Academy of Science, St. Petersburg, Russia (ZISP); Institut royal des Sciences Naturelles, Brussels, Belgium (IRSNB); and the Hungarian Natural History Museum, Budapest, Hungary (HNHM).

Reproductive Isolation. All crosses were conducted in plastic petri dishes maintained under the same conditions as the parent cultures. Virgin females from each population were obtained by isolating homeomorphic nymphs (tritonymphs or protonymphs) from the parent cultures and rearing them to maturity in individual petri dishes. Each virgin female was crossed with two males using a reciprocal crossing scheme. A preference was made for homeomorphic males, because heteromorphic males can kill one another and homeomorphic males using their enlarged third pair of legs as a weapon (Woodring 1969). The groups were checked after different periods of time and new males were added if necessary.

Molecular Analyses. All DNA extractions were obtained from freshly killed mites (adults and deutonymphs) or mites preserved in 100% ethanol. Extraction of whole genomic DNA from a single individual mite was accomplished with a QIAGEN DNeasy tissue kit. We extracted DNA and compared sequences from five specimens of each species. Amplification of a target gene region from extracted DNA was achieved through the polymerase chain reaction (PCR). Domains 2 and 3 of 28S nuclear rDNA were amplified using primers D23 F 5′-GAGAGTTCAAGAGTACGTG-3′ and D6R 5′-CCAGCTATCCTGAGGGAAACTTCG-3′ from Park and Foighil (2000). PCRs were performed in 50-μl volumes containing 3 μl of template DNA, 2.5 μl of each primer, 3.5 μl of dNTPs, 3.5 μl of $MgSO_4$, 5 μl of reaction buffer, and 0.2 μl of Platinum *Taq* polymerase under the under the following conditions: an initial denaturing (at 94°C for 2 min); 40 cycles of denaturation (at 94°C for 30 s), annealing (at 52°C for 20 s), and extension (at 72°C for 1 min and 15 s); an additional extension (at 72°C for 7 min); held at 4°C until the samples were retrieved from the thermal cycler. The amplified DNA was electrophoresed in 1.5% agarose gel and the bands were visualized with ethidium bromide and UV light. Bands corresponding to the desired target region were excised from the agarose and purified using the QIAquick gel extraction kit (QIAGEN, Valencia, CA). Sequence reactions were run with the same primer set as used for the initial amplifications and were sequenced using an ABI PRISM 377 automated cycle-sequencer. The resulting sequences were aligned with the computer program Clustal followed by additional manual adjustments.

Morphometric Analyses. Continuous characters of different morphological structures were measured with an ocular micrometer using an Axioskop (Carl Zeiss, Jena, Germany). Seventy-six measurements of females (Table 7) and 133 measurements of deutonymphs (Table 9) were made for 25 cultured individuals of each species. Additionally, 10 deutonymphs we measured from the pinned *X. lobicollis.*

Missing data are a common problem in mite morphometrics, because the standard technique of mounting mites allows measurements only in the horizontal plane of a slide. Although specimens that allowed maximal numbers of measurements were selected for the analyses, there are some missing data. Variables with >12% missing values for each species were dropped from the model. In the remaining variables (61 for females and 101 for deutonymphs), missing values were replaced by values predicted by a linear regression (X is length of idiosoma).

Values in the resulting matrices were converted 1) to logarithms equalize the variances and 2) logged Darroch and Mosimann shape variables (Darroch and Mosimann 1985) to suppress the size factor and create scale-free, or dimensionless, variables.

There are two procedures of size-adjustment that have usually been used in mite and insect morphometrics: discarding the first principal component and a Burnaby projection onto a plane orthogonal to the first axis (Houck and OConnor 1998, Okabe and OConnor 2000, Sorensen and Foottit 1992). Jungers et al. (1995) evaluated these two and nine other methods of size adjustment on hypothetical individuals known to be different in size but identical in shape to the real individual from their samples. Only variables in the Mosimann family of shape ratios allowed identification of different sized individuals of the same shape after accounting for overall size differences. Darroch and Mosimann shape variables may or may not be correlated with size (Jungers et al. 1995). Principal components of logged raw data can be contrasted with the principal components of logged shape variables to determine the extent to which overall differences among individuals can be attributed to a combination of size and shape versus shape only (Darroch and Mosimann 1985; Simmons et al. 1991). In the present

Table 1. Reproductive isolation trials. *Sancassania salasi* × *S. ochoai* respectively

##	16 April 2001	18 April 2001	20 April 2001	22 April 2001	25 April 2001	30 April 2001	7 May 2001	15 May 2001
2	TN,2m	f, m	f, 1 + 3m	f, 3m	f, 2m*	f, 2m	f, m	-
4	TN,2m	f, m	f, 2 + 2m	f, 4m	f, 4m	f, 4m	f	m
7	PN,2m	(PN), m	f, 1 + 3m	f, 4m	f, 3m	f, 3m	f, m	f, m
11	2m,TN	1 + 3m, f	4m, f	3m, f	3m, f	3m, f	m, f	m
12	2m,TN	1 + 2m, f	3m, f	2 + m, f	3m, f	m, f**	m, f	m
13	2m,TN	m, TN	m, (TN)	+ m, f	m, f	m, f	f	f
14	2m, PN	m, PN	m, PN	m, (TN)	m	m	m	-
15	2m,TN	2m, TN	m, (TN)	m, f	1 + 1m, f	2m, f	2m, f	f
16	2m,TN	m	m, f	+ m, f	m, f**	m, f	f	f
17	2m,TN	m, TN	m, TN	m, f	m, f	+ m, f	m, f*	-
18	2m,TN	m, 1f	2 + 2m, f	3m, f	3m, f	3m, f	2m, f	f
19	2m,TN	2m	1 + 3m, f	1 + 2m, f	2m, f	2m, f	2m, f	m

No viable progeny was detected. *, observed in copula; **, unsuccessful copulation; +, addition of male(s) from the parent culture; f, female; m, male; PN, protonymph; (PN), molting to tritonymph; TN, tritonymph; and (TN), tritonymph molting to adult.

analyses, we follow Darroch and Mosimann (1985) and explicitly define size as the geometric mean of all variables. The size component should be influenced mostly by nongenetic variance because the cultures of each species were started with a few deutonymphs collected from a single host specimen; thus, variation due to genetic factors should be minimal.

Discriminant function analyses (DFAs) were performed on shape variables to discriminate groups by shape rather than size. Variables with significantly lower F values ($\alpha < 0.05$) were dropped from the models. Because the resulting matrices exceeded DFA requirements, 13 and one variables with lowest F values were also dropped from the two and one species analyses of deutonymphs (see below), respectively. Raw data, discriminant function coefficients, the constant terms, and standardized discriminant function coefficients are available upon request.

Males were not included in the analyses, because they, like other *Sancassania* males, display extremely high levels of phenotypic variation (andropolymorphism) (Timms et al. 1981, Woodring 1969), which requires a separate morphometric study.

All morphometric analyses were done with the program SPSS version 10.0.7a for Macintosh (SPSS Science, Chicago IL).

Results and Discussion

Reproductive Isolation. The crosses were conducted as presented in Table 1. The results indicate that the two populations are reproductively isolated, and should thus be considered separate species (hereafter referred to as *S. salasi* sp. nov. and *S. ochoai* sp. nov.). In one mating pair, *S. salasi* male × *S. ochoai* female, copulation was unsuccessful, and the sperm was found on female's hysterosoma rather than in the seminal receptacle. This may indicate either incipient behavioral or mechanical prezygotic isolation, but this is highly speculative at this point. We observed two successful copulations of males of both species with females of the other species. Despite these copulations, we did not detect progeny during a 29-d observation period (the life cycle of mites of the genus *Sancassania* can be completed in ≈10 d), although we found a few eggs laid by one female of *S. salasi* in group 4 (Table 1). Another female of *S. salasi* (7) was moved to an individual rearing cell, but no eggs were found during 21 h of observation. This mite was subsequently dissected, and eggs obtained from its oviducts were examined. All eggs were in the developmental stage containing many yolk spherules and nuclei (Hughes 1959). Thus, all evidence indicates that hybrid zygotes *S. salasi* female × *S. ochoai* male die in the early developmental stages before birth, indicating postzygotic isolation between the two species.

Molecular Analysis. The length of the sequences obtained from each collection was 793 bp (Appendix 1). Although use of 28S rDNA has not been recommended for resolving problems of closely related species (Cruickshank 2002), our analyses showed 1.4% difference between the two sequences. This is about equal to the percentage difference we have observed between two other closely related acarid species, *Acarus siro* L. and *Acarus immobilis* Griffiths (M.L. and A.J.D., unpublished data). The sequences are accessioned in GenBank, accession numbers AY191833 (*S. ochoai*), AY191834 (*S. salasi*).

Morphometric Analyses. *Females.* Principal components derived from log size and shape and log shape variables are summarized in Table 2 and Fig. 1. Principal component analysis of log size and shape variables resulted in nine principal components, with the first three accounting for 62.3% of the total variance. All loadings are positive on the first axis, and scores of 40 variables (66.7%) are high or moderate, indicating influence of size-related variation. The second component contrasts some dorsal posterior setae + leg III-IV measurements versus some leg I-II measurements (Table 2). Among all components, only this component separates the two species, indicating the presence of shape-related variance, but there is a small amount of overlap (Fig. 1A). The third component has high or moderate loading on four body measurements.

Principal component analysis (PCA) based on scale-free information alone resulted in 17 components, with the first three accounting for 43.2% of the total variance. The first principal component explains only 23.1% of the variance and, like PC-2 of logged raw data, serves to separate the two species, although here

Table 2. First three principal components of log size and shape and log shape of *S. ochoai* and *S. salasi* females

Variable	Log size and shape			Log shape		
	PC-1	PC-2	PC-3	PC-1	PC-2	PC-3
Idiosoma, length	0.425	0.231	0.760	−0.326	0.774	0.238
Idiosoma, wt	0.286	0.332	0.768	−0.406	0.666	0.224
Propodosoma	0.438	0.166	0.415	−0.245	0.609	0.110
Hysterosoma	0.355	0.217	0.786	−0.296	0.733	0.247
vl	0.696	−0.338	−0.013	0.476	0.138	−0.115
se	0.728	0.212	0.107	−0.284	0.112	−0.344
c_1	0.464	−0.304	−0.158	0.352	−0.007	0.252
c_p	0.767	0.332	−0.040	−0.354	−0.362	−0.192
d_1	0.755	0.387	−0.084	−0.336	−0.568	−0.050
e_1	0.618	0.707	−0.078	−0.783	−0.402	−0.043
e_2	0.841	−0.023	−0.329	0.230	−0.701	0.082
f_2	0.617	0.520	−0.182	−0.594	−0.332	0.345
h_1	0.688	0.470	−0.248	−0.519	−0.485	0.109
h_2	0.552	0.429	−0.281	−0.441	−0.405	0.067
h_3	0.700	0.418	−0.257	−0.407	−0.610	−0.279
3a	0.485	0.315	0.119	−0.376	0.188	−0.288
3b	0.430	0.420	0.092	−0.467	0.090	0.041
4e	0.693	−0.228	0.120	0.346	0.223	0.122
Leg I	0.900	−0.236	0.055	0.615	0.102	0.391
Tarsus I	0.884	−0.332	−0.143	0.720	−0.349	0.205
ω_1 I	0.456	−0.220	−0.064	0.191	0.158	−0.080
ω_3 I	0.415	0.135	0.011	−0.182	0.175	0.089
ba	0.658	−0.424	0.103	0.601	0.029	−0.223
la I	0.765	−0.278	−0.168	0.600	−0.218	0.395
ae	0.701	−0.588	0.087	0.844	−0.002	−0.028
wa I	0.762	−0.229	−0.224	0.455	−0.447	−0.045
gT I	0.762	−0.418	−0.070	0.689	−0.082	−0.014
hT I	0.696	−0.548	−0.003	0.791	−0.012	0.284
ϕ I	0.467	0.503	−0.035	−0.573	0.155	0.009
mG I	0.738	−0.447	0.065	0.706	−0.028	−0.086
cG I	0.764	−0.165	0.017	0.355	−0.217	−0.498
σ'' I	0.570	0.178	0.172	−0.240	0.283	−0.440
vF I	0.858	0.153	0.078	−0.125	−0.213	−0.173
Leg II	0.887	−0.197	0.077	0.610	0.132	0.432
Tarsus II	0.786	−0.361	0.063	0.643	−0.048	0.240
ω_1 II	0.580	0.282	−0.124	−0.348	0.024	0.249
ba II	0.713	−0.627	−0.181	0.788	−0.199	0.138
la II	0.808	−0.124	−0.238	0.327	−0.416	0.296
wa II	0.574	0.123	−0.158	−0.101	−0.216	−0.351
gT II	0.739	−0.402	0.013	0.842	0.006	0.082
hT II	0.767	−0.322	−0.038	0.555	−0.004	0.438
ϕ II	0.658	0.101	0.220	−0.165	0.392	−0.043
mG II	0.731	−0.397	0.111	0.624	0.086	−0.247
σ II	0.358	−0.008	0.234	−0.005	0.235	−0.648
vF I	0.700	0.382	0.131	−0.532	0.148	−0.251
Leg III	0.862	−0.079	0.033	0.245	0.041	0.363
Tarsus III	0.901	−0.095	0.056	0.368	−0.196	0.086
w III	0.652	0.384	−0.198	−0.408	−0.308	0.366
kT III	0.744	0.103	−0.185	−0.116	−0.113	0.367
ϕ III	0.550	0.453	0.059	−0.548	0.130	−0.348
σ III	0.611	−0.360	0.305	0.491	0.226	−0.398
nG III	0.656	0.187	0.165	−0.226	0.167	−0.146
cR III	0.542	0.581	0.148	−0.704	0.198	−0.194
Leg IV	0.862	0.198	0.186	−0.382	0.434	0.425
Tarsus IV	0.728	0.296	0.213	−0.444	0.335	0.290
d IV	0.577	0.449	0.047	−0.602	−0.103	−0.358
r IV	0.528	0.574	−0.012	−0.670	−0.011	0.373
w IV	0.655	0.212	−0.028	−0.235	−0.048	0.541
kT IV	0.554	0.295	0.030	−0.362	0.129	0.068
ϕ IV	0.370	−0.238	0.397	0.149	0.596	−0.255
wF IV	0.624	0.170	0.208	−0.214	0.225	−0.134
% of Total variance	44.1	13.4	5.8	23.1	12.3	7.8
Total variance	0.223			0.133		

the separation is complete. Respective loadings of these components are highly negatively correlated ($r = -0.98$, $P < 0.05$). PC-1 of log size and shape analysis is therefore very close to the isometric vector that was explicitly removed (40.3% of the total variance) in the shape analysis. This vector may represent

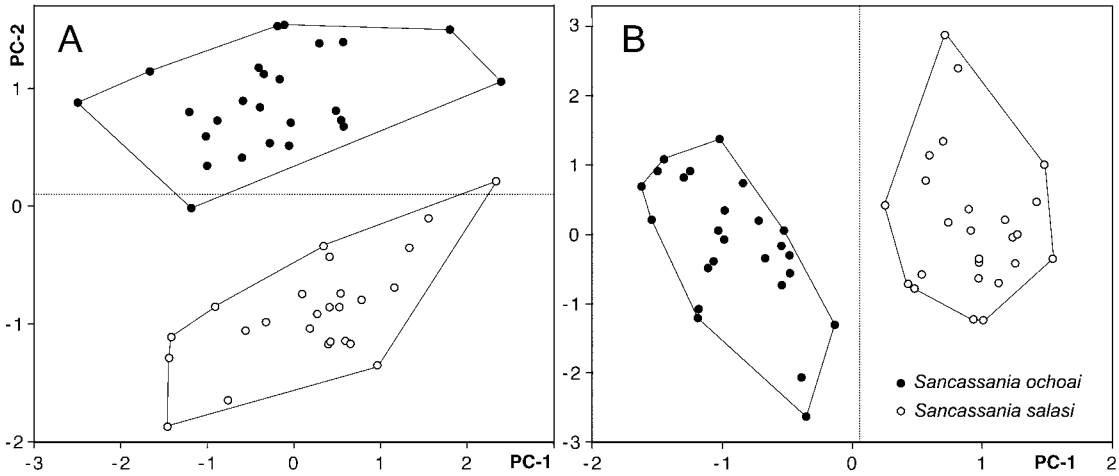

Fig. 1. Scatterplot of the first two principal components of the log size and shape (A) and log shape (B) analyses for females of two *Sancassania* species ($n = 50$).

nongenetic components of variance; 59.2% of such variance is contained in the first three components of log shape and size analysis. The shape versus shape and size scatterplots (Fig. 1) show that the logged measurements contain a great proportion of the size variation; thus, they are not as useful as logged shape data for species discrimination. The variables *aa* and *hT* I have highest positive and the variable e_1 has highest negative loadings on PC-1 and the ratios e_1/hT I and e_1/aa allow for complete bivariate species separation. The other components (PC-4 and beyond) probably represent measurement errors (Houck and OConnor 1998). PC-2 of the shape analysis is very similar to PC-3 of logged raw data ($r = 0.88$, $P < 0.05$) and is probably size-related. PC-3 contrasts some leg setae and solenidia (Table 2).

Discriminant function analysis on the reduced subset of 39 shape variables (see above) produced one function allowing for complete separation of the two species. The largest contribution to discrimination was by the same variables as in the shape PCA, but with the opposite sign: e_1, *aa*, and *hT* I (Table 3). The first variable is widely used in *Sancassania* systematics, usually as a qualitative character. Other variables, beside d_1, listed in Table 3, are metric characters that have not been previously used in *Sancassania* systematics. All of the original grouped individuals were correctly classified, but only 92.0% of the individuals were correctly classified in cross-validation by DFA.

Deutonymphs. Principal component analysis was conducted on three groups (*S. ochoai*, *S. salasi* from culture, and *S. salasi* from beetles) to evaluate the effect of laboratory culture on *S. salasi*.

PCA on log size and shape variables resulted in 12 principal components, with the first three accounting for 72.4% of the total variance. The first component (53.1% of the total variance) is a size component containing residual shape as well. It has all coefficients positive except for *1a*, distance *ba* II base-tarsus II base, and two other variables that have small coefficients (Table 4). The first component partially separates *S. ochoai* and individuals of *S. salasi* collected from beetles (Fig. 2A). No additional separation occurred on the subsequent components. A scatterplot of PC-1 versus PC-2 shows separation between the two species with overlapping groups of *S. salasi* from culture and beetles (Fig. 2A). The two groups from culture are oriented almost parallel to one another, indicating the same pattern of size and shape variance, although variance of *S. salasi* explained by PC-1 and PC-2 has a greater magnitude. Two of 10 individuals collected from beetles are misclassified, suggesting a culture effect on variation.

PCA on log shape variables resulted in 20 components, with the first three accounting for 51.4% of the total variance (Table 4). PC-1 (40.8% of the total variance) consists of 53 positive and 48 negative load-

Table 3. Discriminant character loadings from 40 characters of *S. ochoai* and *S. salasi* females

Variable	DF-1	Variable	DF-1
e_1	0.184	*ba*	−0.085
aa	−0.184	σ III	−0.061
hT I	−0.176	h_3	0.075
Leg I	−0.141	*d* IV	0.076
r IV	0.139	*vF* I	0.073
cR III	0.127	h_2	0.071
Tarsus I	−0.127	*w* III	0.067
ba II	−0.126	*3b*	0.065
Tarsus II	−0.121	*kT* IV	0.064
f_2	0.116	*la* I	−0.063
gT I	−0.114	Tarsus III	−0.063
Leg II	−0.109	*3a*	0.058
mG I	−0.107	d_1	0.055
h_1	0.106	*4a*	−0.054
mG II	−0.101	Leg III	−0.053
hT II	−0.099	Tarsus IV	0.053
ϕ I	0.096	C_p	0.062
ϕ III	0.094	*wa* I	−0.045
gT II	−0.093	ω_1 II	0.044
vl	−0.088		

Variables are ordered by absolute size of correlation within DF-1.

Table 4. First three principal components of log size and shape and log shape of *S. ochoal* and *S. salasi* deutonymphs

Variable	Log size and shape			Log shape		
	PC-1	PC-2	PC-3	PC-1	PC-2	PC-3
Idiosoma, length	0.883	0.415	0.040	0.451	0.202	0.388
Idiosoma, wt	0.887	0.292	0.107	0.155	0.285	−0.189
Propodosoma	0.195	0.514	0.467	0.574	0.438	−0.283
Hysterosoma	0.902	0.350	−0.037	0.129	−0.088	0.552
Length of gnathosoma	0.372	0.834	0.216	0.808	0.291	0.152
Wt of gnathosoma, base	0.030	0.910	−0.018	0.920	−0.007	0.108
Wt of gnathosoma, apex	0.724	0.140	−0.077	0.177	−0.122	−0.179
Distal palpomer	0.721	0.397	0.081	0.338	0.104	−0.054
Posterior gnathosomal setae	0.807	−0.437	0.005	−0.856	−0.011	0.027
Anterior gnathosomal sete	0.800	−0.249	−0.034	−0.676	−0.069	−0.156
Gnathosomal solenldlon	0.670	0.499	0.080	0.620	0.099	−0.154
Sternal shield length	0.670	0.389	0.035	0.270	0.144	0.092
Sternal shield wt, max	0.892	0.299	−0.051	0.320	−0.168	−0.234
Ventral shield length, max	0.838	0.167	−0.115	0.028	−0.207	−0.216
Ventral shield length, up oviposltor	0.886	0.319	−0.108	0.275	−0.265	0.059
Ventral shield wt, max	0.937	0.247	0.003	−0.114	−0.018	0.213
Ventral shield wt min	0.951	0.162	0.031	−0.321	0.111	0.035
Ventral shield wt posterior	0.845	0.406	−0.080	0.494	−0.102	0.217
vi	0.699	0.280	0.174	0.057	0.295	0.352
se	0.482	0.614	0.098	0.441	0.136	0.104
c_2	0.232	0.558	−0.658	0.491	−0.688	0.153
e_2	−0.108	0.548	−0.389	0.651	−0.380	−0.200
h_1	−0.115	0.371	0.213	0.521	0.155	−0.381
h_2	0.255	0.274	−0.239	0.350	−0.242	−0.121
1a	−0.202	0.892	−0.127	0.926	−0.109	0.081
3b	0.372	0.550	−0.136	0.520	−0.134	0.107
4a	0.703	0.333	0.001	0.244	0.002	−0.083
g	0.482	0.128	0.484	0.027	0.549	−0.062
Sternum	0.903	0.015	−0.001	−0.529	−0.019	−0.078
DS1	0.598	0.218	−0.128	0.021	−0.143	0.139
Length of attachment organ[a]	0.745	0.580	0.024	0.621	0.091	0.255
Wt of attachment organ	0.854	0.450	−0.003	0.441	0.048	0.235
DS2	0.752	0.097	0.408	−0.321	0.691	0.308
Anterior sucker (ad_3)	0.727	0.503	0.079	0.570	0.159	−0.080
Median sucker ($ad_1 + ad_2$)	0.929	0.252	0.017	−0.306	0.127	0.619
Anterior lateral sucker (ps_2)	0.874	0.222	0.072	−0.214	0.169	0.170
Posterior lateral sucker (ps_1)	0.766	0.310	0.231	0.184	0.382	−0.168
Anterior cuticular sucker	0.777	0.349	−0.070	0.198	−0.106	0.091
Posterior cuticular sucker	0.763	0.423	−0.057	0.297	−0.047	0.312
Posterior unpaired cuticular sucker	0.751	0.281	−0.131	0.101	−0.165	0.214
Leg I	0.703	0.630	0.075	0.843	0.143	−0.076
Tarsus I	0.568	0.649	0.053	0.760	0.039	−0.288
Empodium I	0.698	0.298	−0.099	0.313	−0.139	0.076
Diam of tarsus I near base	0.759	0.380	0.054	0.342	0.116	0.059
ω_1 I	0.655	0.258	0.111	0.290	0.125	−0.021
ω_2 I	0.665	0.104	0.120	−0.008	0.155	0.110
ω_3 I	0.654	0.252	0.012	0.108	0.050	0.464
Base of ω_3 I-base of tarsus I	0.097	0.824	0.172	0.855	0.140	−0.167
e I	0.807	0.292	−0.026	0.314	−0.044	−0.023
f I	0.816	0.163	0.128	0.062	0.195	−0.209
ra I	0.862	0.359	−0.030	0.341	−0.055	0.004
la I	0.755	0.363	0.034	0.307	0.052	−0.025
Diam of *wa* I	0.190	−0.027	−0.013	0.226	−0.078	−0.792
q I	0.720	−0.068	−0.102	−0.247	−0.159	−0.105
p I	0.850	−0.083	0.080	−0.515	0.130	0.233
gT I	0.663	0.554	0.005	0.590	0.002	−0.060
hT I	0.924	0.066	−0.045	−0.497	−0.076	0.084
mG I	0.744	0.143	0.017	−0.017	−0.001	−0.062
vF I	0.773	−0.268	−0.081	−0.590	−0.136	−0.207
Leg II	0.719	0.512	0.053	0.774	0.153	0.174
Tarsus II	0.514	0.768	0.030	0.864	0.063	−0.052
Empodium II	0.890	0.189	−0.032	−0.079	−0.048	0.271
Diam of tarsus II near base	0.855	0.139	−0.062	−0.044	−0.132	0.021
ω_1 II	0.775	0.179	0.091	0.174	0.106	−0.131
ba	0.873	−0.310	−0.084	−0.829	−0.071	0.161
ba II-tarsus II base	−0.219	0.879	0.138	0.921	0.127	−0.071
e II	0.853	−0.011	−0.040	−0.345	−0.080	0.167
f II	0.806	−0.006	−0.072	−0.178	−0.116	0.144
ra II	0.564	0.632	−0.073	0.683	−0.070	0.297

Table 4. Continued

Variable	Log size and shape			Log shape		
	PC-1	PC-2	PC-3	PC-1	PC-2	PC-3
wa II	0.227	0.558	−0.241	0.630	−0.230	0.077
Diam of *wa* II	0.463	−0.140	0.009	−0.114	−0.029	−0.566
q II	0.771	0.012	−0.016	−0.297	−0.011	−0.006
p II	0.858	−0.252	0.026	−0.755	0.052	0.091
gT II	0.450	0.289	0.196	0.328	0.172	−0.084
hT II	0.838	0.299	−0.062	0.055	−0.114	0.274
ϕ II	0.737	−0.012	0.026	−0.040	−0.013	−0.361
mG II	0.758	0.190	0.017	−0.081	0.005	0.185
cG II	0.681	0.099	0.148	−0.058	0.190	−0.010
vF II	0.836	0.041	−0.137	−0.383	−0.224	0.016
Leg III	0.953	0.126	0.018	−0.496	0.109	−0.042
Tarsus III	0.958	0.126	0.048	−0.509	0.158	0.048
Empodium III	0.897	−0.003	−0.155	−0.464	−0.301	0.138
e III	0.909	−0.118	0.011	−0.613	0.040	−0.048
f III	0.874	−0.328	0.048	−0.842	0.063	0
p III	0.893	−0.118	0.127	−0.685	0.231	−0.015
q III	0.921	−0.185	−0.032	−0.797	−0.071	−0.034
w III	0.799	0.141	0.040	−0.132	0.084	0.154
r III	0.738	−0.540	−0.015	−0.884	−0.032	−0.228
kT III	0.951	−0.109	−0.054	−0.808	−0.103	0.070
nG III	0.752	−0.407	0.024	−0.741	0.011	−0.046
Leg IV	0.953	0.202	0.066	−0.359	0.291	0.204
Tarsus IV	0.966	0.056	0.033	−0.676	0.152	0.214
Empodium IV	0.888	−0.143	−0.194	−0.648	−0.315	−0.025
d IV	0.816	−0.380	−0.242	−0.824	−0.314	0.077
e IV	0.860	−0.303	−0.002	−0.754	−0.024	−0.078
f IV	0.878	−0.322	0.047	−0.858	0.080	0.003
q IV	0.922	−0.118	0.070	−0.725	0.139	0.104
r IV	0.605	0.091	−0.128	−0.326	−0.149	0.383
w IV	0.859	−0.011	−0.152	−0.441	−0.259	0.084
kT IV	0.890	0.100	0.001	−0.417	0.050	0.162
ϕ IV	0.624	−0.036	−0.118	−0.163	−0.177	−0.260
% of Total variance	53.1	16.1	3.2	40.8	5.8	4.8
Total variance	0.461			0.255		

[a] From ovipositor to posterior edge; DS1, distance end of sternum-end of apodemes II; DS2, distance attachment organ-posterior edge of body.

ings. Highest positive loadings are *1a*, *ba* II-tarsus II base, width of gnathosoma (base), tarsus II and base of ω_3 I-base of tarsus I. Highest negative loadings are *r* III, posterior gnathosomal setae, and *f* IV. There is complete separation of the species along the first canonical axis (Fig. 2B). The two deutonymphs from beetles misclassified by PC-1 are the same as in the shape and size analysis. As in the shape analysis of

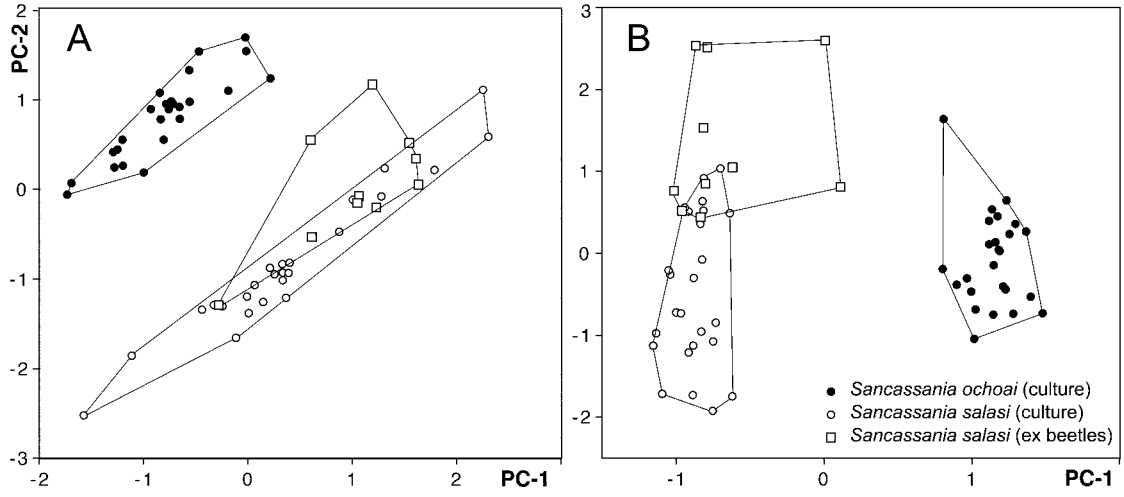

Fig. 2. Scatterplot of the first two principal components of the log size and shape (A) and log shape (B) three-group analyses for deutonymphs of two *Sancassania* species of (n = 60).

Table 5. Discriminant character loadings from 56 characters of *S. ochoai* and *S. salasi* deutonymphs

Variable	DF-1	Variable	DF-1
Wt of gnathosoma, base	0.066	*e* III	−0.020
1a	0.085	*gT* I	0.020
ba II-tarsus II base	0.046	Sternum	−0.019
r III	−0.045	Empodium IV	−0.019
f IV	−0.040	Tarsus III	−0.018
Base of ω_3 I-base of tarsus I	0.039	Length of attachment organ[a]	0.018
f III	−0.039	*vF* I	−0.018
q III	−0.038	*3b*	0.017
Tarsus II	0.037	Ventral shield wt posterior	0.016
Posterior gnathosomal setae	−0.036	Propodosoma	0.016
ba	−0.035	Leg III	−0.016
d IV	−0.033	*p* I	−0.016
Leg I	0.032	Anterior sucker (ad_3)	0.016
kT III	−0.032	h_1	0.014
p II	−0.031	c_2	0.014
Length of gnathosoma	0.030	*hT* I	−0.013
e IV	−0.028	*vF* II	−0.012
Leg II	0.027	Leg IV	−0.012
Tarsus I	0.027	*ae*	0.012
q IV	−0.028	h_2	0.012
p III	−0.026	Idiosoma, length	0.011
Tarsus IV	−0.025	*kT* IV	−0.011
ra II	0.025	*w* IV	−0.011
nG III	−0.024	Wt of attachment organ	0.010
Anterior gnathosomal seta	−0.024	Empodium III	−0.010
we II	0.023	DS2	−0.010
s_2	0.022	Empodium I	0.009
Gnathosomal solenidion	0.020	*ra* I	0.009

Variables ordered by absolute size of correlation within DF-1.
[a] From ovipositor to posterior edge; DS2, distance attachment organ-posterior edge of body.

females, PC-1 is highly correlated with PC-2 of logged raw data ($r = 0.94$, $P < 0.05$). The shape analysis removed 44.7% of the variance being attributable to the size-related variance; 60.8% of such variance was removed from the first three principal components of the logged raw data. Shape and size versus shape scatterplots (Fig. 2) show that the strong shape difference between the species is accompanied by a strong size difference. Cultured individuals of *S. salasi* have much greater magnitude of size-related variance explained by PC-1 than *S. salasi* from beetles. In contrast, *S. salasi* from beetles have much greater magnitude of shape-related variance explained by PC-2. Because there is no complete overlap between the two groups, one can conclude that the rearing technique caused changes in both size and shape. In other words, cultured specimens may differ in shape from their wild type, causing a potential problem with their correlation. Significant differences in shape of adult acarid mites associated with nutritional quality has been demonstrated by Griffiths (1966) for *Acarus immobilis* Griffiths, 1964 and by Gerson and Caupa (1982) for *Rhizoglyphus robini* Claparède, 1869. PC-2 contrasts reared specimens versus specimens collected on beetles, but there is a large overlap (Fig. 2B). No further separation of groups occurred on the subsequent components.

Discriminant function analyses were conducted 1) on *S. ochoai* and the combined group of *S. salasi* from culture and beetles to contrast the interspecific shape variation; and 2) on the two groups of *S. salasi* to contrast the intraspecific shape variance.

The two species DFA was done on the reduced subset of 56 shape variables. The analysis produced one function allowing for complete separation of the two species. The largest contribution to discrimination was by the variables: width of gnathosoma at base, and *1a* (Table 5). The second character, diameter of *1a*, can be used for species identification as an univariate character despite a small overlap. All of the originally grouped individuals were correctly classified and 96.7% of the individuals were classified correctly in cross-validation.

The one species DFA was done on 31 variables. The strongest contributions to the resultant discriminant function were provided by variables: length of gnathosoma, posterior lateral sucker (ps_1), *vi*, and *d* IV. These and other characters ordered by their absolute contribution to DF-1 in Table 6 are most prone to shape changes. Use of them in taxonomic distinction is inappropriate, at least for this data set.

Taxonomy

Sancassania ochoai Klimov, Lekveishvili & OConnor, sp. nov.

(Figs. 3A and B, 4–9, 10, G–K, 11, 12)

Female. (Figs. 3A and B, 4, 5. Table 7; measurements/ratios given for $n = 25$, unless otherwise noted). Idiosoma 650-1180 (939.6 ± 21.45). Internal vertical setae *vi* slightly barbed. Supracoxal setae *scx*

Table 6. Discriminant character loadings from 31 characters of *S. salasi* deutonymphs from culture and beetles

Variable	DF-1	Variable	DF-1
Length of gnethosoma	0.117	Empodium III	−0.042
Posterior lateral sucker (ps_1)	0.081	Distal palpomer	0.040
vl	0.068	Empodium IV	−0.040
d IV	−0.066	Length of attachment organ[a]	0.040
Anterior lateral sucker (ps_2)	0.068	*mG* I	−0.039
DS2	0.058	c_2	−0.038
Wt of gnathosoma, apex	−0.050	*kT* III	−0.038
f II	−0.048	*p* III	0.038
Ventral shield length, up ovipositor	−0.049	*sa*	0.038
Ventral shield length, max	−0.049	Diam of *wa* I	−0.037
Sternal shield wt. max	−0.048	*e* II	−0.036
wa II	−0.047	*ba*	−0.035
Wt of attachment organ	0.043	*re* I	−0.034
f I	0.043	*ba* II-tarsus II base	0.032
ϕ IV	−0.042	Leg II	0.025
Median sucker ($ad_1 + ad_2$)	0.042		

Variables ordered by absolute size of correlation within DF-1.
[a] From ovipositor to posterior edges; DS2, distance attachment organ-posterior edge of body.

short, spiniform. Setae *si* 1.0–2.0 (1.40 ± 0.049, $n = 20$) times longer than c_1. Distance *si-si* longer than length of setae *si*. Anterio-dorsal hysterosomal setae c_1 and c_2 much shorter than other hysterosomal setae, their tips not reaching bases of next setae. Setae d_1 2.2–5.0 (3.77 ± 0.164, $n = 21$) times longer than c_1 and 2.2–4.1 (2.82 ± 0.093, $n = 21$) times shorter than e_1. Setae d_1 and e_1 not reaching or reaching bases of next setae (e_1 and h_1, respectively) in ovigerous females. Setae e_1 2.8–5.3 (4.54 ± 0.141, $n = 23$) times shorter than idiosoma. Posterio-dorsal hysterosomal setae h_1 longer than e_1, smooth, with attenuate tips. Adanal setae ad_1 posterior to ps_1. Duct of spermatheca short, 23–37 (31.0 ± 2.03, $n = 7$), moderately dilated at spermatheca (Fig. 3A and B), width at external opening 8–19 (12.6 ± 1.47, $n = 7$), width at spermatheca 9–17 (12.6 ± 1.01, $n = 7$). Legs and tarsi comparatively long; legs I 2.4–3.4 (3.0 ± 0.057) shorter than idiosoma, tarsus I 2.9–3.7 (3.24 ± 0.04) shorter than leg I. Tarsal setae *aa* setiform, normally slightly anterior to solenidion ω_2. Tarsal setae *ba* I-II setiform, paramedial. Ratio e_1/hT 8.4–14.9 (10.34 ± 0.277, $n = 23$), e_1/aa 8.4–12.7 (10.46 ± 0.243, $n = 22$).

Homeomorphic Male. (Figs. 6 and 7; Table 8; measurements/ratios given for $n = 10$, unless otherwise noted). Idiosoma 696–971 (818.4 ± 24.05). Supracoxal seta short, spiniform. Setae *si* 1.1–1.9 (1.27 ± 0.081) times longer than c_1. Distance *si-si* shorter than length

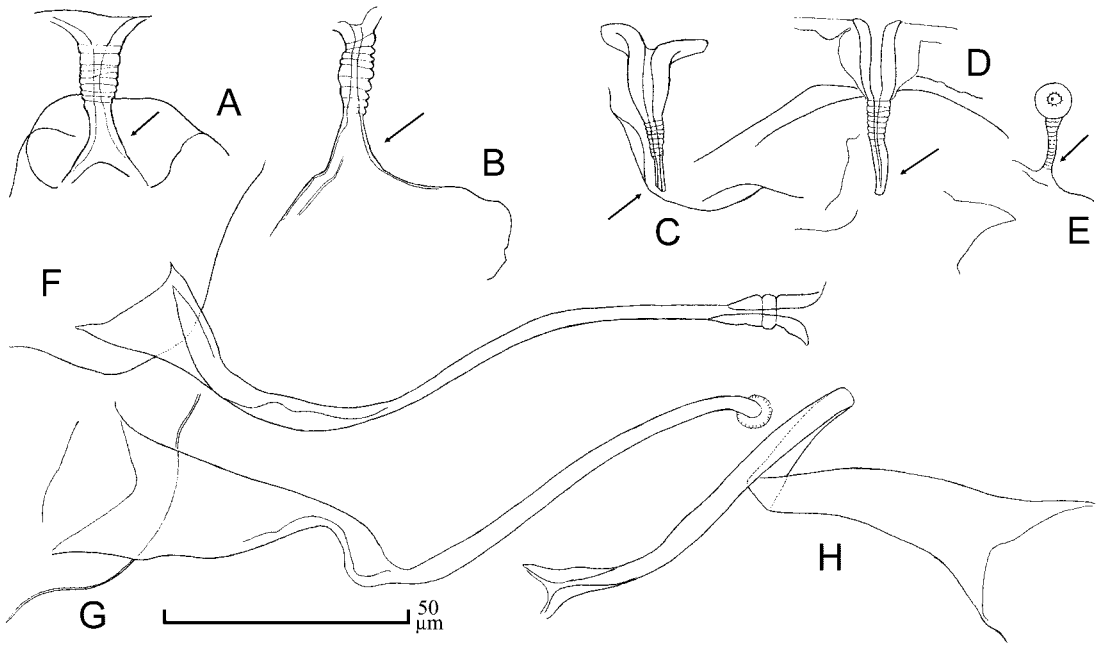

Fig. 3. Spermatheca of three *Sancassania* species. (A and B) *S. ochoai* sp. nov., paratypes. (C–E) *S. salasi* sp. nov., paratypes. (F–H) *S. phyllophagiana* (Oseto & Mayo).

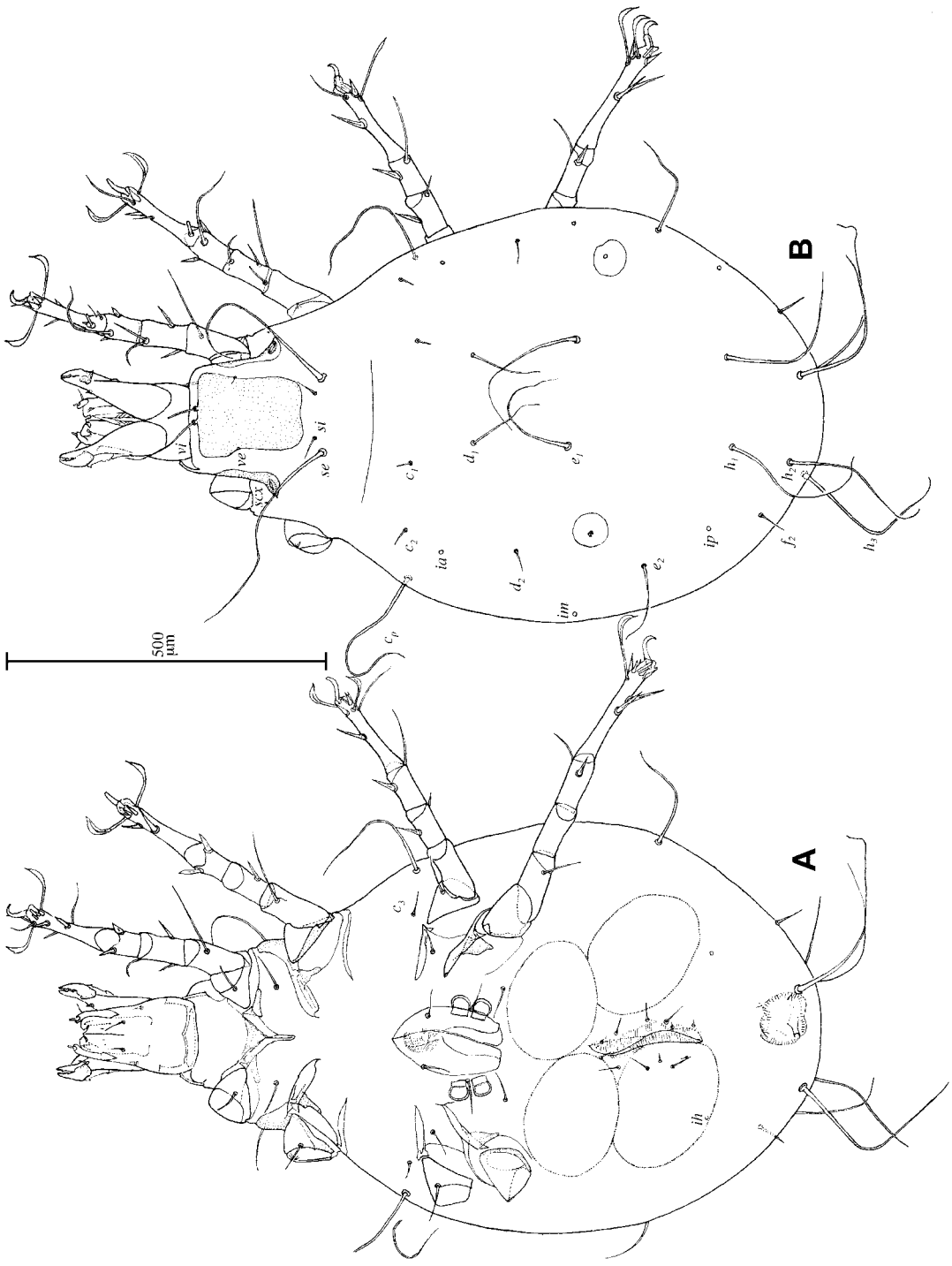

Fig. 4. *S. ochoai* sp. nov. (female, holotype). (A) Ventral view. (B) Dorsal view.

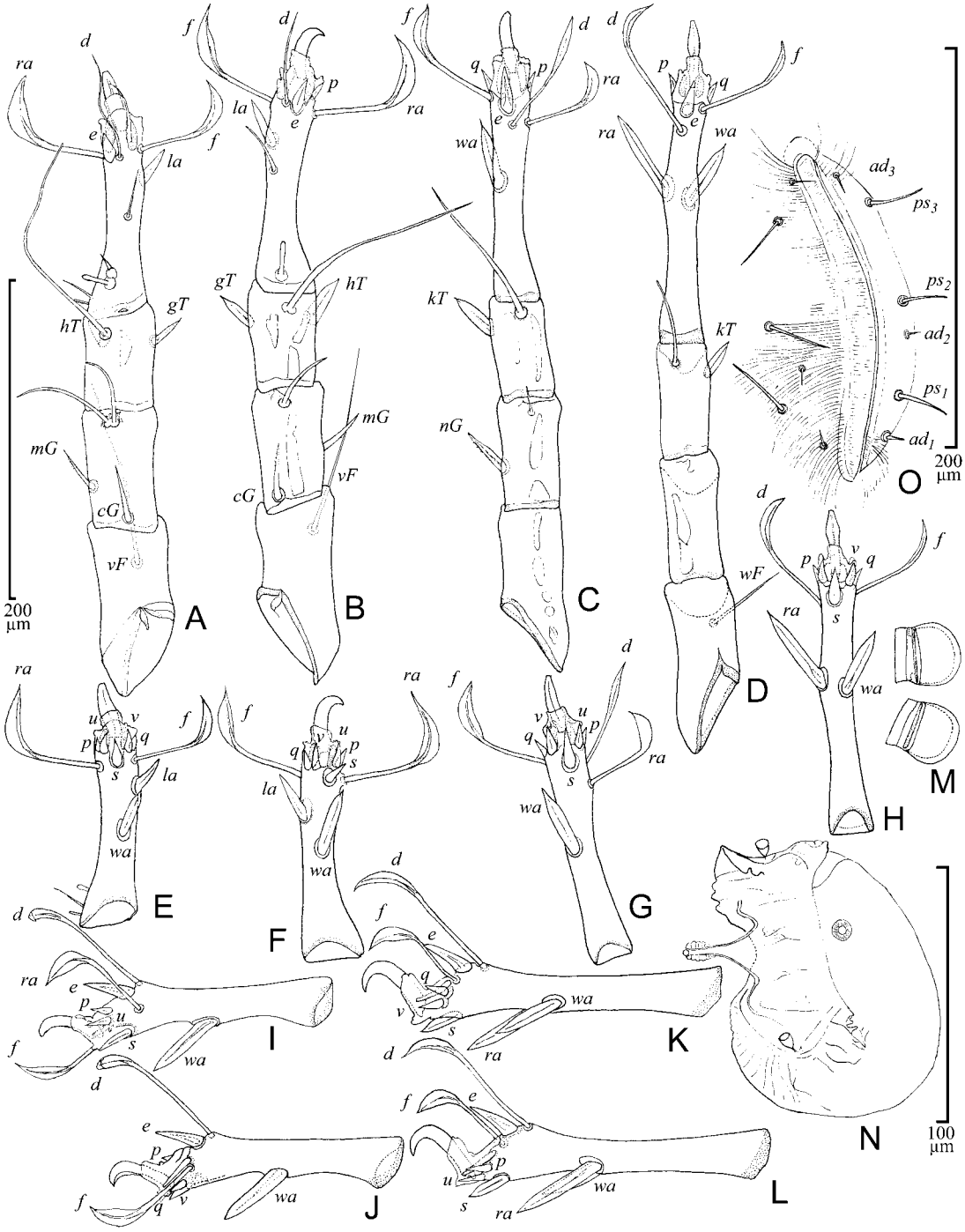

Fig. 5. *S. ochoai* sp. nov. (female, paratype). (A–D) Legs I-IV, dorsal view, respectively. (E–H) Tarsi I-IV, ventral view, respectively. (I and J) Tarsus III, lateral view. (K and L) Tarsus IV, lateral view. (M) Genital papillae. (N) Spermatheca. (O) Anus. Bars, A–L, 200 μm (left); M and O, 200 μm (right); and N, 100 μm.

of setae *si*. Idiosomal setae long, with inflated bases. Setae d_1 very long, 308–374 (339.8 ± 7.20), 2.1–2.8 (2.44 ± 0.077) times shorter than idiosoma 4.4–6.0 (5.38 ± 0.17) times longer than c_1, 1.4–1.7 (1.44 ± 0.038) times shorter than e_1 (n = 9), reaching transverse level of cupules *ip*. Setae e_1 1.5–2.6 (1.79 ± 0.097) times shorter than idiosoma. Setae e_1 and e_2 protruding beyond posterior end of hysterosoma. Setae h_1 nearly as long as h_2 and h_3. Pseudanal setae ps_1 long, 103–264 (229.7 ± 14.73), setiform, with attenuated tips. Setae

Table 7. Measurements (range, mean ± SE) of 76 morphological structures of females of two *Sancassania* species

Variable	*S. ochoai* $n = 25$	*S. salasi* $n = 25$	Character	*S. ochoai* $n = 25$	*S. salasi* $n = 25$
Idiosoma, length	650–1180, 939.6 ± 21.45	740–1250, 943.2 ± 24.07	ϕ I	108–163, 130.1 ± 2.85^{w}	103–143, 121.8 ± 1.97
Idiosoma, wt	355–740, 603.4 ± 16.99	440–900, 587.2 ± 22.11	*mG* I	23–45, 31.9 ± 1.00	30–50, 38.0 ± 0.91
Propodosoma	235–330, 280.0 ± 5.30^{w}	225–350, 284.0 ± 6.09^{x}	*cG* I	25–45, 32.0 ± 0.95^{x}	23–48, 35.7 ± 1.29
Hysterosoma	400–825, 663.0 ± 18.53^{w}	465–950, 660.8 ± 22.09^{x}	σ' I	38–50, 45.6 ± 0.81^{t}	25–50, 37.6 ± 1.32^{u}
vi	75–108, 88.4 ± 1.58^{x}	75–125, 100.3 ± 2.15	σ'' I	45–68, 57.3 ± 1.10	48–73, 58.1 ± 1.32
ve	8–10, 8.4 ± 0.36^{g}	8–13, 9.9 ± 0.54^{j}	*vF* I	75–138, 101.8 ± 2.61	80–138, 104.4 ± 2.93
si	20–43, 28.5 ± 1.15^{u}	25–38, 31.7 ± 0.82^{x}	*pR* I	20–43, 30.8 ± 1.20^{v}	20–50, 31.7 ± 1.94^{r}
se	263–413, 314.7 ± 7.36^{w}	250–425, 320.8 ± 7^{x}	Leg II	270–398, 327.9 ± 6.02	300–413, 360.5 ± 6.56
c_1	13–30, 20.4 ± 0.79^{w}	15–28, 22.7 ± 0.79^{v}	Tarsus II	83–138, 105.0 ± 2.65	88–150, 123.2 ± 2.92
c_2	13–25, 19.2 ± 0.72^{s}	18–33, 25.9 ± 0.85^{v}	ω_1 II	20–30, 22.8 ± 0.47^{v}	18–25, 22.6 ± 0.53
c_3	23–45, 34.0 ± 1.15	25–48, 36.5 ± 1.55^{u}	*ba* II	23–39, 29.7 ± 0.80	27–44, 35.8 ± 0.84
c_p	175–300, 222.2 ± 6.93^{v}	138–300, 215.7 ± 7.12	*la* II	23–35, 28.6 ± 0.64	23–38, 31.0 ± 0.90^{x}
d_1	50–150, 77.0 ± 4.42^{w}	50–125, 70.2 ± 3.47^{v}	*wa* II	30–55, 40.2 ± 1.33^{w}	33–58, 40.5 ± 1.33^{v}
d_2	23–40, 31.5 ± 1.11^{u}	28–68, 41.8 ± 1.82^{t}	*gT* II	20–35, 28.0 ± 0.79	28–40, 32.1 ± 0.59
e_1	164–324, 211.6 ± 8.15^{w}	112–223, 172.9 ± 5.83^{v}	*hT* II	30–40, 35.1 ± 0.73	30–48, 40.1 ± 0.90
e_2	100–213, 138.0 ± 4.82	95–195, 149.1 ± 5.14	ϕ II	100–150, 119.1 ± 2.08	100–163, 121.5 ± 2.63
f_2	26–54, 39.2 ± 1.18^{w}	28–43, 35.4 ± 0.85	*mG* II	30–50, 38.4 ± 0.96	38–60, 44.6 ± 1.14
h_1	165–312, 229.9 ± 7.22^{x}	140–246, 207.4 ± 6.18^{w}	*cG* II	23–43, 30.2 ± 1.19^{u}	23–53, 34.1 ± 1.59^{t}
h_2	175–325, 223.6 ± 7.90	150–250, 205.1 ± 5.60^{x}	σ II	30–48, 37.6 ± 0.91^{w}	20–53, 39.7 ± 1.78^{x}
h_3	163–313, 233.3 ± 8.12	113–288, 212.5 ± 6.85	*vF* I	75–138, 101.8 ± 2.61	80–138, 104.4 ± 2.93
1a	33–63, 48.4 ± 1.39^{x}	38–50, 44.6 ± 1.01^{u}	*pR* I	20–43, 30.8 ± 1.20^{v}	20–50, 31.7 ± 1.94^{r}
3a	33–53, 41.4 ± 1.15^{v}	30–50, 39.6 ± 1.02^{x}	Leg III	270–438, 339.3 ± 6.63	293–438, 365.0 ± 7.32
3b	35–63, 47.8 ± 1.26^{x}	28–58, 44.5 ± 1.48^{x}	Tarsus III	100–200, 121.6 ± 4.01	108–175, 132.3 ± 2.94
4a	35–60, 49.4 ± 1.46^{v}	43–65, 54.6 ± 1.05^{x}	*d* III	65–113, 83.5 ± 2.36^{x}	45–113, 80.8 ± 4.09^{t}
g	33–55, 43.9 ± 1.39^{t}	38–58, 45.3 ± 1.10^{w}	*w* III	35–58, 45.1 ± 1.26	33–55, 42.8 ± 1.09
CSP	13–30, 22.0 ± 1.53^{u}	18–38, 26.8 ± 2.04^{j}	*kT* III	30–43, 37.1 ± 0.69	30–43, 37.8 ± 0.78
Leg I	268–375, 313.7 ± 5.57	288–400, 346.8 ± 6.05	ϕ III	88–138, 105.3 ± 2.11^{x}	75–125, 99.4 ± 2.24^{x}
Tarsus I	77–128, 97.4 ± 2.43	87–129, 112.1 ± 2.48	σ III	18–30, 21.7 ± 0.67^{w}	18–38, 26.6 ± 1.05
ω_1 I	15–23, 18.4 ± 0.53^{v}	18–23, 19.5 ± 0.42^{v}	*nG* III	30–40, 36.5 ± 0.66	25–50, 36.8 ± 1.09
ω_2 I	10–15, 13.1 ± 0.31^{u}	8–13, 9.9 ± 0.35^{t}	*cR* III	53–72, 61.7 ± 1.09	42–72, 57.0 ± 1.25^{w}
ω_3 I	30–45, 35.4 ± 0.80	28–43, 34.9 ± 0.82	Leg IV	338–488, 411.5 ± 6.33^{x}	350–488, 417.3 ± 6.62
Famulus	10–15, 12.3 ± 0.31^{w}	10–13, 10.5 ± 0.23^{r}	Tarsus IV	138–188, 158.1 ± 2.58^{x}	125–193, 157.1 ± 3.25
ba	20–38, 27.1 ± 0.85	25–43, 31.7 ± 0.75	*d* IV	75–120, 87.9 ± 2.32^{x}	58–125, 82.0 ± 3.06
la I	18–30, 22.9 ± 0.60^{x}	20–33, 25.5 ± 0.63	*r* IV	49–74, 64.2 ± 1.33^{x}	43–70, 57.9 ± 1.47^{v}
aa	13–30, 20.6 ± 0.67^{x}	23–34, 26.7 ± 0.61^{w}	*w* IV	35–63, 48.7 ± 1.23	33–63, 48.5 ± 1.34^{x}
wa I	20–40, 27.9 ± 1.13^{w}	25–38, 30.8 ± 0.83^{x}	*kT* IV	23–35, 29.9 ± 0.73	25–35, 28.6 ± 0.58^{x}
gT I	18–30, 24.7 ± 0.54	22–34, 28.6 ± 0.59	ϕ IV	50–75, 60.7 ± 1.37^{x}	50–80, 66.0 ± 1.39
hT I	16–26, 20.6 ± 0.50	20–31, 25.9 ± 0.59	*wF* IV	43–63, 50.3 ± 1.02	40–68, 50.8 ± 1.38^{x}

Superscript denotes number of measurements if <25 (a = 1, b = 2 . . . x = 24).
CSP, canal of spermatheca.

ps_2 48–77 (69.9 ± 2.65), shifted posteriorly from anus by 44–70 (57.2 ± 2.70), reaching or not reaching ps_1 bases, usually with obtuse tips (sometimes attenuated). Distance ps_1-ps_2 62–117 (84.4 ± 5.50). Aedeagus elongated, with free end bent upward (Fig. 7R). Position of leg I-III elements similar to female. Legs I 1.8–2.3 (1.99 ± 0.055) times shorter than idiosoma; tarsus I 2.5–3.3 (2.79 ± 0.08) times shorter than leg I. Distal tarsal sucker *e* IV placed on apex of tarsus. Distances between suckers and ends of tarsus IV given in Table 8.

Heteromorphic Male. (Figs. 8 and 9; Table 8; measurements/ratios given for $n = 10$, unless otherwise noted). Idiosoma 702–907 (826.0 ± 19.57). Supracoxal seta short, spiniform. Ratio si/c_1 0.8–1.3 (1.07 ± 0.047). Distance *si-si* shorter than length of setae *si.* Idiosomal setae long with inflated bases. Setae d_1 very long, 308–374 (351.1 ± 6.82), 2.2–2.9 (2.36 ± 0.065) times shorter than idiosoma, 2.6–5.2 (4.36 ± 0.222) times longer than c_1, 2.2–2.9 (2.36 ± 0.065) times shorter than e_1, reaching transverse level of cupules *ip.* Setae e_1 1.5–2.0 (1.69 ± 0.051) times shorter than idiosoma. Setae e_1 and e_2 protruding beyond posterior end of hysterosoma. Setae h_1 nearly as long as h_2 and h_3. Pseudanal setae ps_1 long, 205–268 (249.8 ± 6.80, $n = 9$), setiform, with attenuated tips. Setae ps_2 62–79 (71.0 ± 1.67), shifted posteriorly from anus by 55–88 (65.6 ± 3.95), usually approximating bases of ps_1, with obtuse tips. Distance ps_1-ps_2 57–84 (70.4 ± 2.97). Aedeagus elongated, with free end bent upward. Position of leg I-II and IV elements similar to homeomorphic male, legs III typical for *Sancassania.* Legs I 1.6–1.9 (1.74 ± 0.023) times shorter than idiosoma; tarsus I 2.7–3 (2.81 ± 0.034) times shorter than leg I. Distances between suckers and ends of tarsus IV given in Table 8.

Deutonymph. (Figs. 10G–K, 11, 12; Table 9; measurements/ratios given for $n = 25$). Form of gnathosoma variable (Fig. 10G–K); subcapitulum usually with convex, weakly sclerotized sides; palpi 2.3–3.0 (2.60 ± 0.034) times shorter than length of subcapitulum. Posterior gnathosomal setae usually shorter than in *S. salasi*, 5.5–7.8 (7.07 ± 0.152), approximately equal with *1a;* posterior gnathosomal setae/*1a* 0.8–1.2 (0.95 ± 0.02). Idiosoma ovoid, 1.3–1.6 (1.45 ± 0.015) times longer than wide, dorsal surface covered with small pores. Propodosoma 4.4–7.3 (6.13 ± 0.146) times shorter than hysterosoma; rostral projection broadly

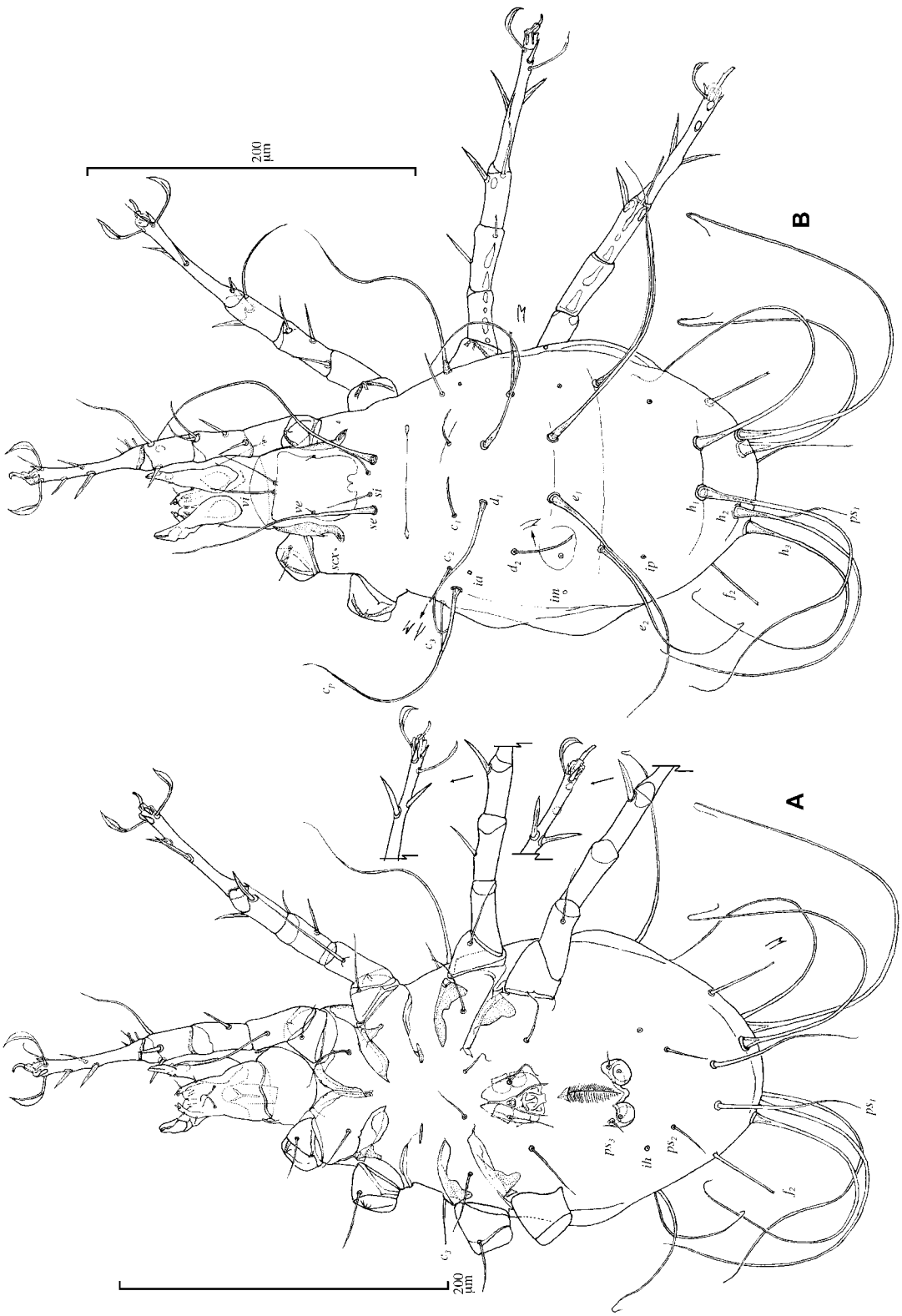

Fig. 6. *S. ochoai* sp. nov. (homeomorphic male, paratype). (A) Ventral view. (B) Dorsal view.

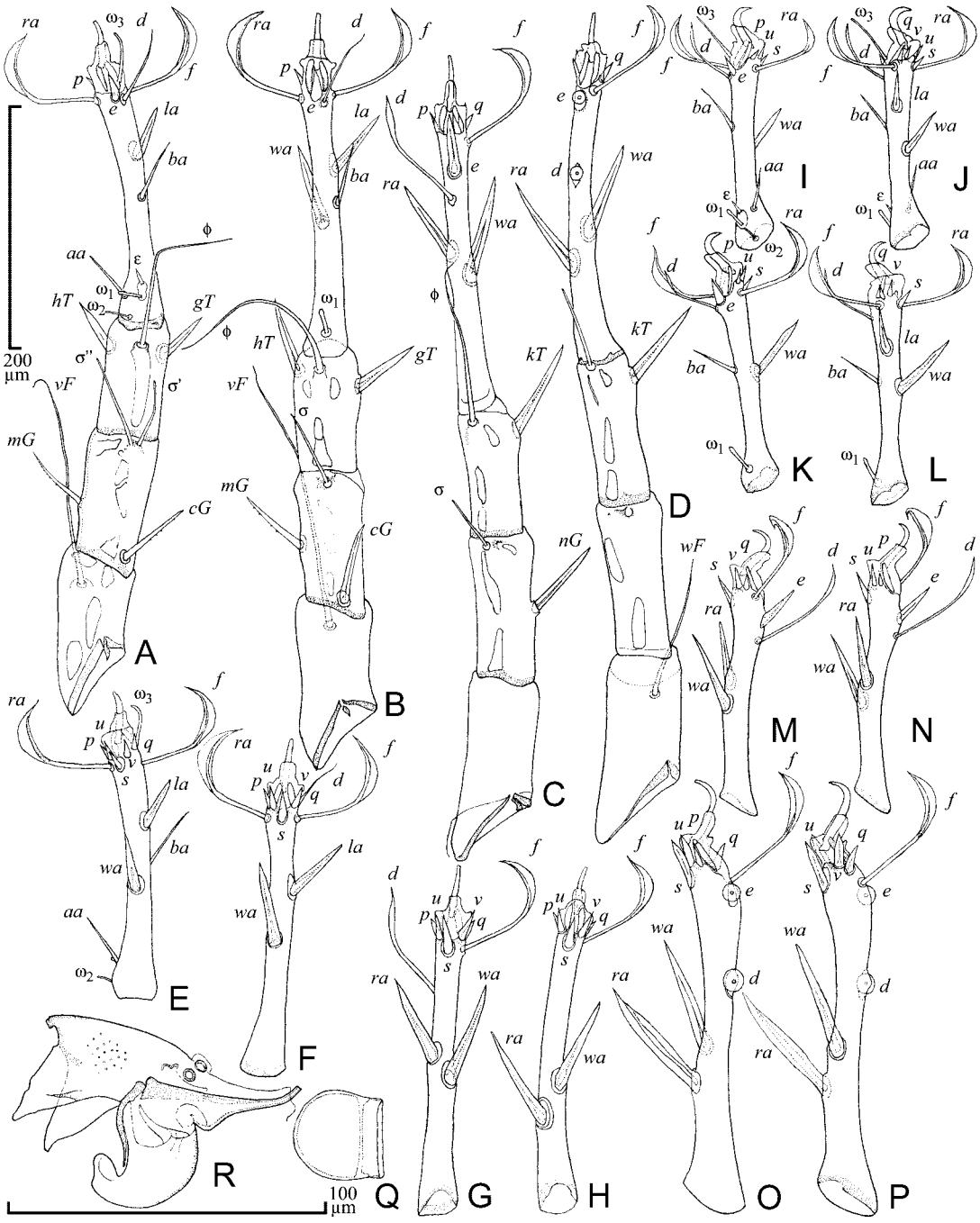

Fig. 7. *S. ochoai* sp. nov. (homeomorphic male, paratype). (A–D) Legs I-IV, dorsal view, respectively. (E–H) Tarsi I–IV, ventral view, respectively. (I and J, K and L, M and N, O and P) Tarsi I, II, III, IV lateral view, respectively. (Q) Genital papillae. (R) Aedeagus. Bars, A–P, 200 μm (left); Q and R, 100 μm.

angled, with *vi* at its apex; *si* distinctly shorter than *SE*, slightly shifted anteriorly (by a distance much less than length of *SE*). Dorsal hysterosomal setae short. Posterior edge of sternal shield touching anterior edge of ventro-genital shield, slightly concave. Sternal apodeme not reaching posterior ends of apodemes II. Conoids *1a* large compared with *S. salasi*, 6.6–8.7 (7.43 ± 0.114), 2.3–3.2% (2.60 ± 0.043) of length of idiosoma, elongated, usually protruding beyond sclerotized bases, smooth. Coxal fields II open, with very short unsclerotized gap between anterior and posterior apodemes; apodemes not reaching posterior edge

Table 8. Measurements (range, mean ± SD) of 90 morphological structures of males of two *Sancassania* species

Variable	Homeomorphic males		Heteromorphic males	
	S. ochoai $n = 10$	*S. salasi* $n = 10$	*S. ochoai* $n = 10$	*S. salasi* $n = 10$
Idiosoma, length	696–971, 818.4 ± 24.05	617–944, 803.9 ± 27.66	702–907, 826.0 ± 19.57	794–1006, 904.7 ± 24.28
Idiosoma, wt	363–497, 455.7 ± 13.18	344–559, 459.6 ± 19.08	410–556, 468.6 ± 14.76	431–638, 528.0 ± 20.23
Propodosoma	211–328, 248.6 ± 13.54[h]	192–272, 228.7 ± 7.73	234–293, 262.3 ± 10.29[f]	228–300, 270.2 ± 7.00
Hysterosoma	480–644, 566.0 ± 16.87[h]	425–672, 575.2 ± 21.02	556–614, 581.1 ± 9.87[f]	566–741, 634.5 ± 19.28
vi	86–121, 102.7 ± 2.93	75–122, 100.0 ± 4.42	81–136, 115.1 ± 5.13	82–138, 111.6 ± 6.21
ve	11–15, 12.7 ± 0.42[i]	11–23, 16.7 ± 1.15	10–15, 12.6 ± 0.43	14–33, 18.1 ± 1.73
si	46–86, 72.8 ± 3.64	48–97, 71.7 ± 4.57	64–103, 87.9 ± 4.54	62–209, 98.7 ± 13.27
se	264–506, 398.2 ± 19.53	379–465, 415.8 ± 9.84[i]	345–473, 433.8 ± 14.0	400–518, 461.3 ± 13.49
c_1	24–73, 59.6 ± 4.31	41–136, 101.1 ± 7.56	64–117, 82.5 ± 4.46	98–178, 134.2 ± 8.37
c_2	31–73, 60.1 ± 3.77	42–164, 110.8 ± 11.53	59–88, 77.3 ± 2.50	75–214, 153.4 ± 14.62
c_3	53–99, 81.2 ± 3.76	69–136, 105.5 ± 6.80	84–110, 99.4 ± 2.60	125–179, 150.6 ± 5.53[i]
c_p	209–429, 364.1 ± 18.94	307–418, 358.2 ± 11.82	341–506, 454.3 ± 14.58	343–563, 432.7 ± 22.46
d_1	308–374, 339.8 ± 7.20[i]	223–388, 303.7 ± 18.34	308–374, 351.1 ± 6.82	292–426, 379.2 ± 14.42[i]
d_2	53–121, 96.4 ± 5.96	103–353, 184.1 ± 20.77	106–132, 122.8 ± 2.95	153–402, 259.9 ± 21.45
e_1	286–528, 467.5 ± 21.58	345–544, 465.0 ± 20.22	451–550, 490.6 ± 11.15	410–601, 517.5 ± 21.59
e_2	154–374, 303.6 ± 18.64	308–403, 349.4 ± 8.99	308–440, 376.2 ± 11.10	288–550, 409.0 ± 25.23
f_2	70–132, 110.4 ± 5.47	72–150, 120.8 ± 6.71	99–139, 125.0 ± 3.53	113–160, 138.1 ± 5.24
h_1	484–616, 559.9 ± 12.96	493–710, 599.3 ± 26.1	550–660, 588.5 ± 13.45	518–738, 654.0 ± 21.06
h_2	484–682, 619.3 ± 21.13	520–723, 643.4 ± 26.25	594–682, 637.3 ± 9.18	555–783, 665.4 ± 23.17
h_3	396–704, 526.9 ± 25.95	445–648, 540.3 ± 25.28[i]	506–616, 558.8 ± 12.57	488–658, 578.9 ± 22.63[i]
1a	35–99, 73.5 ± 5.57	47–83, 69.0 ± 3.69	70–114, 90.9 ± 4.06	73–114, 90.8 ± 4.13
3a	44–66, 55.4 ± 2.31	39–65, 50.4 ± 3.16[h]	44–66, 54.2 ± 2.69[h]	49–71, 59.3 ± 2.44[i]
3b	37–103, 75.2 ± 6.92	72–101, 83.5 ± 3.06[i]	66–121, 84.7 ± 5.83	86–114, 97.0 ± 3.34
4a	55–99, 78.5 ± 4.02[i]	59–83, 75.4 ± 2.71	70–103, 84.1 ± 3.91[i]	62–106, 87.2 ± 3.85
g	35–75, 61.6 ± 4.31[i]	51–89, 66.1 ± 3.67	55–88, 70.1 ± 3.75[h]	66–97, 78.4 ± 3.09[i]
ps_1	103–264, 229.7 ± 14.73	151–314, 222.8 ± 13.66	205–268, 249.8 ± 6.80[i]	206–306, 251.9 ± 11.02[i]
ps_2	48–77, 69.9 ± 2.65	53–134, 80.2 ± 8.03	62–79, 71.0 ± 1.67	58–137, 88.7 ± 7.15
ps_3	15–22, 19.8 ± 0.73	17–25, 21.3 ± 0.82	15–22, 18.4 ± 0.71[h]	23–34, 25.7 ± 1.19[i]
ps_1-ps_1	33–66, 45.5 ± 2.58	45–67, 56.6 ± 2.72[h]	37–57, 41.5 ± 2.69[g]	50–66, 58.3 ± 1.58
ps_2-ps_2	79–110, 95.9 ± 3.06	87–120, 104.2 ± 3.46	77–110, 89.2 ± 3.87[i]	83–152, 109.0 ± 6.90
ps_1-ps_2	62–117, 84.4 ± 5.50	28–61, 51.4 ± 2.85	57–84, 70.4 ± 2.97	47–75, 57.0 ± 2.53
ps_2-anus	44–70, 57.2 ± 2.70	51–133, 92.3 ± 7.13	55–88, 65.6 ± 3.95	70–117, 90.2 ± 4.33
Leg I	315–451, 413.6 ± 14.13	365–535, 440.1 ± 15.07	411–532, 474.3 ± 12.68	450–611, 518.5 ± 14.71
Tarsus I	95–176, 150.0 ± 8.22	149–220, 177.4 ± 6.43	147–194, 168.7 ± 4.44	188–250, 210.2 ± 5.89
ω_1 I	14–20, 18.5 ± 0.56	18–23, 20.2 ± 0.90[f]	18–21, 19.3 ± 0.41	20–23, 22.0 ± 0.41[i]
ω_2 I	11–20, 14.9 ± 0.96	10–18, 14.9 ± 0.76	13–21, 17.1 ± 1.04[i]	13–42, 18.8 ± 2.64
ω_3 I	40–46, 42.2 ± 0.72	34–50, 43.4 ± 1.31	35–51, 42.6 ± 1.62	39–49, 43.1 ± 0.97
Famulus	9–13, 10.9 ± 0.42	9–14, 11.2 ± 0.53	9–15, 11.7 ± 0.80[i]	11–15, 12.5 ± 0.57
ba I	33–44, 40.9 ± 0.94	34–44, 38.1 ± 1.16	40–57, 48.2 ± 1.92	34–55, 44.0 ± 2.25
la I	24–47, 37.8 ± 2.04	29–42, 35.4 ± 1.30	35–51, 40.8 ± 1.74	34–53, 42.8 ± 1.70
aa I	24–42, 35.2 ± 1.47	27–51, 36.8 ± 2.14	31–46, 40.3 ± 1.57	33–48, 40.8 ± 1.68
wa I	35–52, 45.1 ± 1.45	34–54, 41.1 ± 2.62[g]	42–59, 51.9 ± 1.69	35–61, 50.0 ± 2.42[i]
gT I	25–62, 43.0 ± 2.80	34–47, 40.7 ± 1.39	40–51, 44.6 ± 1.04	33–55, 44.4 ± 1.99
hT I	25–44, 38.4 ± 1.68	30–46, 37.8 ± 1.54	33–46, 40.5 ± 1.15	34–48, 43.2 ± 1.64
ϕ I	55–88, 67.3 ± 2.92	128–160, 139.0 ± 4.45[g]	77–110, 93.6 ± 3.93[i]	125–153, 138.8 ± 5.36[e]
mG I	35–57, 49.3 ± 2.25	45–62, 51.8 ± 1.59	42–57, 48.4 ± 1.86	47–67, 57.5 ± 1.97
cG I	31–59, 51.2 ± 2.58	42–64, 52.2 ± 2.35[i]	40–62, 53.7 ± 2.11	50–80, 61.3 ± 2.66
σ' I	44–51, 48.6 ± 0.69	39–55, 47.2 ± 1.99[h]	44–57, 50.8 ± 1.52	47–57, 52.6 ± 1.28
σ'' I	61–70, 65.7 ± 0.90	58–72, 65.8 ± 1.67[i]	57–79, 68.4 ± 2.16	61–80, 71.5 ± 2.06
vF I	99–158, 142.3 ± 5.09	111–176, 147.2 ± 7.59	117–176, 149.4 ± 5.73	133–200, 167.5 ± 6.69
pR I	31–70, 58.1 ± 3.33	51–67, 61.0 ± 2.61[f]	55–77, 65.6 ± 2.60	42–89, 68.6 ± 4.80[i]
Leg II	319–513, 436.5 ± 18.21	369–530, 451.2 ± 15.03	429–568, 501.4 ± 12.3	458–615, 539.6 ± 14.07
Tarsus II	99–194, 166.5 ± 8.63	156–228, 189.9 ± 6.89	158–205, 184.8 ± 4.24	193–263, 228.2 ± 6.46
ω_1 II	20–24, 22.0 ± 0.46	20–27, 23.7 ± 0.82[i]	21–27, 23.7 ± 0.51	26–29, 26.9 ± 0.41[i]
ba II	29–48, 41.3 ± 1.67	30–45, 37.2 ± 1.68	31–52, 46.2 ± 1.90	36–162, 56.9 ± 11.84
la II	32–55, 46.3 ± 1.98	33–56, 43.1 ± 2.00	40–57, 50.4 ± 1.65	42–62, 53.5 ± 1.94
wa II	35–67, 57.5 ± 2.94	44–67, 56.1 ± 2.40[i]	55–75, 67.4 ± 1.77	48–81, 67.8 ± 3.09
gT II	32–55, 50.1 ± 2.15	37–53, 44.4 ± 1.60	45–64, 54.1 ± 1.54	48–68, 55.7 ± 2.12
hT II	43–66, 56.9 ± 1.98	43–66, 54.8 ± 2.38	51–70, 61.1 ± 1.73	51–73, 64.6 ± 2.59
ϕ II	66–88, 75.5 ± 2.76	120–153, 137.6 ± 3.89[i]	88–121, 104.9 ± 3.38	115–164, 144.0 ± 7.08[g]
mG II	35–66, 57.1 ± 2.79	46–74, 58.0 ± 2.64	46–62, 55.3 ± 1.54	53–78, 64.1 ± 2.62
cG II	26–63, 52.9 ± 3.06	36–62, 46.5 ± 2.95[h]	46–66, 57.2 ± 1.70	49–69, 60.4 ± 2.38[h]
σ II	46–58, 51.9 ± 1.27	42–59, 50.4 ± 2.06[h]	46–62, 54.3 ± 1.50	49–69, 59.7 ± 2.11
vF II	143–231, 191.6 ± 7.64	146–222, 185.1 ± 7.27	165–224, 200.2 ± 5.95	173–248, 205.9 ± 7.34
pR II	66–101, 85.6 ± 4.04[i]	48–78, 65.2 ± 2.90	73–110, 94.4 ± 4.39	73–104, 84.9 ± 2.95[i]
Leg III	315–517, 450.3 ± 20.13	413–598, 504.6 ± 16.80	385–539, 441.1 ± 14.71	393–502, 451.2 ± 12.54
Tarsus III	143–205, 181.9 ± 5.66	183–255, 213.0 ± 6.63	110–165, 124.3 ± 5.92	75–152, 125.1 ± 7.88
d III	57–99, 81.8 ± 3.53	87–117, 96.6 ± 3.23[h]	198–242, 212.5 ± 4.73	203–335, 253.6 ± 14.79[i]
f III	77–88, 83.8 ± 1.62	73–101, 86.2 ± 2.73	183–209, 196.0 ± 2.46	176–278, 213.8 ± 9.00
e III	35–48, 42.4 ± 1.34	27–41, 33.8 ± 1.50[i]	42–77, 56.0 ± 3.58[i]	32–80, 54.2 ± 5.44
w III	55–77, 70.8 ± 2.09	53–83, 65.7 ± 4.04[g]	79–121, 96.6 ± 3.87	88–145, 116.6 ± 5.32
r III	53–75, 62.4 ± 2.07	47–72, 62.4 ± 2.43	99–121, 103.9 ± 2.88[i]	103–184, 139.4 ± 7.49

Table 8. Continued

Variable	Homeomorphic males		Heteromorphic males	
	S. ochoai $n = 10$	*S. salasi* $n = 10$	*S. ochoai* $n = 10$	*S. salasi* $n = 10$
s III	Not measured	Not measured	29–42, 34.9 ± 1.33	33–46, 39.7 ± 1.79[i]
kT III	51–79, 69.0 ± 2.75	49–73, 62.8 ± 2.17	64–86, 73.4 ± 2.42	58–93, 76.3 ± 3.22
ϕ III	114–139, 124.5 ± 2.65	108–148, 125.3 ± 4.10	119–165, 140.1 ± 4.51	125–161, 143.9 ± 3.61
σ III	22–48, 38.7 ± 2.28	27–59, 42.3 ± 3.16[i]	44–59, 52.3 ± 1.36	44–60, 54.1 ± 1.40
nG III	44–66, 60.3 ± 1.97	45–62, 53.6 ± 1.67	48–66, 58.6 ± 1.79	51–83, 67.3 ± 2.96
cR III	59–110, 95.1 ± 5.22[i]	62–122, 95.5 ± 5.27	95–121, 110.2 ± 2.71	97–139, 122.4 ± 4.19
Leg IV	400–550, 501.8 ± 14.38	425–574, 508.4 ± 13.74	495–623, 567.6 ± 12.29	505–665, 592.7 ± 16.29
Tarsus IV	132–198, 175.1 ± 6.49	173–228, 202.4 ± 5.46	178–220, 200.4 ± 4.13	198–275, 236.8 ± 7.56
e IV	10–15, 12.3 ± 0.56	11–15, 13.3 ± 0.43	11–15, 12.5 ± 0.52[i]	12–16, 13.6 ± 0.42
d IV	10–15, 12.5 ± 0.50	12–16, 13.9 ± 0.35	11–15, 13.2 ± 0.54	11–17, 13.8 ± 0.55
ef	22–46, 33.0 ± 3.06	37–51, 43.9 ± 1.19	37–44, 43.0 ± 0.74[i]	34–56, 46.0 ± 2.60
cd	15–40, 24.4 ± 2.28	34–47, 39.4 ± 1.29	19–42, 27.0 ± 2.74[i]	30–51, 42.0 ± 2.07
ab	86–136, 118.8 ± 4.51	80–123, 99.7 ± 4.01	132–161, 148.5 ± 2.63	111–159, 128.2 ± 4.42
r IV	53–77, 65.9 ± 1.92	56–78, 67.4 ± 2.17	68–95, 81.4 ± 2.25	68–94, 79.7 ± 3.04
w IV	59–81, 72.4 ± 1.80	45–78, 63.0 ± 4.09[h]	68–92, 82.7 ± 2.28	55–88, 77.6 ± 3.45[i]
kT IV	54–73, 62.8 ± 2.03	46–64, 56.9 ± 2.15	55–77, 69.7 ± 2.38	51–82, 68.5 ± 2.89
ϕ IV	57–88, 71.3 ± 2.65	45–66, 54.6 ± 1.93	77–121, 85.8 ± 4.12	55–80, 65.8 ± 2.65
wF IV	62–111.3 ± 3.81	73–129, 104.5 ± 5.68	81–106, 93.7 ± 2.63	97–123, 112.3 ± 3.29

Superscript denotes number of measurements if <10 (a = 1, b = 2 . . . i = 9).

of sternal shield. Coxal setae *3b* and *4a* conoidal, usually with concentric peripheral pattern. Attachment organ typical for *Sancassania;* large, 2.1–2.5 (2.28 ± 0.021) times shorter than width of idiosoma, maximum ventro-genital shield width/attachment organ width 0.9–1.0 (0.94 ± 0.005), minimum ventro-genital shield width/attachment organ width 1.5–1.6 (1.56 ± 0.007); ps_1 and ps_2 large, diameter about half of ad_{1+2}; ps_2

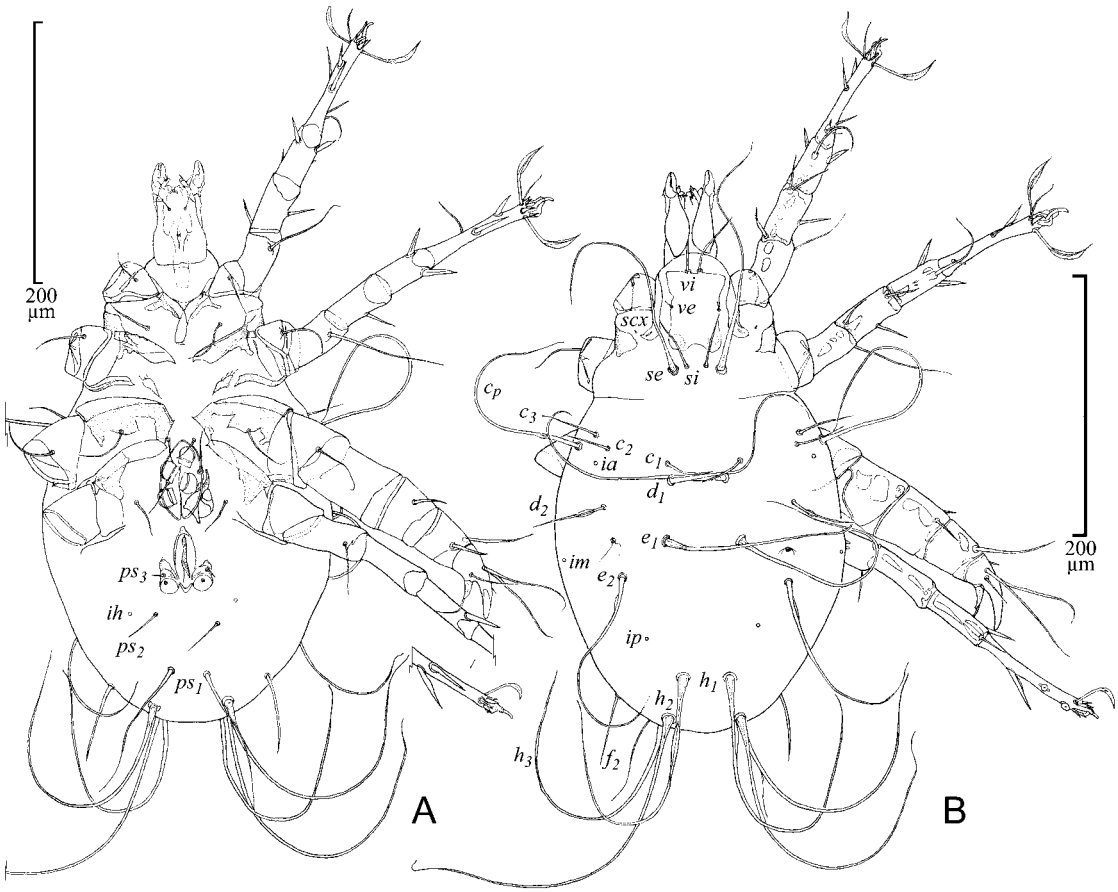

Fig. 8. *S. ochoai* sp. nov. (heteromorphic male, paratype). (A) Ventral view. (B) Dorsal view.

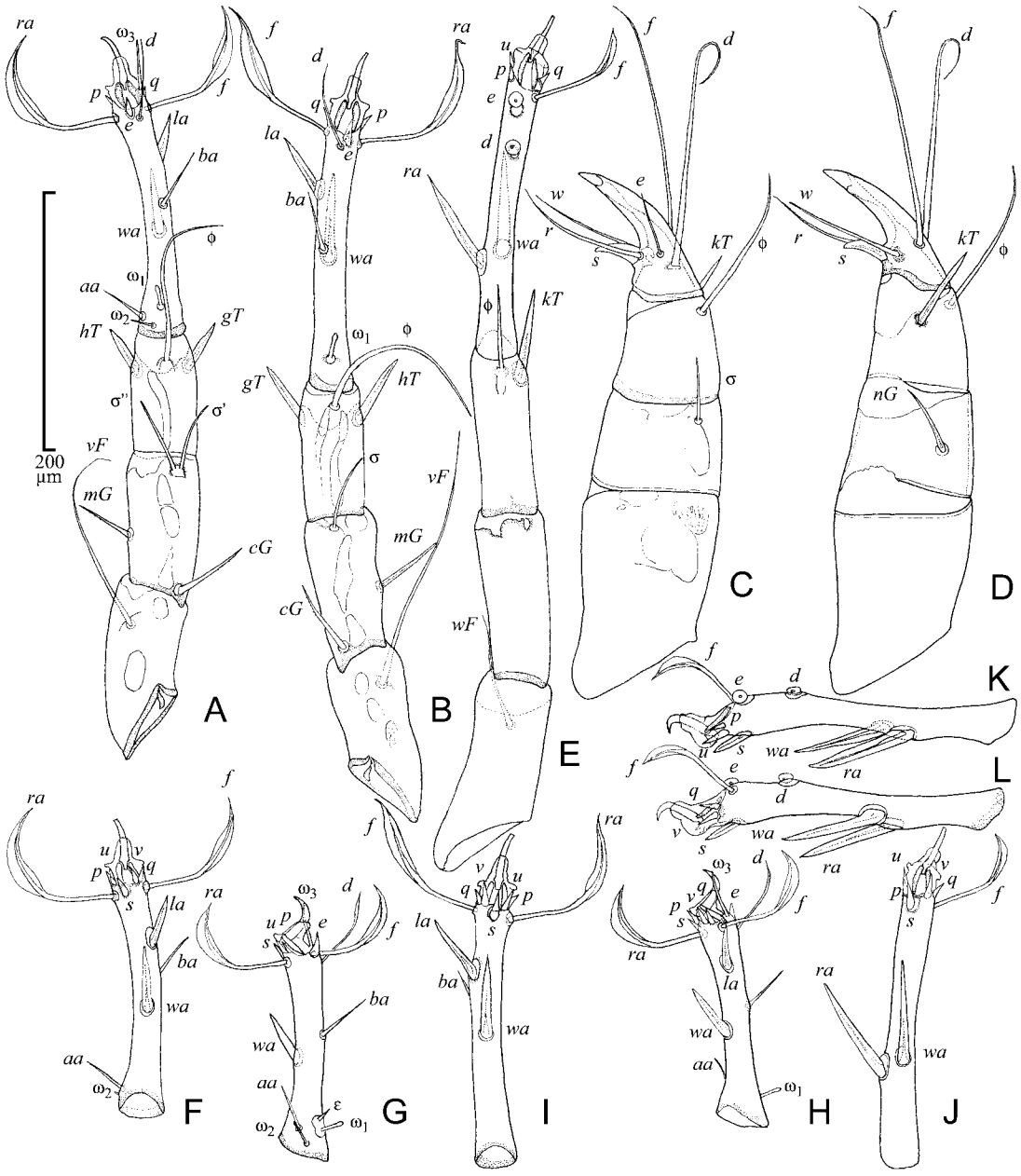

Fig. 9. *S. ochoai* sp. nov. (heteromorphic male, paratype). (A and B) Legs I-II, dorsal view. (C and D) Leg III, lateral view. (E) Leg IV, dorsal view. (F–H) Tarsus I. (I and J) Tarsi II, IV, ventral view. (K and L) Tarsus IV, lateral view.

placed approximately at level of ad_{1+2} center; peripheral cuticular suckers well-developed. Legs I-II protruding beyond edges of propodosoma to level of femora. Tarsi I-II comparatively long; tarsus I 2.7–4.1 (3.34 ± 0.062) and tarsus II 3.2–4.0 (3.45 ± 0.048) times longer than their respective width. Tarsal setae *aa* and solenidion ω_3 placed approximately at middle of tarsus I. Dorso-apical setae *d* on tarsi I-II not protruding beyond *e* I-II. Setae *la* I-II and *ra* I-II not shifted from *wa* I-II, distance *wa* I – *la* I/ diam-eter of *wa* I 0.1–0.8 (0.36 ± 0.045). Solenidion σ I comparatively long, distinctly extending beyond base of ω_1. Dorso-apical setae on tarsi III-IV comparatively short, usually ending near level of claw tip. Ventral tarsal seta *w* IV attenuated; *w* IV and *kT* IV smooth or rarely and weakly toothed.

Morphological Abnormalities. Deutonymph: bases of *SE* touching bases of *si* on one-half of propodosoma (#168). Homeomorphic male: proximal tarsal sucker *e* IV shifted to level of distal sucker (distance between them 6.2) on one tarsus.

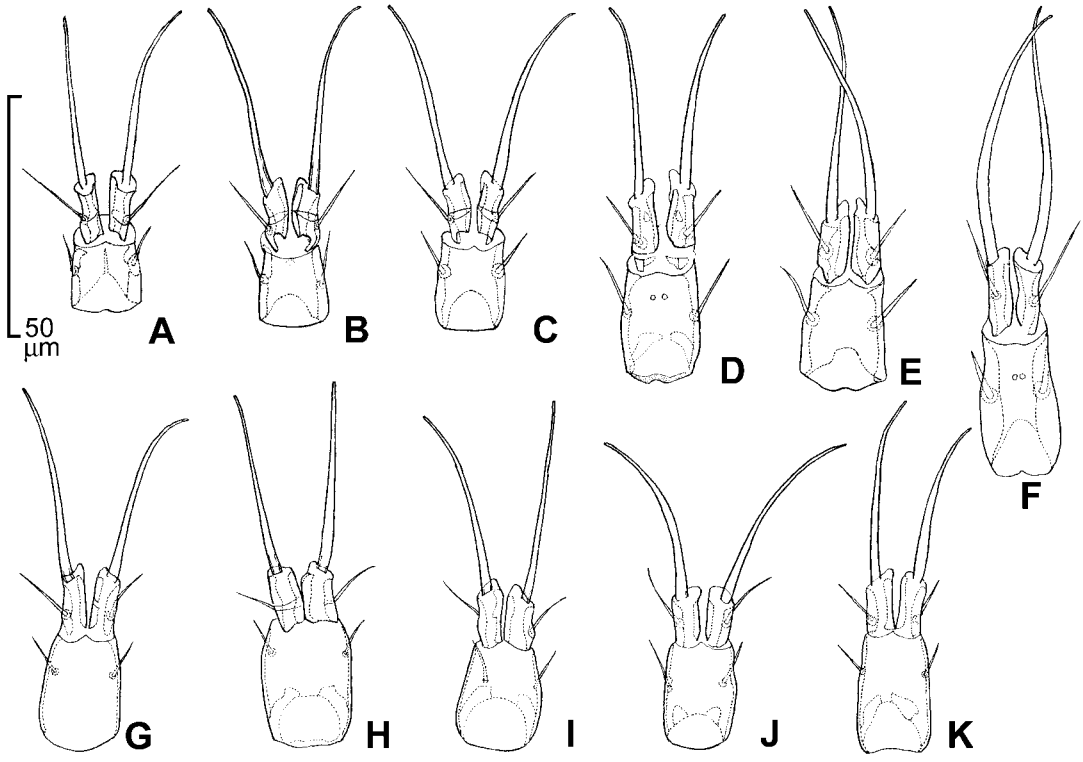

Fig. 10. Variability of gnathosoma in *S. salasi* sp. nov. (A–F) and *S. ochoai* sp. nov. (G–K). (A–C, G–K) From culture. (D–F) From beetle host.

Type Material. HOLOTYPE: female, COSTA RICA: Heredia Prov., Estacion Biologica La Selva nr. Sarapiquí, 10° 26′ N, 84° 01′ W, 29-IV-97, reared from deutonymph *ex Passalus spiniger* Bates (Coleoptera: Passalidae), R. Ochoa, mites cultured on *Botryotinia fuckeliana*, BMOC 97-0430-056. PARATYPES: 48 females, 28 homeo-, 17 heteromorphic males, three trito-, 86 deutonymphs, same data. Holotype in UMMZ, paratypes there and in USNM, INBio, ZISP, IRSNB, HNHM.

Etymology. The species is named for the collector, Dr. Ronald Ochoa.

Diagnosis. Most similar to *S. salasi* (see keys below for specific differences).

Sancassania salasi Klimov, Lekveishvili & OConnor, sp. nov.
(Figs. 3C–E, 10 A–F)

Females. (Figs. 3C–E; Table 7; measurements/ratios given for $n = 25$, unless otherwise noted). Idiosoma 740-1250 (943.2 ± 24.07). Internal vertical setae *vi* slightly barbed. Supracoxal setae *scx* short, spiniform. Setae *si* 1.0–2.5 (1.46 ± 0.08, $n = 21$) times longer than c_1. Distance *si-si* longer than length of *si*. Anteriodorsal hysterosomal setae c_1 and c_2 much shorter than other hysterosomal setae, their tips not reaching bases of next setae. Setae d_1 2.0–7.1 (3.25 ± 0.258, $n = 20$) times longer than c_1 and 1.8–3.2 (2.50 ± 0.076, $n = 20$) times shorter than e_1. Setae d_1 and e_1 usually not reaching bases of next setae (e_1 and h_1, respectively) in ovigerous females. Setae e_1 4.6–7.6 (5.58 ± 0.202, $n = 22$) times shorter than idiosoma. Posterio-dorsal hysterosomal setae h_1 longer than e_1, smooth, with attenuate tips. Adanal setae ad_1 posterior to ps_1. Duct of spermatheca short, 20–39 (31.4 ± 3.01, $n = 7$), constricted at spermatheca (Fig. 3C–E), width at external opening 4–19 (11.2 ± 1.89, $n = 7$), width at spermatheca 2–5 (3.1 ± 0.34, $n = 7$). Legs and tarsi comparatively long; legs I 2.3–3.8 (2.73 ± 0.072) shorter than idiosoma, tarsus I 2.9–3.5 (3.11 ± 0.035) shorter than leg I. Tarsal setae *aa* setiform, normally slightly anterior to solenidion ω_2. Tarsal setae *ba* I-II setiform, paramedial. Ratio e_1/hT I 5.1–8.2 (6.78 ± 0.159, $n = 22$), e_1/aa 5.2–8.2 (6.61 ± 0.182, $n = 20$).

Homeomorphic Male. (Table 8; measurements/ratios given for $n = 10$). Idiosoma 617–944 (803.9 ± 27.66). Supracoxal seta short, spiniform. Setae *si* shorter or longer than c_1, ratio si/c_1 0.6–1.2 (0.74 ± 0.059). Distance *si-si* shorter than length of setae *si*. Idiosomal setae long, with inflated bases. Setae d_1 very long, 223–388 (303.7 ± 18.340), 2.2–3.2 (2.69 ± 0.110) times shorter than idiosoma, 2.5–5.4 (3.15 ± 0.277) times longer than c_1, 1.4–1.7 (1.55 ± 0.048) times shorter than e_1, reaching transverse level of cupules *ip*.

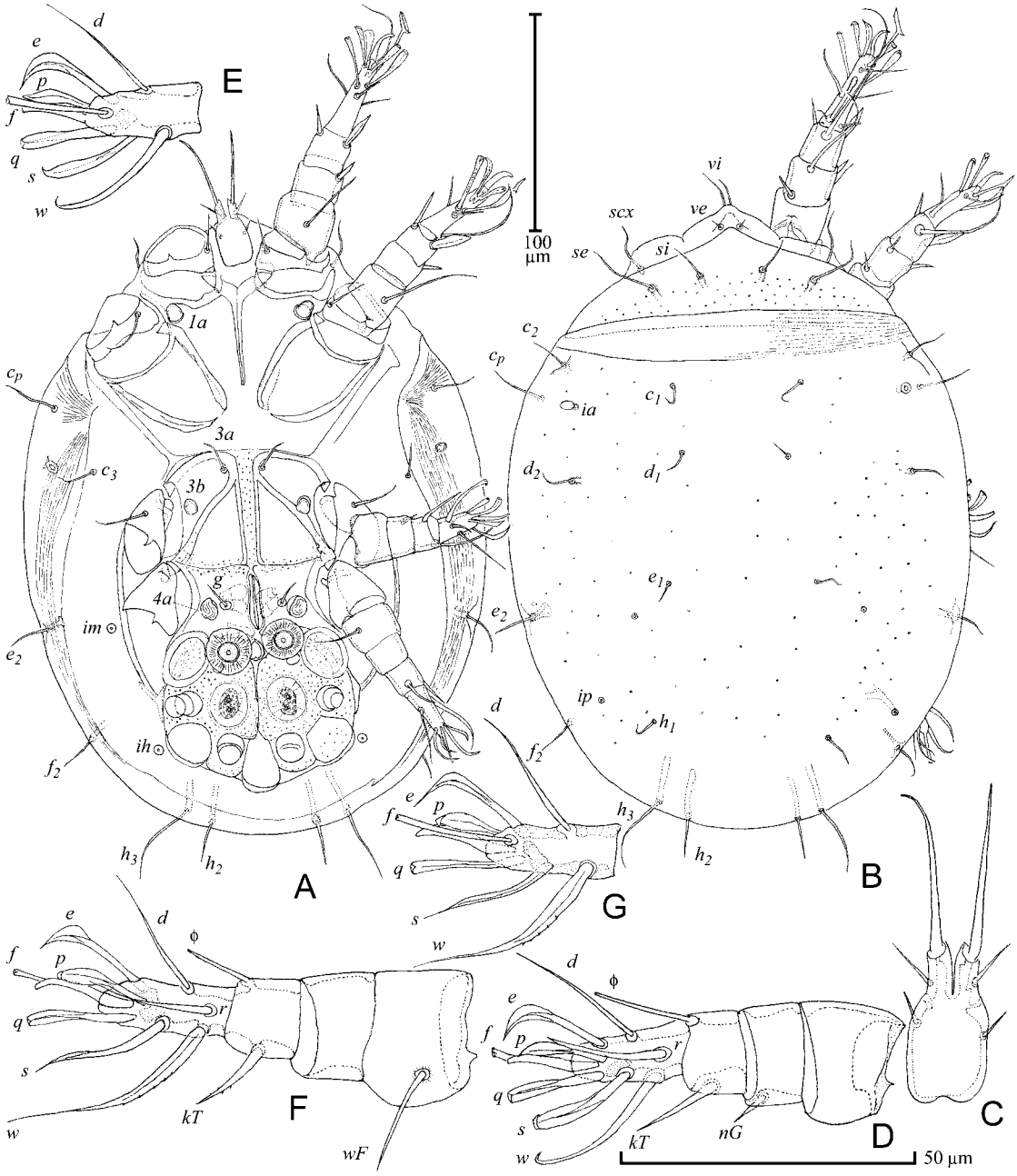

Fig. 11. *S. ochoai* sp. nov. (deutonymph, paratype). (A) Ventral view. (B) Dorsal view. (C) Gnathosoma. (D and F) Legs III-IV. (E and G) Tarsi III-IV. Bars, A and B, 100 μm; C–G, 50 μm.

Setae e_1 1.5–2.1 (1.74 ± 0.05) times shorter than idiosoma. Setae e_1 and e_2 protruding beyond posterior end of hysterosoma. Setae h_1 nearly as long as h_2 and h_3. Pseudanal setae ps_1 long, 151–314 (222.8 ± 13.66), setiform, with attenuated tips. Setae ps_2 53–134 (80.2 ± 8.03), shifted posteriorly from anus by 51–133 (92.3 ± 7.13), reaching ps_1 bases (sometimes not reaching), with obtuse tips (sometimes attenuated). Distance ps_1-ps_2 28–61 (51.4 ± 2.85). Aedeagus elongated, with free end bent upward. Position of leg I-III elements similar to female. Legs I 1.7–2.1 (1.83 ± 0.038) times shorter than idiosoma; tarsus I 2.3–2.6 (2.48 ± 0.021) times shorter than leg I. Distal tarsal sucker *e* IV placed on apex of tarsus. Distances between suckers and ends of tarsus IV given in Table 8.

Heteromorphic Males. (Table 8; measurements/ratios given for $n = 10$, unless otherwise noted). Idiosoma 794-1006 (904.7 ± 24.28). Supracoxal seta short,

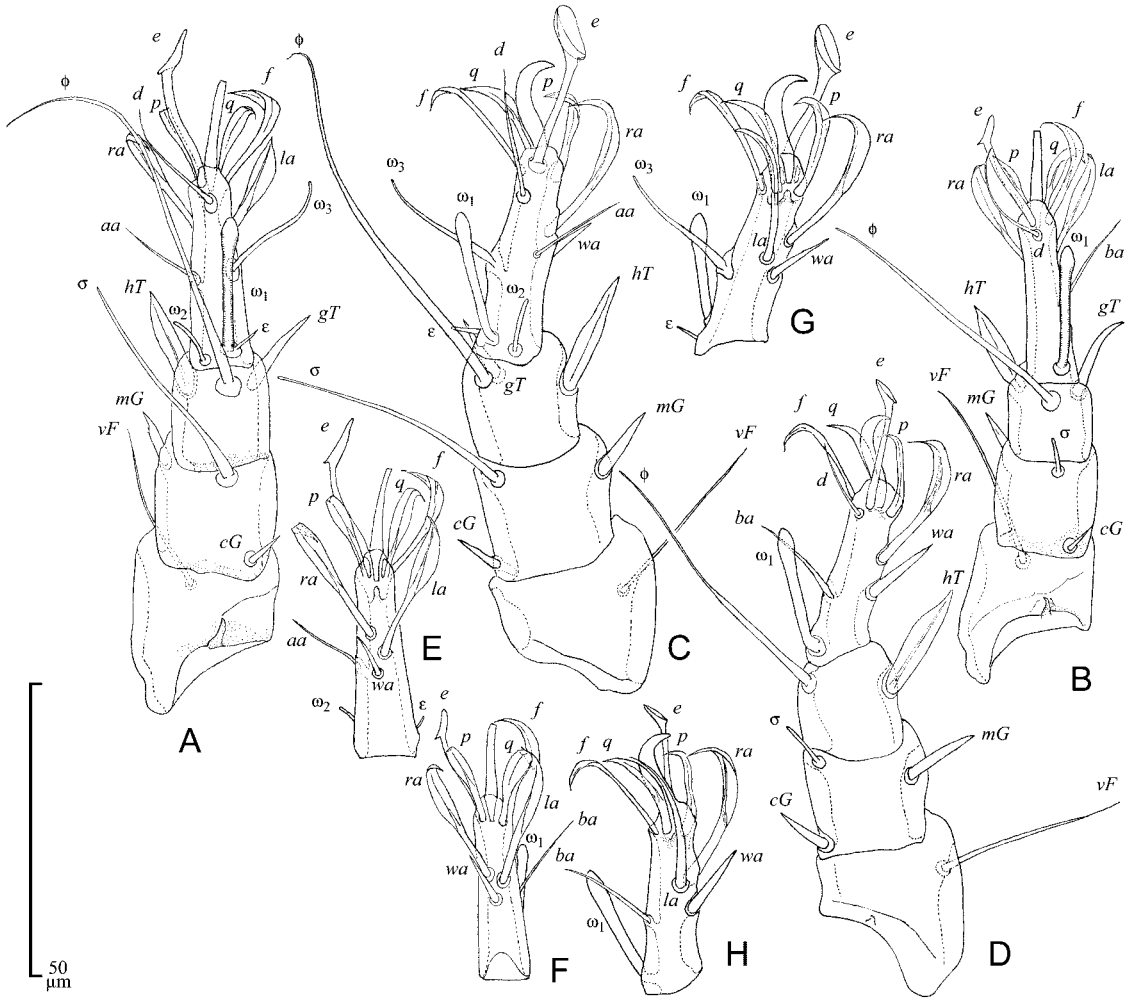

Fig. 12. *S. ochoai* sp. nov. (deutonymph, paratype). (A and B) Legs I-II, dorsal view. (C and D) Legs I-II, lateral view. (E and F) Tarsi I-II, ventral view. (G and H) Tarsi I-II, lateral view.

spiniform. Ratio si/c_1 0.5–1.4 (0.73 ± 0.08). Distance *si-si* shorter than length of setae *si*. Idiosomal setae long with inflated bases. Setae d_1 very long, 292–426 (379.2 ± 14.42), 2.1–2.7 (2.43 ± 0.076) times shorter than idiosoma, 2.2–3.2 (2.79 ± 0.107) longer than c_1, 1.3–1.5 (1.39 ± 0.021, $n = 9$) times shorter than e_1, reaching transverse level of cupules *ip*. Setae e_1 1.5–2.0 (1.76 ± 0.052) times shorter than idiosoma. Setae e_1 and e_2 protruding beyond posterior end of hysterosoma. Setae h_1 nearly as long as h_2 and h_3. Pseudanal setae ps_1 long, 206–306 (251.9 ± 11.02, $n = 9$), setiform, with attenuated tips. Setae ps_2 58–137 (88.7 ± 7.15), shifted posteriorly from anus by 70–117 (90.2 ± 4.33), usually reaching ps_1 bases, with obtuse (rarely attenuated) tips. Distance ps_1-ps_2 47–75 (57.0 ± 2.53). Aedeagus elongated, with free end bent upward. Position of leg I-II and IV elements similar to homeomorphic male, legs III typical for *Sancassania*. Legs I 1.6–1.9 (1.75 ± 0.033) times shorter than idiosoma; tarsus I 2.4–2.5 (2.47 ± 0.011) times shorter than leg I. Distances between suckers and ends of tarsus IV given in Table 8.

Deutonymph. (Fig. 10A–F; Table 9; measurements/ratios given for $n = 35$). Gnathosoma not protruding beyond anterior edge of propodosoma; its form variable (Fig. 10A–F); subcapitulum usually with straight (sometimes slightly convex), well-sclerotized sides; palpi comparatively long, 1.9–2.7 (2.22 ± 0.036) times shorter than length of subcapitulum. Posterior gnathosomal setae usually longer than in *S. ochoai*, 7.8–14.0 (10.68 ± 0.253), 1.3–2.7 (2.04 ± 0.056) times longer than *1a*. Idiosoma ovoid, 1.3–1.7 (1.43 ± 0.012) times longer than width, dorsal surface covered with small pores. Propodosoma 5.1–10.7 (7.14 ± 0.205) times shorter than hysterosoma; rostral projection broadly-angled, with *vi* at its apex; *si* distinctly shorter than *SE*, slightly shifted anteriorly (much less than length of *SE*). Dorsal hysterosomal setae short. Posterior edge of sternal shield touching anterior edge of ventro-genital shield, slightly concave. Sternal

Table 9. Measurements (range, mean ± SE) of 133 morphological structures of *S. ochoai* and *S. salasi* heteromorphic deutonymphs

Variable	*S. ochoai* (culture) $n = 25$	*S. salasi* (culture) $n = 25$	*S. salasi* (ex beetles) $n = 10$	*S. salasi* (combined) $n = 35$
Idiosoma, length	234–325, 286.3 ± 4.59	221–391, 301.2 ± 8.13	275–373, 333.0 ± 7.92	221–391, 310.3 ± 6.65
Idiosoma, wt	165–234, 198.0 ± 3.44	161–264, 211.9 ± 5.39	193–259, 232.0 ± 6.07	161–264, 217.7 ± 4.46
Propodosoma	34–50, 40.4 ± 0.77	29–50, 36.8 ± 1.07	31–55, 43.7 ± 2.44	29–55, 38.8 ± 1.15
Hysterosoma	190–277, 245.9 ± 4.45	192–349, 264.4 ± 7.62	243–321, 289.3 ± 6.72	192–349, 271.5 ± 6.03
Length of gnathosoma	25–36, 30.3 ± 0.57	18–36, 25.7 ± 0.79	28–40, 33.2 ± 1.11	18–40, 27.8 ± 0.86
Wt of gnathosoma, base	11–18, 15.0 ± 0.31	10–16, 11.8 ± 0.32	11–16, 13.3 ± 0.39	10–16, 12.2 ± 0.28
Wt of gnathosoma, apex	8–11, 9.1 ± 0.15	8–11, 9.8 ± 0.20	9–11, 9.8 ± 0.27	8–11, 9.8 ± 0.16
Distal palpomar	9–14, 11.7 ± 0.21	9–16, 11.9 ± 0.32	12–17, 14.0 ± 0.49	9–17, 12.5 ± 0.31
Posterior gnathosomal setae	5–8, 7.1 ± 0.15	8–14, 10.5 ± 0.29	8–14, 11.0 ± 0.52	8–14, 10.7 ± 0.25
Anterior gnathosomal seta	8–13, 10.9 ± 0.28	10–20, 14.9 ± 0.49	12–19, 15.5 ± 0.53	10–20, 15.1 ± 0.38
Gnathosomal solenidion	31–39, 34.1 ± 0.34	27–43, 34.2 ± 0.76	33–44, 37.2 ± 0.99	27–44, 35.0 ± 0.65
Sternal shield length	62–84, 75.2 ± 1.13	58–108, 80.4 ± 2.26	70–98, 87.2 ± 2.59	58–108, 82.3 ± 1.83
Sternal shield wt, max	105–136, 122.4 ± 1.66	103–162, 131.1 ± 2.93	115–150, 137.4 ± 3.11	103–162, 132.9 ± 2.30
Ventral shield length, max	78–103, 90.9 ± 1.25	74–126, 100.9 ± 2.64	88–110, 101.1 ± 2.20	74–126, 100.9 ± 1.97
Ventral shield length, up ovipositor	69–98, 85.8 ± 1.48	70–119, 92.5 ± 2.29	81–109, 95.7 ± 2.50	70–119, 93.4 ± 1.78
Ventral shield wt, max	66–94, 81.4 ± 1.42	68–116, 89.1 ± 2.27	81–106, 96.9 ± 2.38	68–116, 91.3 ± 1.84
Ventral shield wt, min	48–62, 55.6 ± 0.81	50–78, 61.5 ± 1.41	54–73, 68.1 ± 1.76	50–78, 63.4 ± 1.23
Ventral shield wt, posterior	69–95, 80.2 ± 1.15	65–106, 83.2 ± 2.08	74–99, 91.4 ± 2.31	65–106, 85.5 ± 1.73
vi	15–23, 18.9 ± 0.52^{x}	14–23, 19.2 ± 0.53	20–28, 24.3 ± 0.89	14–28, 20.7 ± 0.60
ve	3–9, 5.7 ± 0.37^{s}	4–9, 5.5 ± 0.24	7–10, 8.5 ± 0.30	4–10, 6.4 ± 0.30
si	9–21, 13.8 ± 0.62^{w}	8–11, 9.0 ± 0.27^{r}	8–16, 11.9 ± 0.94	8–16, 10.0 ± 0.46^{ab}
se	16–32, 23.3 ± 0.92^{x}	17–27, 22.3 ± 0.69^{v}	22–28, 25.6 ± 0.63	17–28, 23.3 ± 0.58^{af}
scx	22–27, 24.2 ± 0.29^{u}	21–33, 25.9 ± 0.58^{x}	23–29, 26.2 ± 0.72^{h}	21–33, 26.0 ± 0.47^{af}
c_1	9–13, 10.5 ± 0.25^{w}	7–9, 8.2 ± 0.14^{r}	5–16, 9.5 ± 1.43^{f}	5–16, 8.5 ± 0.37^{x}
c_2	9–20, 15.1 ± 0.57	9–24, 14.0 ± 0.77	8–17, 12.8 ± 0.94	8–24, 13.7 ± 0.61
c_3	10–17, 13.9 ± 0.35	12–28, 20.2 ± 0.93^{u}	16–22, 19.2 ± 1.04^{f}	12–28, 20.0 ± 0.75^{aa}
c_p	19–28, 24.3 ± 0.48	16–36, 26.4 ± 0.99^{x}	20–36, 25.3 ± 1.68^{h}	16–36, 26.1 ± 0.84^{af}
d_1	6–12, 10.0 ± 0.35^{v}	5–13, 9.1 ± 0.48^{u}	6–12, 8.7 ± 0.86^{f}	5–13, 9.0 ± 0.42^{aa}
d_2	9–17, 12.4 ± 0.39^{w}	5–12, 9.0 ± 0.47^{u}	6–12, 8.8 ± 0.64^{h}	5–12, 8.9 ± 0.38^{ac}
e_1	8–14, 10.7 ± 0.31^{w}	5–12, 8.4 ± 0.65^{n}	6–11, 9.5 ± 1.64^{c}	5–12, 8.6 ± 0.59^{q}
e_2	14–23, 17.6 ± 0.48	11–23, 14.6 ± 0.67^{x}	11–20, 14.8 ± 0.94	11–23, 14.6 ± 0.54^{ah}
f_2	10–20, 14.6 ± 0.47	9–21, 14.0 ± 0.78^{r}	8–17, 11.4 ± 1.07^{h}	8–21, 13.2 ± 0.67^{z}
h_1	8–17, 11.5 ± 0.50^{x}	8–13, 9.6 ± 0.34^{x}	9–16, 11.4 ± 0.83^{i}	8–16, 10.1 ± 0.36^{ag}
h_2	12–18, 15.5 ± 0.28	11–21, 15.1 ± 0.54	11–22, 16.1 ± 0.98	11–22, 15.4 ± 0.47
h_3	28–41, 32.8 ± 0.66^{u}	34–75, 52.2 ± 1.93	39–64, 50.5 ± 3.34^{g}	34–75, 51.8 ± 1.66^{af}
1a	7–9, 7.4 ± 0.11	4–7, 5.2 ± 0.19	5–6, 5.7 ± 0.16	4–7, 5.3 ± 0.15
3a	13–18, 15.7 ± 0.26	9–25, 16.1 ± 0.85^{v}	13–20, 17.3 ± 0.81^{h}	9–25, 16.4 ± 0.66^{ad}
3b	6–8, 6.7 ± 0.11	4–9, 6.3 ± 0.25	5–9, 6.9 ± 0.35	4–9, 6.4 ± 0.21
4a	6–9, 8.0 ± 0.16	6–11, 8.3 ± 0.23	8–11, 9.3 ± 0.30	6–11, 8.6 ± 0.20
g	10–14, 12.3 ± 0.19	9–20, 13.4 ± 0.70^{v}	11–21, 16.1 ± 1.08^{i}	9–21, 14.2 ± 0.62^{ae}
Sternum	40–51, 46.4 ± 0.64	39–75, 56.2 ± 1.74	47–67, 58.1 ± 1.90	39–75, 56.7 ± 1.35
DS1	8–16, 11.7 ± 0.38	8–19, 12.9 ± 0.60	10–16, 12.7 ± 0.48	8–19, 12.9 ± 0.45
Ventrum (only sclerotized part)	19–31, 25.5 ± 0.76	24–44, 32.4 ± 1.09^{x}	31–34, 32.7 ± 0.48^{h}	24–44, 32.4 ± 0.82^{af}
Length of attachment organ*	57–78, 69.6 ± 1.10	52–90, 69.5 ± 1.97	62–94, 79.3 ± 2.67	52–94, 72.3 ± 1.75
Wt of attachment organ	75–100, 86.9 ± 1.30	66–119, 90.1 ± 2.39	78–123, 102.5 ± 3.74	66–123, 93.6 ± 2.21
DS2	16–25, 19.1 ± 0.44	14–37, 22.1 ± 1	23–47, 30.8 ± 2.14	14–47, 24.6 ± 1.14
Anterior sucker (ad_3)	16–23, 19.3 ± 0.30	16–26, 19.4 ± 0.52	18–25, 22.1 ± 0.74	16–26, 20.2 ± 0.47
Median sucker ($ad_1 + ad_2$)	16–23, 20.0 ± 0.39	16–31, 22.6 ± 0.82	20–29, 26.2 ± 0.85	16–31, 23.6 ± 0.69
Anterior lateral sucker (ps_2)	9–12, 11.1 ± 0.15	8–17, 12.2 ± 0.42	12–16, 14.6 ± 0.45	8–17, 12.9 ± 0.37
Posterior lateral sucker (ps_1)	9–13, 11.2 ± 0.17	9–14, 11.6 ± 0.27	11–16, 14.1 ± 0.45	9–16, 12.3 ± 0.30
Anterior cuticular sucker	20–29, 24.2 ± 0.40	19–35, 25.9 ± 0.78	20–36, 28.2 ± 1.49	19–36, 26.5 ± 0.71
Posterior cuticular sucker	19–29, 24.2 ± 0.48	19–33, 24.9 ± 0.75	20–34, 28.3 ± 1.28	19–34, 25.9 ± 0.69
Posterior unpaired cuticular sucker	19–28, 24.0 ± 0.47	20–35, 25.9 ± 0.78	19–33, 27.8 ± 1.41	19–35, 26.4 ± 0.70
Leg I	85–109, 96.0 ± 1.11	73–120, 94.7 ± 2.14	86–125, 105.1 ± 3.17	73–125, 97.7 ± 1.93
Tarsus I	31–41, 36.1 ± 0.55	27–44, 35.1 ± 0.78	31–45, 38.0 ± 1.17	27–45, 35.9 ± 0.68
Empodium I	16–22, 18.7 ± 0.29	15–25, 19.4 ± 0.50	19–22, 20.5 ± 0.44	15–25, 19.7 ± 0.38
Diam of tarsus I near base	9–12, 10.9 ± 0.19	9–14, 11.3 ± 0.26	10–14, 12.4 ± 0.33	9–14, 11.6 ± 0.22
ω_1 I	19–27, 22.5 ± 0.40	19–28, 23.1 ± 0.45	23–28, 26.0 ± 0.46	19–28, 23.9 ± 0.41
ω_2 I	8–15, 9.5 ± 0.31	8–13, 10.2 ± 0.24	9–12, 10.9 ± 0.26	8–13, 10.4 ± 0.19
ω_3 I	16–32, 21.8 ± 0.73	19–30, 22.7 ± 0.64	21–29, 25.1 ± 0.88	19–30, 23.4 ± 0.55
Famulus	4–8, 6.1 ± 0.36^{o}	5–8, 6.6 ± 0.25^{u}	6–9, 7.3 ± 0.27^{i}	5–9, 6.8 ± 0.20^{ad}
d I	16–28, 21.6 ± 0.72^{t}	14–34, 23.3 ± 1^{x}	21–27, 23.7 ± 0.76^{i}	14–34, 23.5 ± 0.75^{ag}
e I	27–36, 30.8 ± 0.51	27–40, 32.5 ± 0.65	29–37, 34.1 ± 0.86	27–40, 33.0 ± 0.53
f I	22–30, 24.9 ± 0.39	22–34, 26.4 ± 0.48^{x}	27–33, 30.2 ± 0.77	22–34, 27.5 ± 0.50^{ah}
ra I	26–36, 30.0 ± 0.62	23–41, 31.4 ± 0.85	27–37, 32.0 ± 1.15	23–41, 31.6 ± 0.68
la I	22–33, 27.6 ± 0.47^{w}	24–39, 29.5 ± 0.91	28–34, 30.9 ± 0.69	24–39, 29.9 ± 0.68
aa I	13–17, 15.5 ± 0.13	11–26, 16.7 ± 0.80^{x}	14–19, 16.4 ± 0.77^{f}	11–26, 16.6 ± 0.65^{ad}
wa I	9–15, 11.7 ± 0.32^{t}	9–16, 12.7 ± 0.45^{g}	10–14, 12.0 ± 0.42^{h}	9–16, 12.5 ± 0.34^{aa}
Diam of *wa* I	2–4, 2.8 ± 0.08	2–4, 3.0 ± 0.05	2–3, 2.9 ± 0.11	2–4, 2.9 ± 0.05
q I	16–23, 19.0 ± 0.39	18–28, 21.9 ± 0.52	16–27, 22.7 ± 1.18	16–28, 22.1 ± 0.49
p I	16–25, 19.7 ± 0.36	19–30, 23.2 ± 0.60	22–31, 26.3 ± 1.01^{i}	19–31, 24.0 ± 0.56^{ah}

Table 9. Continued

Variable	*S. ochoai* (culture) $n = 25$	*S. salasi* (culture) $n = 25$	*S. salasi* (ex beetles) $n = 10$	*S. salasi* (combined) $n = 35$
gT I	13–18, 15.5 ± 0.21	11–20, 15.3 ± 0.46	13–19, 16.8 ± 0.52	11–20, 15.7 ± 0.38
hT I	17–23, 20.2 ± 0.32	16–34, 23.6 ± 0.70	21–27, 24.6 ± 0.56	16–34, 23.9 ± 0.53
ϕ II	62–87, 70.7 ± 1.27	59–98, 79.7 ± 2.56[t]	67–95, 81.3 ± 2.50	59–98, 80.2 ± 1.88[ad]
mG I	11–16, 13.7 ± 0.36	12–21, 15.0 ± 0.38	13–16, 15.3 ± 0.34	12–21, 15.1 ± 0.28
cG I	8–11, 9.0 ± 0.23[t]	8–13, 9.9 ± 0.24	8–12, 10.2 ± 0.40	8–13, 10.0 ± 0.20
σ I	27–43, 34.9 ± 0.79[w]	27–48, 39.3 ± 1.51[n]	25–47, 38.7 ± 2.62[h]	25–48, 39.1 ± 1.32[v]
vF I	25–37, 31.6 ± 0.66[x]	28–51, 40.5 ± 1.21[x]	36–47, 41.3 ± 1.31	28–51, 40.7 ± 0.93[ah]
pR I	14–21, 17.5 ± 0.45[g]	17–31, 21.5 ± 0.80[r]	17–27, 22.9 ± 0.97	17–31, 22.0 ± 0.62[ab]
Leg II	75–105, 87.6 ± 1.45	66–111, 86.6 ± 2.02	76–114, 96.3 ± 3.10	66–114, 89.3 ± 1.83
Tarsus II	28–37, 32.9 ± 0.47	23–41, 31.1 ± 0.73	28–41, 34.1 ± 1.15	23–41, 32.0 ± 0.65
Empodium II	14–20, 16.5 ± 0.28	13–23, 18.2 ± 0.47	17–23, 19.2 ± 0.55	13–23, 18.5 ± 0.38
Diam of tarsus II near base	8–11, 9.6 ± 0.17	8–13, 10.5 ± 0.24	9–12, 11.0 ± 0.22	8–13, 10.7 ± 0.19
ω_1 II	18–26, 22.4 ± 0.36	20–29, 23.6 ± 0.42[x]	23–28, 26.2 ± 0.48	20–29, 24.3 ± 0.38[ah]
ba	16–22, 18.5 ± 0.39	18–31, 25.2 ± 0.64	23–30, 25.8 ± 0.81	18–31, 25.4 ± 0.51
ba II-tarsus II base	9–17, 13.1 ± 0.35	6–12, 8.4 ± 0.27	8–16, 10.5 ± 0.83	6–16, 9.0 ± 0.34
d II	16–20, 17.8 ± 0.51[j]	18–28, 23.2 ± 0.84[o]	20–27, 23.5 ± 0.88[g]	18–28, 23.3 ± 0.63[v]
e II	18–29, 23.4 ± 0.49	22–33, 26.9 ± 0.61	23–32, 27.8 ± 0.95	22–33, 27.2 ± 0.51
f II	19–27, 23.3 ± 0.43	22–33, 26.2 ± 0.59	23–31, 26.5 ± 0.73	22–33, 26.3 ± 0.46
ra II	24–36, 29.4 ± 0.64	23–37, 28.4 ± 0.75	27–36, 30.3 ± 1.06	23–37, 28.9 ± 0.62
la II	22–30, 26.9 ± 0.60[p]	20–36, 28.0 ± 0.76	23–32, 27.6 ± 0.97[i]	20–36, 27.9 ± 0.61[ah]
wa II	11–16, 13.5 ± 0.27[x]	9–16, 12.8 ± 0.33[w]	10–16, 12.4 ± 0.54	9–16, 12.7 ± 0.26[ag]
Diam of *wa* II	2–3, 2.4 ± 0.06	2–3, 2.8 ± 0.07	2–4, 2.9 ± 0.19	2–4, 2.8 ± 0.07
q II	15–21, 18.1 ± 0.36[x]	14–29, 21.0 ± 0.67	19–29, 22.5 ± 1.28	14–29, 21.4 ± 0.60
p II	12–20, 16.3 ± 0.34	17–27, 21.6 ± 0.51	18–28, 24.2 ± 0.97	17–28, 22.4 ± 0.49
gT II	13–20, 16.0 ± 0.28	12–22, 16.0 ± 0.46	16–21, 18.0 ± 0.53	12–22, 16.5 ± 0.39
hT II	16–23, 20.5 ± 0.36	16–31, 22.1 ± 0.78[w]	19–27, 23.8 ± 0.84	16–31, 22.6 ± 0.61[ag]
ϕ II	39–55, 47.5 ± 0.79[x]	45–62, 52.8 ± 1.15[v]	47–66, 56.4 ± 2.18	45–66, 53.9 ± 1.08[af]
mG II	10–16, 12.3 ± 0.35	11–20, 13.5 ± 0.47	12–16, 14.1 ± 0.44	11–20, 13.7 ± 0.36
cG II	7–12, 9.2 ± 0.24	8–14, 10.2 ± 0.30	9–13, 11.1 ± 0.40	8–14, 10.4 ± 0.25
σ II	8–15, 10.8 ± 0.42[u]	7–12, 9.4 ± 0.23[w]	8–10, 9.3 ± 0.27	7–12, 9.4 ± 0.18[ag]
vF II	31–50, 37.1 ± 0.91	33–64, 44.5 ± 1.40	36–56, 46.4 ± 2.11	33–64, 45.0 ± 1.16
pR II	14–23, 18.1 ± 0.42[x]	16–27, 21.6 ± 0.84[o]	23–30, 26.0 ± 1[g]	16–30, 23.0 ± 0.78[v]
Leg III	52–68, 59.3 ± 0.79	50–89, 67.6 ± 1.79	56–79, 72.9 ± 2.08	50–89, 69.1 ± 1.45
Tarsus III	19–25, 22.1 ± 0.32	19–34, 25.1 ± 0.67	23–31, 27.7 ± 0.70	19–34, 25.9 ± 0.55
Empodium III	15–19, 16.5 ± 0.22	15–26, 19.2 ± 0.56	16–22, 19.4 ± 0.62	15–26, 19.3 ± 0.43
d III	16–28, 22.1 ± 0.59[w]	25–44, 33.1 ± 0.95	27–39, 30.7 ± 1.78[h]	25–44, 32.5 ± 0.64[ag]
e III	19–25, 23.0 ± 0.41[w]	23–35, 27.3 ± 0.57	25–32, 28.9 ± 0.72	23–35, 27.7 ± 0.47
f III	19–27, 22.7 ± 0.47[x]	25–38, 30.7 ± 0.65	27–40, 32.5 ± 1.36[i]	25–40, 31.2 ± 0.60[ah]
s III	18–23, 19.7 ± 0.30[w]	17–31, 22.8 ± 0.74[x]	20–28, 24.4 ± 1.03[f]	17–31, 23.1 ± 0.63[ad]
p III	13–16, 15.0 ± 0.24[v]	14–27, 18.9 ± 0.64[w]	19–25, 21.8 ± 0.84[i]	14–27, 19.7 ± 0.56[af]
q III	16–23, 19.8 ± 0.38[w]	19–33, 25.3 ± 0.57	21–30, 26.9 ± 0.92[i]	19–33, 25.7 ± 0.49[ah]
w III	27–34, 30.6 ± 0.44[x]	22–45, 34.0 ± 1.01	31–44, 37.9 ± 1.34	22–45, 35.1 ± 0.86
r III	9–20, 13.0 ± 0.72[v]	19–34, 25.6 ± 0.82[v]	20–32, 26.9 ± 1.13	19–34, 26.0 ± 0.66[af]
kT III	16–23, 18.9 ± 0.31	18–32, 23.7 ± 0.67	19–28, 24.6 ± 0.91	18–32, 24.0 ± 0.54
ϕ III	16–25, 20.8 ± 0.55[v]	20–39, 28.1 ± 0.85	24–32, 27.9 ± 1.14[h]	20–39, 28.0 ± 0.70[ag]
nG III	7–11, 8.2 ± 0.18	9–16, 11.7 ± 0.43	10–13, 12.0 ± 0.47	9–16, 11.8 ± 0.33
cR III	16–27, 20.8 ± 0.66[x]	20–44, 28.5 ± 1.14[v]	28–35, 30.7 ± 0.90[h]	20–44, 29.1 ± 0.88[ad]
Leg IV	59–78, 67.9 ± 1.05	58–97, 75.5 ± 1.93	67–89, 83.9 ± 2.17	58–97, 77.9 ± 1.63
Tarsus IV	21–29, 24.5 ± 0.38	21–39, 28.9 ± 0.82	26–34, 31.9 ± 0.82	21–39, 29.7 ± 0.67
Empodium IV	16–20, 17.3 ± 0.22	16–29, 21.4 ± 0.67	18–24, 21.5 ± 0.65	16–29, 21.4 ± 0.51
d IV	16–28, 22.5 ± 0.63[w]	23–51, 35.5 ± 1.29	25–39, 32.5 ± 1.56	23–51, 34.6 ± 1.04
e IV	20–28, 23.4 ± 0.42	24–35, 30.1 ± 0.61	27–36, 31.6 ± 1.12	24–36, 30.5 ± 0.55
f IV	23–30, 25.5 ± 0.46[w]	24–44, 34.7 ± 0.90	33–42, 37.7 ± 1.12	24–44, 35.6 ± 0.74
s IV	21–28, 24.9 ± 0.44[t]	23–36, 28.9 ± 0.79[u]	24–34, 29.3 ± 1.04[i]	23–36, 29.0 ± 0.63[ad]
p IV	15–21, 17.6 ± 0.44[r]	16–33, 20.3 ± 0.70[x]	19–25, 21.7 ± 0.86	16–33, 20.7 ± 0.56[ah]
q IV	19–27, 22.0 ± 0.47	20–34, 27.3 ± 0.73	26–34, 29.6 ± 0.89	20–34, 27.9 ± 0.60
r IV	11–19, 14.5 ± 0.41[x]	11–24, 16.8 ± 0.69[w]	16–20, 18.5 ± 0.51	11–24, 17.3 ± 0.52[ag]
w IV	33–47, 40.3 ± 0.77	35–65, 47.1 ± 1.31	41–62, 50.2 ± 2.13	35–65, 48.0 ± 1.13
kT IV	16–23, 19.3 ± 0.32	14–30, 22.4 ± 0.74	20–32, 25.3 ± 1.18	14–32, 23.2 ± 0.66
ϕ IV	10–16, 13.4 ± 0.35[x]	12–22, 15.7 ± 0.55	12–17, 14.9 ± 0.57	12–22, 15.5 ± 0.42
wF IV	17–25, 20.1 ± 0.39[w]	20–41, 28.5 ± 1.15[s]	28–37, 32.7 ± 0.80	20–41, 29.9 ± 0.88[ac]

Superscript denotes number of measurements if less than value indicated in the first row (a = 1, b = 2, ... ah = 34).

[a] From ovipositor to posterior edge DS1, distance end of sternum-end of apodemes II, DS2, distance attachment organ-posterior edge of body.

apodeme not reaching posterior ends of apodemes II. Conoids *1a* comparatively small, 3.7–7.5 (5.33 ± 0.148), 1.4–2.1% (1.72 ± 0.028) of length of idiosoma, rounded, not protruding, or slightly protruding beyond their sclerotized bases, smooth. Coxal fields II open, with very short unsclerotized distance between anterior and posterior apodemes; apodemes not reaching posterior edge of sternal shield. Coxal setae *3b* and *4a* conoidal, usually with concentric peripheral pattern. Attachment organ as in *S. ochoai*, 2.0–2.7

(2.34 ± 0.028) times shorter than width of idiosoma, maximum ventro-genital shield width/attachment organ width 0.9–1.1 (0.98 ± 0.008), minimum ventro-genital shield width/attachment organ width 1.3–1.7 (1.47 ± 0.012). Legs I-II protruding beyond edges of propodosoma to level of femora. Tarsi I-II comparatively long; tarsus I 2.7–3.5 (3.11 ± 0.034) and tarsus II 2.4–3.6 (3.0 ± 0.034) times longer than their respective width. Tarsal setae *aa* and solenidion ω_3 placed approximately at middle of tarsus I. Dorso-apical setae *d* on tarsi I-II not protruding beyond *e* I-II. Setae *la* I-II and *ra* I-II not shifted from *wa* I-II, distance *wa* I – *la* I/ diameter of *wa* I −0.3–1.5 (0.29 ± 0.061). Solenidion σ I comparatively long, distinctly extending beyond base of ω_1. Dorso-apical setae on tarsi III-IV comparatively short, usually ending near level of claw tip. Ventral tarsal seta *w* IV attenuated; *w* IV and *kT* IV smooth or rarely and weakly toothed.

Morphological Abnormalities. Female: *aa* shifted distally, placed between ω_1 and *ba* I levels (#22, 23); σ I short and thick, bifurcate and σ' bifurcate on one leg I (#6); an additional solenidion posterior to σ' and σ" on one leg I (#5). Deutonymph: *3b* on one side short, setiform (#12); two *r* on one tarsus III (#19); σ absent on both genua I (#*4a*). Homeomorphic male: one *vi* approximately three-fourths shorter than the other, more heavily serrate on tip (#1); one c_2 very long, 197, another one 117 (#9).

Type Material. HOLOTYPE: female, COSTA RICA: Cartago Prov., Orosí, Parque Nacional Tapantí, 9° 46′ N, 83° 46′ W, 28-IV-97, reared from deutonymph ex *Xyloryctes lobicollis* Bates (Coleoptera: Scarabaeidae), R. Ochoa, mites cultured on *Botryotinia fuckeliana*, BMOC 97-0430–029a. PARATYPES: 31 females, 26 homeo-, 12 hetero-, three ambiomorphic males, two trito-, 80 deuto-, two protonymphs, same data; 7, 1, and two deutonymphs, ex *Xyloryctes lobicollis* BMOC 97-0430-029a, BMOC 97-0430-029b, and BMOC 97-0430-029c, respectively, locality, data and collector as holotype. Holotype in UMMZ, paratypes there and in USNM, INBio, ZISP, IRSNB, HNHM.

Etymology. The species is named after the late Mr. Luis Angel Salas-Fonseca in recognition of his contribution to Costa Rican acarology.

Diagnosis. Very close to *S. phyllophagiana* and *S. ochoai*. See differences in keys below. Note that the original description of *S. phyllophagiana* (Oseto and Mayo 1975) contains some errors and should be used with caution. Our comparisons are based on material reared from the type-host, *Phyllophaga anxia* (LeConte).

Key to *Sancassania* Species Associated with Scarabaeoid Beetles in North and Central America

Females

1. Duct of spermatheca very long, 156–176 (164.3 ± 6.13, *n* = 3) (Fig. 3F–H) . . . . . *S. phyllophagiana* (Oseto and Mayo 1975)
   Duct of spermatheca shorter, 20–37 (Fig. 3A–E) 2
2. Duct of spermatheca dilated at spermatheca (Fig. 3A and B). Ratio e_1/hT 8.4–14.9 (10.34 ± 0.277), e_1/aa 8.4–12.7 (10.46 ± 0.243) . . . . . *S. ochoai* Klimov, Lekveishvili & OConnor, sp. nov.
   Duct of spermatheca constricted at spermatheca (Fig. 3C–E). Ratio e_1/hT I 5.1–8.2 (6.78 ± 0.159), e_1/aa 5.2–8.2 (6.61 ± 0.182). . . . *S. salasi* Klimov, Lekveishvili & OConnor, sp. nov.

Homeomorphic Males

1. Aedeagus straight . . . . . *S. phyllophagiana* (Oseto and Mayo 1975)
   Apex of aedeagus bent upward 2
2. Distance between pseudanal setae ps_1-ps_2 62–117 (84.4 ± 5.50). . . . . *S. ochoai* Klimov, Lekveishvili & OConnor, sp. nov.
   Distance ps_1-ps_2 28–61 (51.4 ± 2.85) . . . . . *S. salasi* Klimov, Lekveishvili & OConnor, sp. nov.

Deutonymphs

1. Dorso-apical setae *d* on tarsi I-II protruding beyond *e* I-II. Ventral tarsal seta *wa* on tarsi I-II shifted from *ra* and *la* I-II on distance that exceeds its diameter; ratio distance *wa* I – *la* I/ diameter of *wa* I 1.2–3.1 (1.64 ± 0.06, *n* = 40). . . . . *S. phyllophagiana* (Oseto and Mayo 1975)
   Dorso-apical setae *d* on tarsi I-II not protruding beyond *e* I-II. Distance between *wa* and *la* usually not exceeding diameter of *wa* on tarsi I-II 2
2. *1a* larger, 6.6–8.7 (7.43 ± 0.114), 2.3–3.2% (2.60 ± 0.043) of length of idiosoma. Posterior gnathosomal setae shorter, 5.5–7.8 (7.07 ± 0.152), approximately equal with *1a*: posterior gnathosomal setae/*1a* 0.8–1.2 (0.95 ± 0.02) . . . *S. ochoai* Klimov, Lekveishvili & OConnor, sp. nov.
   1a smaller, 3.7–7.5 (5.33 ± 0.148), 1.4–2.1% (1.72 ± 0.028) of length of idiosoma. Posterior gnathosomal setae longer, 7.8–14.0 (10.68 ± 0.253), 1.3–2.7 (2.04 ± 0.056) times longer than *1a* . . . . . *S. salasi* Klimov, Lekveishvili & OConnor, sp. nov.

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References Cited

Cruickshank, R. H. 2002. Molecular markers for the phylogenetics of mites and ticks. Syst. Appl. Acarol. 7: 3–14.

Darroch, J. N., and J. E. Mosimann. 1985. Canonical and principal components of shape. Biometrika 72: 241–252.

Gerson, U., and U. Caupa. 1982. Allometric variation in *Rhizoglyphus robini* Claparede (Acari: Acaridae). Israel J. Entomol 16: 69–72.

Grandjean, F. 1939. La chaetotaxie des pattes chez les Acaridiae. Bull. Soc. Zool. France 64: 49–60.

Griffiths, D. A. 1966. Nutrition as a factor influencing hypopus formation in the *Acarus siro* species complex (Acarina, Acaridae). J. Stored Prod. Res. 7: 325–340.

Griffiths, D. A., W. T. Atyeo, R. A. Norton, and C. A. Lynch. 1990. The idiosomal chaetotaxy of astigmatid mites. J. Zool. (Lond.) 220: 1–32.

Houck, M., and B. M. OConnor. 1998. Morphological variation in *Hemisarcoptes* (Acari: Hemisarcoptidae): application of multivariate morphometric analyses. Ann. Entomol. Soc. Am. 91: 335–349.

Hughes, A. M. 1976. The mites of stored food and houses. HM Stationery Office, London, United Kingdom.

Hughes, T. E. 1959. Mites or the Acari. Athlone Press, London, United Kingdom.

Jungers, W. L., A. B. Falsetti, and Ch. E. Wall. 1995. Shape, relative size, and size-adjustments in morphometrics. Yearb. Phys. Anthropol. 38: 137–161.

Mullen, G. R., and B. M. OConnor. 2002. Mites (Acari), pp. 449–516. *In* G. Mullen and L. Durden [eds.], Medican and Veterinary Entomology. Academic, San Diego, CA.

OConnor, B. M., and M. A. Houck. 1991. Preparation of mite specimens, pp. 243–245. *In* D. Rosen [ed.], Armored scale insects, their biology, natural enemies and control, vol. B. Elsevier, Amsterdam.

Okabe, K., and B. M. OConnor. 2000. Morphometric and systematic analyses of populations of the *Schwiebea bar-bei* – group (Acari: Acaridae) with particular reference to populations from North America and Japan. Int. J. Acarol. 26: 115–126.

Okabe, K., and B. M. OConnor. 2001. A method for both mass and individual rearing of fungivorous astigmatid mites (Acari). Exp. Appl. Acarol. 25: 493–504.

Oseto, C. Y., and Z. B. Mayo. 1975. A new species of *Caloglyphus* (Acarina: Acaridae) associated with *Phyllophaga anxia* (Coleoptera: Scarabaeidae). J. Kans. Entomol. Soc. 48: 212–223.

Park, J.-K., and D. Ó Foighil. 2002. Sphaeriid and corbiculid clams represent separate heterodont bivalve radiations into freshwater environments. Mol. Phylogenet. Evol. 14: 75–88.

Simmons, T., A. B. Falsetti, and F. H. Smith. 1991. Frontal bone morphometrics of southwest Asian Pleistocene hominids. J. Hum. Evol. 20: 249–269.

Sorensen, J. T., and R. Foottit (eds). 1992. Ordination in the study of morphology, evolution and systematics of insects: applications and quantitative genetic rationals. Elsevier, Amsterdam.

Timms, S., D. N. Ferro, and R. M. Emberson. 1981. Andropolymorphism and its heritability in *Sancassania berlesei* (Michael) (Acari: Acaridae). Acarologia 27: 391–398.

Woodring, J. P. 1969. Environmental regulation of andropolymorphysm in tyroglyphids (Acari), pp. 433–440. *In* G. O. Evans [ed.], Proceedings of the 2nd International Congress of Acarology, Sutton Bonington, England, 19–25 July, 1967, Akadémiai Kiadó. Budapest, Hungary.

Zachvatkin, A. A. 1941. [Tyroglyphoid mites Tyroglyphoidea], pp. 1–475. *In* S. A. Zernov [ed.], Fauna SSSR: Paukoobraznuye, vol. 6, issue 1. Akademiya Nauk SSSR Publ. Moscow-Leningrad, USSR. [in Russian, French (abstr.)]

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Appendix 1. Sequences of 28S rDNA gene of two *Sancassania* species

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                10        20        30        40        50        60        70        80        90       100
           ....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|
S.salasi   TGACAGGCAAACGGGTGGAACCaCGAAGTATGCCTGGCAGGCAATTCAGCTACGATCGACGGTTTGTGTCGCATGCAGTGGGTCCGTCTTTTCTGGCCAT
S.ochoai   ..................................................................................A.....................

               110       120       130       140       150       160       170       180       190       200
           ....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|
S.salasi   GCTAGTGACGCATCCAACCGGCGATTGTAGTGCATTTTGTCCTGCCAGTGCTAAAGCCACGTCCGATTAGGTGGCTGGAATGGCCGTAGTGAGCTGTCGC
S.ochoai   ............A...T.....................................................................................

               210       220       230       240       250       260       270       280       290       300
           ....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|
S.salasi   AAGGAAGGTGGCCGGATAGTGCTTGCATTATTCGGTGTTATAGCCTTGTGGCCGTGCCATTGCCTAGCGTGCTGATCGGTGTAAAAACTCCGAAAGGAGT
S.ochoai   ..................................................................................C.....................

               310       320       330       340       350       360       370       380       390       400
           ....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|
S.salasi   ATTGCCAGTAATGGGCTGTTGTGCTTTGCGGTGCCATGTGTGTCGTGCCATTTTGCGCTTTCGTGTCTTCGGGCTCGTAAAGACGGAGTGGTATCGTGTG
S.ochoai   ..................................G..A.................GC..........A.....................................

               410       420       430       440       450       460       470       480       490       500
           ....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|
S.salasi   CTCATTGGTGTCGATTGCATGAGCGGCTTGCGCAAACTGTGGTGCGAGTAGGTCGGTCTCCACCCGACCCGTCTTGAAACACGGACCAAGGAGCCTAACA
S.ochoai   ..................................................................................................

               510       520       530       540       550       560       570       580       590       600
           ....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|
S.salasi   CACACGCAAGTCGCACGGTCTTGTTTAGGCCTGTGAGGCGTAATGAAAATAAACTGCTATGAGGTTGTGCGCTCAAAAgGCAAGCAATCGCAATAGCGGC
S.ochoai   ..................................................................................................

               610       620       630       640       650       660       670       680       690       700
           ....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|
S.salasi   CTGCcTACTTcCTTTATCGGGGATATGGTGGAGCTGGAgCGTGTGCgTTGGTACCCgAAAGATGGtGAACTATGCCTGGgCAGGACGAAGCCAGAGGAAA
S.ochoai   ..................................................................................A.................

               710       720       730       740       750       760       770       780       790
           ....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|...
S.salasi   CTCTGGtGGAGGtCCGtAgCGAtTCTgACGTGCAAATCGATCGTcAgACCTGGGTaTAgGGGcGAAAgAcTAATCgAACCATCTAGTtGCTGG
S.ochoai   ..............T...................................................................................
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