

ARRHENOSEIUS GLORIOSUS N. G., N. SP.
(ACARI: MESOSTIGMATA: ASCIDAE),
AN ARRHENOTOKOUS MITE FROM RAINFORESTS
IN QUEENSLAND, AUSTRALIA.

BY David Evans WALTER * and Evert E. LINDQUIST **

ACARI
ASCIDAE
NEW GENUS
AUSTRALIA
ARRHENOTOKY

ABSTRACT: We describe a new genus and species of ascid mite, *Arrhenoseius gloriosus*, from rainforests in Queensland, Australia. This heavily armoured predatory mite can complete a generation in less than a week when fed nematodes at 25° C. The new genus belongs to the tribe Blattisociini Lindquist and Evans and appears to be most closely related to the northern hemisphere genus *Zercoseius*. However, unlike other Blattisociini for which the sex determination mechanism has been determined, *A. gloriosus* is arrhenotokous instead of pseudoarrhenotokous. We describe sexual dimorphism in the deutonymphal instar and ontogenetic changes in form of tarsal setae of legs II–IV. These attributes have not been previously noted among mites of the family Ascidae.

ACARI
ASCIDAE
GENRE NOUVEAU
AUSTRALIE
ARRHÉNOTOQUIE

RÉSUMÉ : Nous décrivons un nouveau genre et une nouvelle espèce d'acarien Ascidae, *Arrhenoseius gloriosus*, des forêts humides du Queensland, Australie. Une génération de cet acarien prédateur bien sclérifié peut se développer en moins d'une semaine à 25° C. avec des nématodes comme proies. Le nouveau genre appartient à la tribu des Blattisociini Lindquist and Evans et le genre *Zercoseius* de l'hémisphère nord semble le plus proche. Contrairement aux autres Blattisociini pour lesquels nous connaissons le déterminisme sexuel, *A. gloriosus* est arrhénotoque plutôt que pseudo-arrhénotoque. Nous décrivons un dimorphisme sexuel de la deutonymphe et des changements ontogénétiques de forme des poils tarsaux des pattes II–IV. Ces caractéristiques n'ont jamais été observées auparavant parmi les acariens de la famille des Ascidae.

INTRODUCTION

Rainforests have an unrivalled reputation for biological diversity and unusual species. This is certainly true of the acarofauna of Australian rainforests

(WALTER & PROCTOR, 1998, 1999). In this paper, we continue a series of studies dealing with the Australian fauna of mites in the family Ascidae. The family as a whole was reviewed recently for Australia by HALLIDAY *et al.* (1998), with the genera *Asca*, *Lasio-*

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seius (in part), *Hoploseius*, and the newly described *Ectoantennoseius* treated further in separate papers by WALTER *et al.* (1993), WALTER & LINDQUIST (1997), and WALTER (1998a, 1998b), respectively. The present paper contains the description, ontogeny, and biological observations of an unusual new species of ascid mite for which we propose a new genus belonging to the tribe Blattisociini sensu LINDQUIST & EVANS (1965). Among the known taxa in the Ascidae, this mite is highly distinctive morphologically and genetically, especially as it is one of the few species for which an arrhenotokous sex mechanism is demonstrated (NORTON *et al.*, 1993; WALTER & PROCUTOR, 1999). The ontogenetic changes in form of setae on tarsi II to IV in this species are also noteworthy, as is the sexual dimorphism in the ventral chaetotaxy of the deutonymph.

Material representing but one species of the new genus is available. Recognition of attributes that may be practically and phylogenetically diagnostic at the generic level, as distinct from the specific level, is always problematical for such monobasic taxa. In this case we have been guided primarily by the attributes used by previous authors, including ourselves, to distinguish between the currently recognized genera of Ascidae, particularly of the tribe Blattisociini.

MATERIALS AND METHODS

Mites were cleared in Nesbitt's solution, and mounted in Hoyer's medium or Heinze polyvinyl alcohol on microscope slides (KRANTZ, 1978; EVANS, 1992). Measurements are given in parentheses (in micrometres), and were made from flattened, slide-mounted specimens using stage-calibrated ocular micrometers. All shield measurements refer to lengths (measured along their midlines), unless width is specified (shield width is often strongly distorted in slide-mounts). The system of setal notation for the idiosoma follows LINDQUIST & EVANS (1965), with modifications for the posterior region as given by LINDQUIST (1994). Setae were measured from the bases of their insertions to their tips, and distance between setae as the minimum distance between their insertions. Notation for porelike structures of the

idiosoma as either gland pores (solenostomes) or poroids (lyrifissures) follows JOHNSTON & MORAZA (1991), based on morphological and physiological distinctions reported by ATHIAS-HENRIOT (1969a, 1969b) and KRANTZ & REDMOND (1987), respectively. Leg lengths were measured from the base of coxa to apex of tarsus excluding the pretarsus. Leg and palpal setal notation and chaetotaxy follow EVANS (1963, 1964, 1965), with modifications for tarsi II to IV as given by EVANS (1969).

Behavioural and other biological observations are based on a culture established from two adult females collected from subtropical rain-forest litter along Dawson Creek, Mt Glorious, Queensland (17.vii.1997). Mites were reared in culture jars (7 cm diameter), or in small glass vials (5 cm high, 1 cm diameter) with charcoal-plaster floors (WALTER & IKONEN, 1989) and fed nematodes [*Panagrellus silusiae* (de Man)]. Arrhenotoky was established by using isolated, virgin females and rearing any offspring they produced. Slide preparations of the larva, protonymph, deutonymph and adult female and male of *Zercoseius spathuliger* (Leonardi, 1899) were borrowed from the collections of Dr M. L. MORAZA, University of Navarra, Spain, for comparison with these instars of *A. gloriosus*.

Collection Abbreviations

- QM: Queensland Museum, South Brisbane, Queensland 4101, Australia
- UQIC: Department of Zoology & Entomology, University of Queensland, St. Lucia, Queensland 4072, Australia
- CNC: Canadian National Collection of Insects and Arachnids, Research Branch, Agriculture & Agri-Food Canada, Ottawa, Ontario K1A 0C6, Canada

Arrhenoseius new genus

TYPE SPECIES. *Arrhenoseius gloriosus* n. sp. Genus based on adult, nymphal and larval material representing one species.

DIAGNOSIS. Protonymph with expansive opisthonotal shield bearing 14 pairs of setae including 6 pairs, *J1*, *J2*, *Z1*, *Z2*, *S2*, *S3*, that are on soft cuticle in other known protonymphal Ascidae. Deutonymph with single dorsal shield bearing deep mid-lateral incisions. Adult female and male with entire dorsal shield; humeral setal pair *r3* erect but simple (not tricarinate); marginal *R*-series reduced to one pair on soft cuticle. Female with metapodal plates insensibly fused to peritrematal shields, and with expansive ventrianal shield bearing 7 pairs of ventral setae plus the 3 circumanals. Male with holovenal shield, including its union with peritrematal-exopodal shields. On deutonymph and adult: leg IV tibia with 9 setae, lacking *pl-2*; tarsus II with two elongate whiplike setae, *ad-3*, *pl-2*; tarsus III with one elongate whiplike seta, *ad-3*; tarsus IV with two elongate whiplike setae, *ad-3*, *pd-3*.

DESCRIPTION. With character states of tribe Blattisociini, including: fixed chela with setiform pilus dentilis; movable chela without mucro or denticles on proximal ventral surface; peritrematal shield broadly united with exopodal plate curving behind coxa IV; para-anal setae inserted at mid-level of anus, and similar in length or shorter than postanal seta; female spermathecal apparatus of phytoseioid-type, with conspicuous, well-sclerotized cervix and long, slender minor duct.

Idiosomal dorsum. Female and male with expansive dorsal shield with complete series of *j*, *z*, *s* and all *r*-marginal setae present on anterior region and complete *J*, *Z* and *S* series on posterior region; only one pair of marginals, *R1*, on lateral soft cuticle in both sexes; submarginal series lacking. Most dorsal setae of adults curved, tapered and slightly barbed, except humeral seta *r3* which is smooth and nearly perpendicular to body. Deutonymph with single dorsal shield, with deep midlateral incisions. Protonymph with separate podonotal and opisthonotal shields, the latter expansive, bearing setae *J1-J5*, *Z1-Z5*, *S2-S5*. Larva with separate podonotal and small pygidial shield, the latter bearing setae *Z3*, *Z4* and at least vestiges of setae *J3*, *J4*.

Idiosomal venter. Female sternal shield with endopodal extensions connected to exopodal projections of peritrematal-exopodal shield between bases of legs I-II and II-III, and with three pairs of setae, *st1-st3*,

and two pairs of poroids, *iv1-iv2*; fourth sternal setae and third sternal poroids on separate metasternal plates; genital shield widened and truncated posteriorly, but paragenital poroids *iv5* on soft cuticle closely beside its posterolateral corners; ventrianal shield expansive, bearing setae *JV1-JV4*, *ZV1-ZV3* and the circumanal setae; para-anal setae inserted at mid-level of anus, subequal to or slightly shorter than postanal seta; setae *JV5* inserted on narrow strip of soft cuticle between ventrianal and dorsal shields; peritrematal shields expansive, fully united to exopodal plates running alongside coxae I to IV, united to dorsal shield anteriorly, and their posterior extremities broadly truncated and consolidated with metapodal plates; spermatheca with sclerotized cervix and long, fine accessory duct. Male with sternogenital-endopodal, peritrematal-exopodal and ventrianal shields connected to form holovenal shield; endopodal projections of sternogenital shield connected with exopodal projections of peritrematal shield between bases of legs I-II, II-III, III-IV.

Gnathosoma. Base of tritosternum slender, bases of laciniae bordered by several denticles at level of their fusion. Tectum triramous. Deutosternum with seven rows of denticles, all connected by lateral margins of deutosternal groove. Corniculi well developed, stout, entire apically, well separated. Fixed chela multidentate, with small pilus dentilis and small offset subapical tooth; movable chela tridentate, with fringed hyaline envelope around base. Male spermatodactyl curving ventrally beyond tip of movable chela. Palpus normal in size and form, its trochanter and femur similar in length; palptrochanter with one seta on protonymph, *v-2* added on deutonymph; deutonymphal and adult setation of palpal trochanter, femur, genu, tibia, tarsus, respectively 2-5-6-14-15.

Legs. Tarsus I with pretarsus and paired claws, with dorsal subapical sensillus *s* slightly clavate-tipped, strongly recurved distally. Femur I typically shaped, gradually narrowing basally. Legs II-IV with paired claws and median lobe of pulvillus broadly rounded. Leg II of female not thicker than legs III-IV, and without opposable spinelike setae on ventral surfaces of segments. Deutonymphal and adult setation of legs I-II-III-IV, trochanters: 6-5-5-5; femora: 12-11-6-6; genua: 13-11-9-9; tibiae: 13-10-8-9; setae *av-2* and *pv-1* present on genua II and III;

seta *pl-2* absent on genu III and tibiae III and IV. None of leg setae dimorphically thickened or otherwise modified on male.

RELATIONSHIPS. *Arrhenoseius* is uniquely apomorphic among the genera of Ascidae in its protonymph having an expansive opisthonotal shield that captures setae *J1*, *J2*, *Z1*, *Z2*, *S2*, *S3* and bears a total of 14 pairs of setae, and in its female having the metapodal plates fused to the posterior margins of the peritrematal shield. It is unusual among Ascidae in its male having a holovenral shield, an apomorphy otherwise known only in the genera *Antennoseius* (Ascini), *Zercoseius* (Blattisociini) and, rarely, *Lasioseius* (Blattisociini).

Within the tribe Blattisociini, adult *Arrhenoseius* most closely resemble *Zercoseius* which is also monobasic, and with it shares two putative apomorphies: *R*-marginal series reduced to just the protonymphal pair, *R1* (which is the only pair of marginal setae on soft cuticle) and male ventral shielding consolidated into a holovenral shield. Both genera also have females without free metapodal plates; however, the metapodal plates are incorporated into the posterior margins of the peritrematal shields in *Arrhenoseius*, whereas they are incorporated into the anterolateral areas of the ventrianal shield in *Zercoseius*. Similarly, tarsi II to IV of deutonymph and adults in both genera each have one or two long whiplike setae; however, the setae elongated as whiplike structures in *Arrhenoseius* are *ad-3* and *pl-2* on tarsus II, *ad-3* alone on tarsus III, and *ad-3* and *pd-3* on tarsus IV, whereas in *Zercoseius* they are *ad-3* and *pd-3* on tarsi II and III, and *ad-3* alone on tarsus IV. Also, females have expansive ventrianal shields bearing 7 pairs of opisthogastric setae in addition to the circumanals, but in *Arrhenoseius* these include *ZV1* and exclude *JV5* which remains on soft cuticle (as in *Lasioseius*), whereas in *Zercoseius* *ZV1* is absent and *JV5* is on the shield. *Zercoseius* also differs from *Arrhenoseius* in having a typical, dorso-ventrally flattened dorsal shield; fixed digits with 4–5 teeth; movable digits with 2 teeth; deutonymphs and adults without podonotal setae *z1*, *s1*, *s2*; exopodal elements that remain free from the peritrematal shields between legs I–II and II–III in adults; no recognizable calyx of the spermathecal apparatus (ATHIAS-HENRIOT, 1967); the paragenital poroids captured by the posterolateral corners

of the female epigynial shield; the male opisthogastric region with setae *ZV2*, *ZV3*, *JV4*; and genu III, tibia III and tibia IV with one more seta, *pl-2*, in deutonymphs and adults. Moreover, *Zercoseius* is known only from North America and Europe, *Arrhenoseius* only from Australia.

Protonymphs in both *Zercoseius* and *Lasioseius* have a pygidial shield with setae *J1-2*, *Z1-2* and *S2-3* inserted on the soft cuticle, rather than being captured on an expanded shield as in *Arrhenoseius*. The deutonymph of *Zercoseius spathuliger*, however, resembles that of *Arrhenoseius gloriosus* in having a well sclerotized, heavily ornamented dorsal shield with lateral incisions. In contrast with *A. gloriosus*, however, in *Z. spathuliger* setae *s3* are enlarged and erect on the dorsal shield margin so as to resemble a humeral pair of setae above short, curved *r2* and short, smooth *r3* on soft cuticle. In transforming to the adult, setae *r2* (erroneously denoted *r3* in LINDQUIST & EVANS, 1965) become enlarged and erect to resemble humeral setae in their new position on the dorsal shield, *s3* become smaller and curved like other adjacent setae, and *r3* become curved, slightly barbed, and undifferentiated from *r4*, *r5*. These transformations in setal forms do not occur in *A. gloriosus*; instead, setae *r3* change from being curved and slightly barbed on the deutonymph to erect and smooth on the adult. The deutonymph of *Z. spathuliger* also differs in having a small ventrianal shield bearing setae *JV3* and usually *JV2* in addition to the circumanals, instead of an anal shield as in *A. gloriosus* (also in *Lasioseius*).

There are a number of species of *Lasioseius* whose females have heavily sclerotized and highly ornamented dorsal and ventral shielding and a spermathecal apparatus without a clearly developed cervix. At least a dozen such species have been described, including *L. imitans* (Berlese), *L. scutalis* (Banks), *L. alter* Vitzthum, *L. humberti* Athias-Henriot, *L. vitzthumi* Westerboer, *L. tectus* Hyatt, *L. convexus* Krantz, *L. americanus* Chant, *L. araucariae* Hirschmann, *L. mouchei* Loots, *L. rugosa* (Halliday), *L. zaluckii* Walter & Lindquist, representing two or more species groups. The male has been described for only one of these species, *L. vitzthumi*, and it is unusually apomorphic in *Lasioseius* in having a holovenral shield (although a line of delineation remains evident at the

junction of the sternogenital and ventrianal shields). A few of the *Lasioseius* species discussed above have been confused with the pachylaelapid genus *Zygo-seius* by some authors (VITZTHUM, 1925; WESTERBOER, 1963; HYATT, 1964). Adult females of *Arrhenoseius* and *Zygo-seius* both have metapodal plates consolidated with peritrematal shields and their males have a holovertral shield. However, the variety of attributes that exclude *Zygo-seius* from the family Ascidae, including a 3-tined apotele on the palptarsus, 13 setae on femur I, a divided dorsal shield in the deutonymph but an entire dorsal shield in the adult, fusion of the metasternal and endopodal plates in the female, a non-phytoseiid type spermathecal apparatus with an unpaired sperm reservoir in the female, and an S-shaped spermatodactyl with a basal posteroventral bend in the male, indicate that any similarities between these two taxa are superficial. Also, the protonymph of *Zygo-seius* does not have an expanded posterior dorsal shield.

In the key to world genera of Ascidae recently published by HALLIDAY *et al.* (1998), *Arrhenoseius* keys readily to couplets 24 and 25, which are end points for the genera *Zerco-seius*, *Aceodromus* and *Lasioseius*. Couplet 24 can be modified, and an additional couplet, 24A, inserted to include *Arrhenoseius*, and to correct for the presence of setae *r2* in *Zerco-seius*, as follows, with no changes needed for couplet 25:

24(23). Adults with 1 pair of marginal setae (*R1*) on soft lateral cuticle; female metapodal plates incorporated into ventrianal or peritrematal plates, and ventrianal shield with 7 pairs of setae in addition to circumanals; male with holovertral shield... 24A

Adults with 3–9 pairs of marginal setae (*r-R*) on soft lateral cuticle; female metapodal plates free on soft cuticle, and ventrianal shield with 6 or fewer pairs of setae in addition to circumanals; male usually with separate sternogenital, ventrianal and peritrematal-exopodal shields... 25

24A(24) Podonotal region of adult dorsal shield lacking setae *z1*, *s1*, *s2*; female with metapodal plates incorporated into ventrianal shield; female ventrianal shield lacking setae *ZVI* but with *JV5* on its posterolateral margins; genu III with 10, tibiae III and IV with 9 and 10 setae, respectively (*pl-2* present on each of these segments)... *Zerco-seius*

Podonotal region of adult dorsal shield holotrichous; female with metapodal plates incorporated into posterior margins of peritrematal shields; female ventrianal shield with setae *ZVI* but with *JV5* inserted on soft cuticle

behind its posterolateral margins; genu III with 9, tibiae III and IV with 8 and 9 setae, respectively (*pl-2* absent from each of these segments)... *Arrhenoseius*

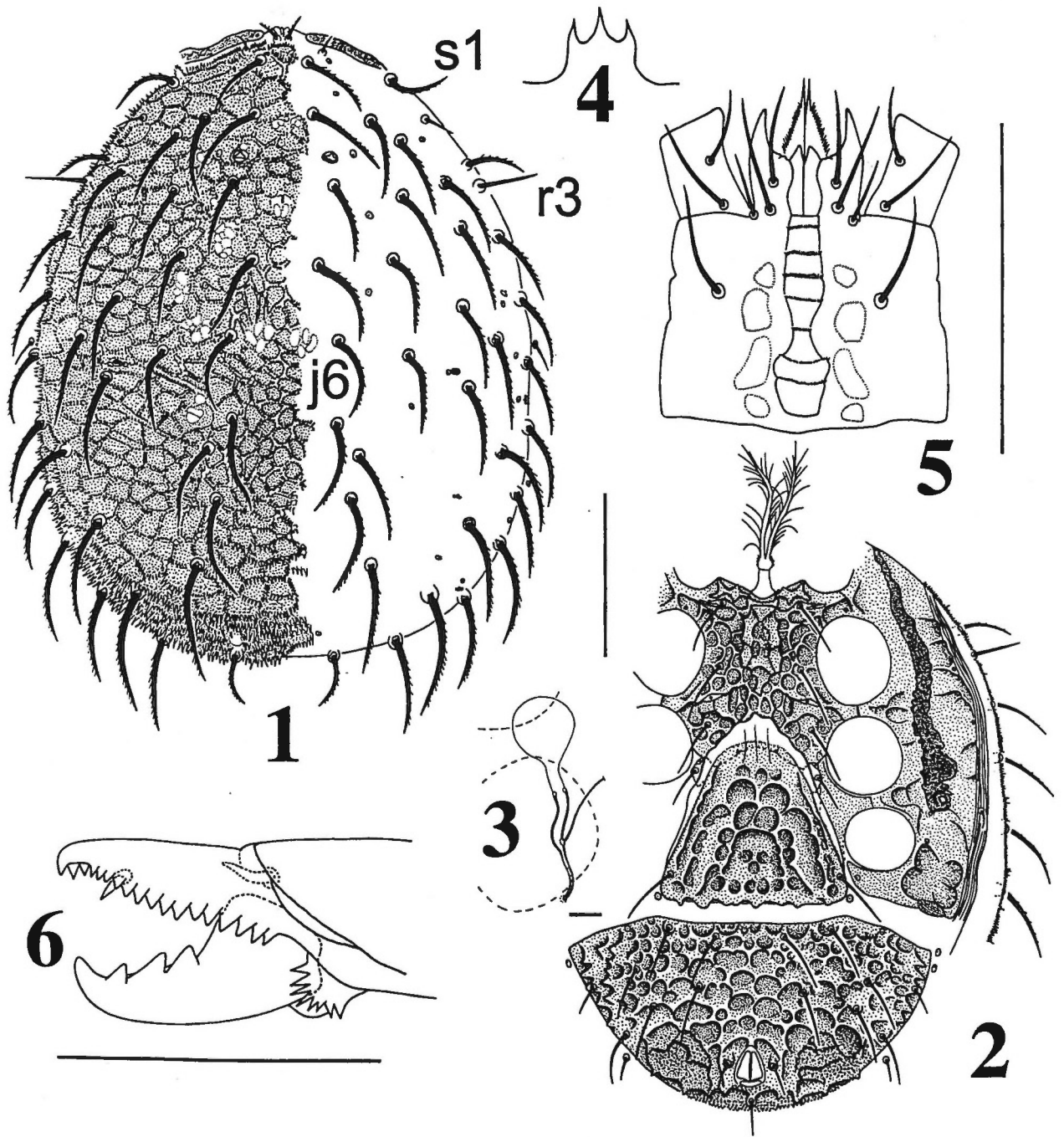
Arrhenoseius gloriosus n. sp.

(Figs 1–24)

MATERIAL EXAMINED. QUEENSLAND: Holotype female, subtropical rainforest litter along Dawson Creek, Manorina National Park (27°23'S, 152°47'E), 17.vii.1997. In QM. Paratypes: 1 female, 2 males, same data as holotype; 2 females, 19 males, 2 deutonymphs, 6 protonymphs, 5 larvae from culture from same site; 3 females, 1 male, Maiala National Park, Mt Glorious, 17 Oct. 191994; 1 female, 2 males, Cedar Creek (27°19'S, 152°46'E), Mt Glorious, 5.vii.1995; 2 females, Kilcoy Creek (26°46'S, 152°35'E), Conondale Ranges, 14.ii.1996; 3 females, Bundaroo Creek (26°42'S, 152°36'E), Conondale Ranges, 13.vii.1995; 2 females, 1 male, Little Paradise Falls (26°32'S, 151°35'E), Bunya Mountains, 13.ii.1996; 4 females, Darraboola Creek, Lamington National Park, Green Mountains Section 23.vii–3.viii.1995; 13 females, 9 males, Border Track, Lamington National Park, Green Mountains Section, 5.i–2.ii.1995, ex litter from crow's nest ferns in rainforest canopy, D.E. WALTER & D. RODGERS. All other collections by D.E. WALTER from rainforest leaf litter. In UQIC, CNC.

DIAGNOSIS. With characteristics of the genus and: dorsal shield of adults entirely covered with reticula outlined by spiculate tubercles, with nearly all setae thick, curved, barbed, longer than intervals between their bases; ventral shielding of adults entirely ornamented with embossed, smooth reticula and fovea; sternal shield of female with anteromedial patch of reticula somewhat elevated from adjacent surfaces; spermatodactyl of male with foot-like apex with anterior rounded toe and posterior pointed heel.

ADULT FEMALE. *Idiosomal dorsum* (Fig. 1). Holodorsal shield (length 370–410, greatest width at level of setae *s6* 325–330) hemispherical, extending latero-ventrally, leaving only narrow band of soft striated cuticle between it and peritrematal and ventrianal



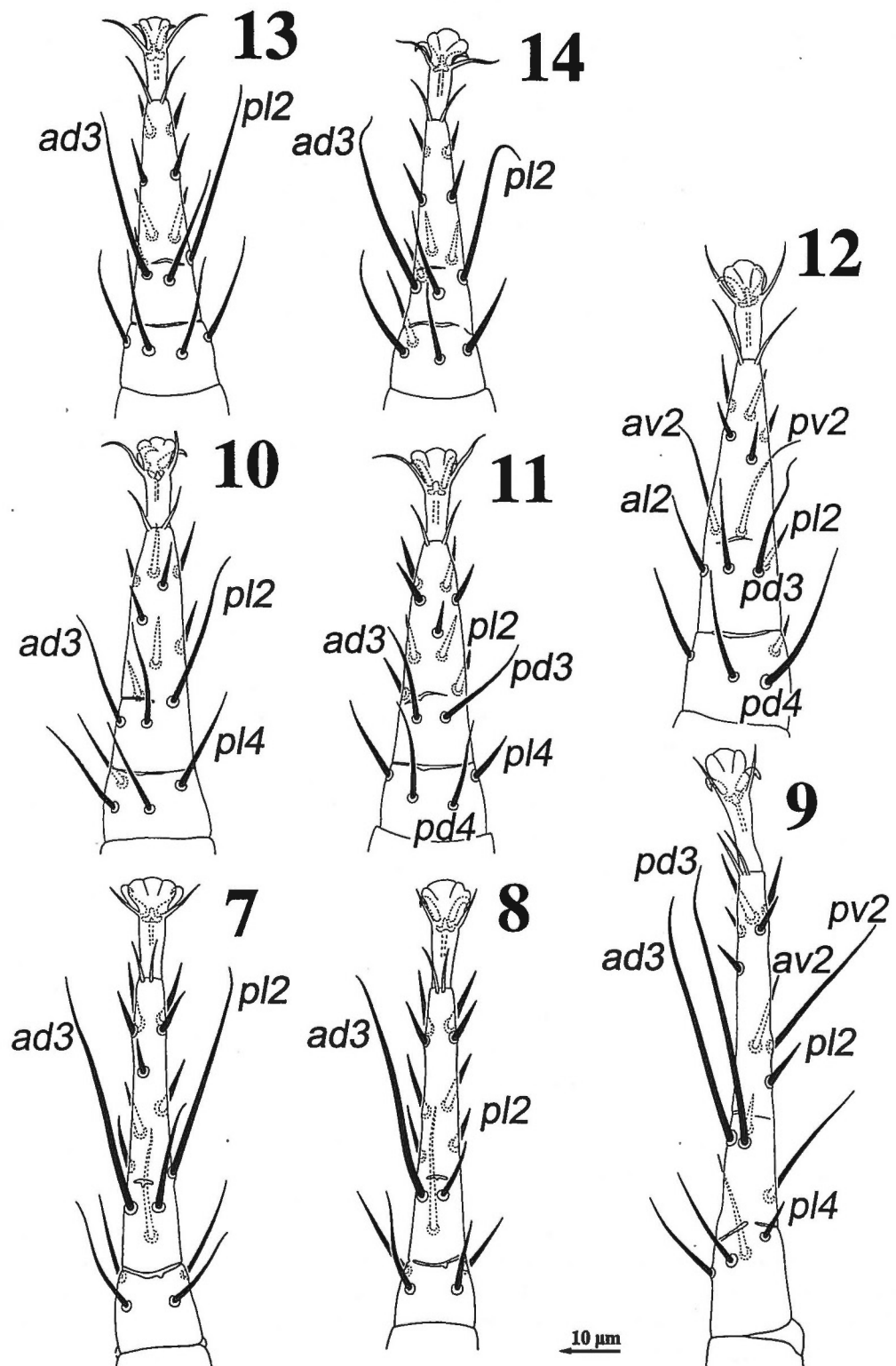
FIGS. 1-6. *Arrhenoseius gloriosus* n. sp., adult female. 1. — Dorsal shield and peripheral structures on soft cuticle. 2. — Ventral shielding. 3. — Spermathecal apparatus. 4. — Gnathotectum. 5. — Hypognathum. 6. — Distal part of chelicera, paraxial view. Scale bars = 100 μ m (1, 2 and 4, 5); 10 μ m (3); 50 μ m (6).

shields; shield covered in dense reticulate array of spiculate tubercles; reticulations filled with smaller spiculate tubercles; shield bearing 37 pairs of mostly elongate, curved, thick, sparsely barbed setae, except *j1* short (18), *z1*, *s2* short (12–15), simple, and humeral *r3* (28–30) straight, erect, simple; all setae set on tubercles; setal lengths *j2–j4*, *j6*, *z2–z4*, *z6*, *s3–s6* (45–60), *j5*, *z5*, *s1*, *r4*, *r5* (38–40), *r2* (28–30); *J1–J4* (50–57), *J5* (32), *Z1–Z3* (55–60), *Z4* (70–73), *Z5* (53–56), *S1–S3* (45–50), *S4*, *S5* (48–53); *z5* displaced anteriorly, in transverse line with *j5*; dorsal shield complement of poroids and gland pores difficult to discern amidst ornamentation, but 7 pairs of gland pores denotable as *gdj2*, *gdj4*, *gdz5*, *gdz6*, *gdZ3*, *gds4*, *gdS4* and 13 pairs of poroids denotable as *idj1*, *idj3*, *idj6*, *idJ2*, *idJ4*, *idJ5*, *idz3*, *idz6*, *ids4*, *ids6*, *idS1*, *idS3*, *idS4* evident. Setae *R1* short (10) simple, in soft cuticle along with marginal poroids *idR3* between dorsal and ventral shields.

Idiosomal venter (Fig. 2). Covered with strongly sclerotised shields ornamented with embossed reticula or fovea, without tubercles or spicules except sparsely on anal region. Tritosternum (85–95) with elongate trapezoidal base (15) and paired, sparsely plumose laciniae (68–70) separate for nearly (all but basal 8) entire length; laciniae flanked by several denticles at level of their fusion. Presternal region lacking separate platelets or ornamented cuticle, but sternal shield extended anteriorly into this region. Sternal shield (median length 90–95, narrowest width between legs II 78–80) with three pairs of simple setae (30–35) and two pairs of poroids; with anteromedial patch of reticula somewhat elevated from adjacent surfaces; endopodal extensions of shield between coxae I–II with conspicuous gland pore near their lateral extremities; endopodal extensions between coxae I–II and II–III contiguous with exopodal extensions of peritrematal-exopodal shields. Fourth pair of sternal setae (23–25) and third pair of poroids on separate metasternal plates closely surrounded by sternal, genital and endopodal shielding. Endopodal plates present as free strips alongside coxae III–IV. Epigynial shield broadly subtriangular, its median length (110–115, including hyaline anterior extension) subequal to its greatest width (117–125) along truncate posterior margin; hyaline anterior margin of shield convexly rounded, extending over posterior

region of sternal shield to level of setae *st3*; genital setae (35) inserted on lateral edges near posterior margin of shield; paragenital poroids *iv5* on soft cuticle adjacent to posterolateral corners of shield. Peritrematal shield expansive, fully consolidated with exopodal shield alongside coxae II–IV, united with dorsal shield at level of setae *s1*; metapodal plate incorporated into truncated posterior margin of shield; shield with poroid *ip1* at level of coxa II, gland pore *gp1* at level of coxa III, poroid *ip2* closely posterad stigma, and gland pore *gp2* and poroid *ip3* further posterad stigma at level of coxa IV; inguinal gland pore *gv2* on exopodal extremity of shield curving behind coxa IV; peritreme extending anteriorly nearly to vertical setae *j1*, with crenulated margins, especially along inner (ventral) margin. Ventrianal shield expansive, its greatest width (247–250) along anterior margin over twice its median length (115–120), abutting posterior margins of epigynial and peritrematal shields, with 7 pairs of simple ventral setae (*JV1–JV4*, *ZV1–ZV3*), *ZV3* shortest (15–20), others subequal (25–30), and three simple, subequal circumanal setae (15–20); one pair of poroids *ivo1* near anterolateral margin of shield, para-anal gland pores *gv3* indiscernible; cribrum a broad strip behind postanal seta. Narrow strip of soft cuticle between ventrianal and dorsal shields with 3 pairs of poroids *ivo2–ivo4*, and simple setae *JV5* (12–15). Spermathecal apparatus (Fig. 3) with short (15–20) major duct leading from orifice between bases of legs III–IV to slender, cylindrical calyx whose sclerotized length (18–20 including atrium) about 5 to 6 times its width (3.5); atrium with long, fine minor duct ending without discernible enlargement.

Gnathosoma (Figs. 4–6). Gnathotectum (Fig. 4) with three simple, sharply pointed tines. Base of fringed labrum with short (6–11) spearlike supralabral process. Hypognathum (Fig. 5) with corniculi (11–12) hornlike, parallel; internal malae with fringed lateral margins and acute apices extending slightly beyond tips of corniculi; 7 moderately broad rows of deutosternal denticles, each finely multidenticulate (14–30 denticles per row), all connected by lateral margins of deutosternal groove, 5th row constricted to about half width of 4th row, 6th row widened beyond lateral margins of groove; four pairs of sim-



FIGS. 7–14. *Arrhenoseius gloriosus* n. sp., leg tarsi, dorsal aspect. 7, 8 & 9. — Tarsi II, III, IV respectively, female. 10, 11 & 12. — Tarsi II, III, IV respectively, protonymph. 13 & 14. — Tarsi II, III respectively, larva. Scale bar = 10 μm excluding arrowhead, which points to anterolateral face of tarsi.

ple subcapitular setae, anterior pair similar in length to 2nd and 4th pairs (30), 3rd pair shorter (20). Second article of chelicera (95–100) with smooth hyaline rim along its paraxial face above base of movable chela, ending in fixed digit with row of 15–17 closely spaced teeth decreasing in size apically, offset subapical tooth, and distal hook (Fig. 6); dorsal cheliceral seta (6–8) simple, somewhat flattened; pilus dentilis (3) simple. Movable digit (38–40) with 3 strong teeth; margin of hyaline envelope at base of movable chela fringed. Palpal length 112–114, chaetotaxy as described for genus, all setae smooth; palptrochanter with seta *av* (25) slightly stouter and less tapered than *pv* (27); setae *al* of femur and *al-1*, *al-2* of genu spatulate; palp tarsus with no setae enlarged, but one sigmoid.

Legs (Figs 7–9). All legs with well developed pretarsi (12–15) and paired claws. Excluding ambulacra, lengths of leg I 285–290, leg II 260–265, leg III 235–242, leg IV 285–290. Ventral surfaces of coxae I–IV embossed with reticula or fovea; coxa I with denticulate ridge near dorsal anterior margin, and cluster of 2 poroids and gland pore ventroproximally. Tarsus I (80) twice as long as subequal tibia or genu (each 40); subapical lanceolate-tipped sensillus *s* of moderate length (20), narrowly expanded and strongly recurved distally. Tarsi II–IV (75–100) each longer than combined length of subequal tibia and genu (60–75), with apical setal processes *ad-1*, *pd-1* short (10–12); pretarsi II–IV with paradactyli simple, short (9–10). All leg setae smooth; setation of legs I–II–III–IV, respectively: coxae: 2-2-2-1; trochanters: 6-5-5-5; femora: 12-11-6-6; genua: 13-11-9-9; tibiae: 13-10-8-9; leg chaetotactic formulae as given for deutonymph. Tarsus II (Fig. 7) with setae *ad-3* (50–52) and *pl-2* (45–47) long, untapered, whiplike, reaching to base of pretarsus; *pd-3* moderately short (22–24), slender, similar to *ad-4* (25–27) on basitarsus; telotarsus with midventral seta *av-3* (25–27) also slender, other setae short (10–15), stout. Tarsus III (Fig. 8) with *ad-3* (50) formed as on tarsus II, but *pl-2* short (9), stout; *pd-3*, *av-3* slender as on tarsus II, but basitarsal *al-4* (22) stouter and *pl-4* shorter and stouter than on II. Tarsus IV (Fig. 9) with most setae similar in form and length as on III, except *pd-3* (not *pl-2*) elongated (61–63) closely beside elongated *ad-3* (52–57), midventral *av-3*

slightly longer (32–33), and *pv-2* moderately long (38–40), slender.

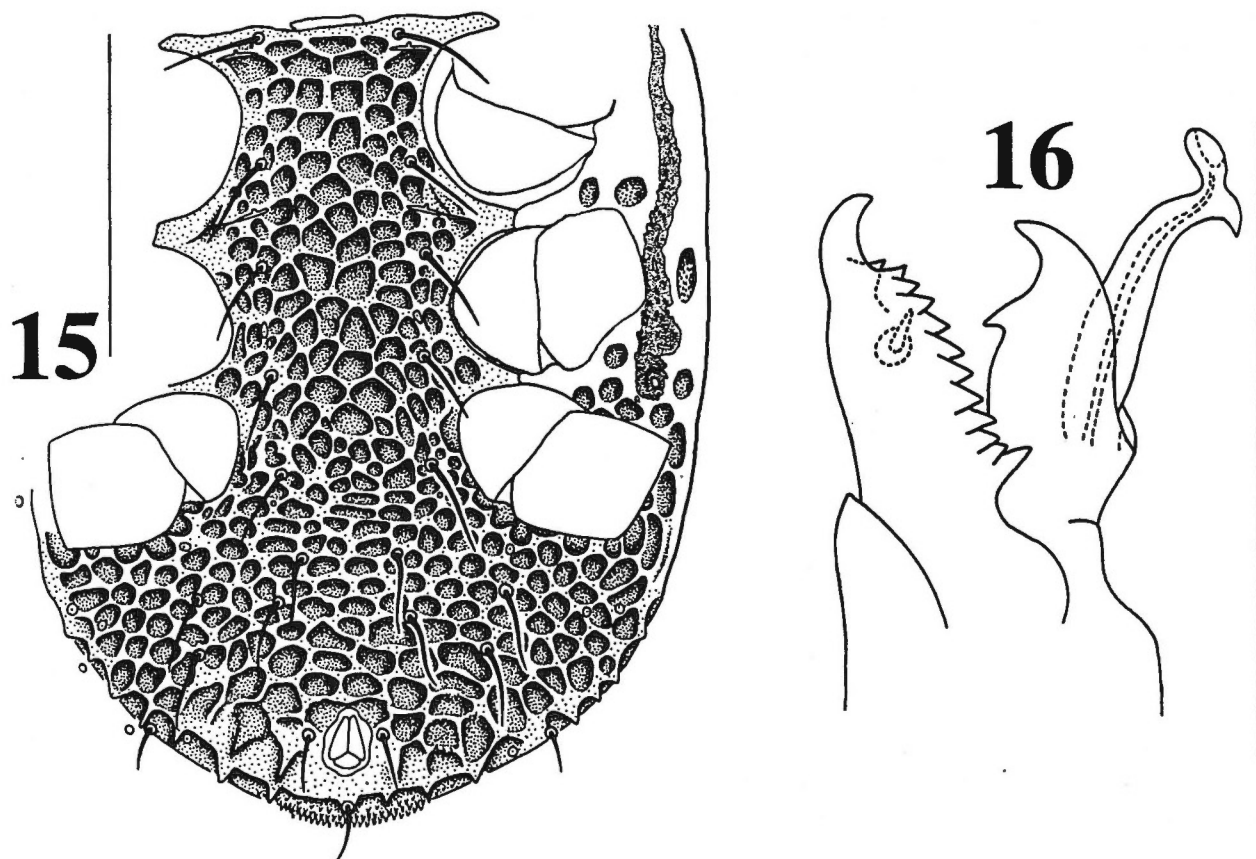
ADULT MALE. *Idiosomal dorsum*. Dorsum entirely covered by strongly sclerotised, hemispherical holo-dorsal shield as in female but about 0.7 smaller (length 275–310, greatest width at level of setae *s6* 210–220); dorsal shield ornamentation, setation and porelike structures as in female; setae *R1* on narrow strip of soft cuticle as in female.

Idiosomal venter (Fig. 15) entirely covered by strongly sclerotised holovenral shield consisting of consolidated sternogenital, ventrianal and peritrematal-exopodal elements; transverse rim — or line-like vestige of division between sternogenital and ventrianal shields sometimes evident between setae *st5* and *JV1*; shield length medially 232–240, width at posterior margin of coxae IV 182–190, ornamented with embossed reticula or fovea much as in female; setal and porelike elements as in female, except: paragenital poroids *iv5* on shield behind setae *st5*, poroids *ivo2-ivo4* on shield laterad setae *ZV2*, setae *JV5* on posterolateral margins of shield, and setae *JV4*, *ZV1*, *ZV3* absent.

Gnathosoma. Gnathotectum, hypognathum and palpi as in adult female, except corniculi slightly more incurved and internal malae extended slightly farther beyond tips of corniculi. Cheliceral structures (Fig. 16) as in adult female except fixed chela (79–82) with row of 10–11 teeth and offset subapical tooth, separated by edentate interval (5) before distal hook; movable chela (28–29) with one tooth and spermatodactyl (length from basal union with chela to apex 27–29) which in lateral view curves gradually anteroventrally and ends with rounded anterior lobe and pointed posterior spur, phytoseiid-like; apex of spermatodactyl in dorsoventral view resembles a foot (9) with rounded anterior toe and pointed heel.

Legs. Excluding ambulacra, lengths of leg I 232–240, leg II 200–208, leg III 192–195, leg IV 232–238. Form, setation and other structures of legs as in adult female, with no dimorphism evident.

LARVA. *Idiosomal dorsum* (Fig. 17). Dorsum (length 175–215) with lightly sclerotised, unornamented podonotal shield (length 107–140, width at level of setae *s4* 135–140) bearing 9 pairs of well developed, simple setae, 3 pairs of poroids, and 1 pair of



FIGS. 15-16. *Arrhenoseius gloriosus* n. sp., adult male. 15. — Ventral shielding. 16. — Distal part of chelicera with spermatodactyl, paraxial view. Scale bars = 100 μ m.

gland pores; setal lengths: *j1* (19–20), *j3* (25–28), *j4* (28–30), *j5* (21–25), *j6* (41–44), *z2* (28–32), *z4* (38–40), *s4* (40–42), *z5* (34–37). Pygidial shield (length 52–55, width at level of setae *Z3* 93–105) unornamented, with 2 pairs of well developed, sparsely barbed setae on lateral margins, *Z3* (50–62), *Z4* (60–82), 2 pairs of minute (<1 μ m), rudimentary setae *J4*, *J5*, 2 pairs of poroids, and 2 pairs of gland pores. Soft cuticle between shields with 3 pairs of oval platelets (sigilla), 3 simple pairs of setae *s6* (35–40), *S3* (31–34), *S4* (15–16), 2 pairs of minute (1–3 μ m) or rudimentary setae *J2*, *J3*, and 2 pairs of poroids; cluster of 2 poroids and 1 gland pore laterad *s6* on either side.

Idiosomal venter. Tritosternum well developed (Fig. 18), with elongate trapezoidal base (10–11); laciniae (49–52) free along 80 percent of length, sparsely plumose. Sternal setae *st1* on faintly sclerotized rectangular plate; *st2-st3* on separate faintly sclerotized,

quadrate plate. Setae *JV1*, *JV2*, *JV5*, *ZV2*, *S5*, *Z5*, 1 pair of poroids in soft cuticle. Anal shield (Fig. 19) broadly oval (length 28–30, width at level of para-anal gland pores 34–40), with simple para-anal (30–35) and postanal (16–20) setae; euanal setae (2) rudimentary; cribrum absent.

Gnathosoma. Gnathotectum (Fig. 20) with anterior margin triramous, each tine serrated, dorsal surface covered with minute denticles except smooth medially. Hypostome with 7 finely multidenticulate rows of deutosternal denticles of similar width (posterior rows slightly wider), bordered and connected on either side by a longitudinal line; hypognathum with a transverse, serrated rim on either side of deutosternal gutter just behind attachment of palpi; 2 pairs (*h1-h2*) of simple subcapitular setae (22–24); corniculi well developed, simple, well separated; internal malae with lateral margins fringed, and with

acute apices extending slightly beyond tips of corniculi. Fixed cheliceral digit (62–68) with dorsal cheliceral seta (5) and row of 9–10 closely set teeth of which apicalmost 2 or 3 smaller than others, a tiny offset subapical tooth, distal hook, and minute pilus dentilis; movable digit (25–28) with 2 teeth. Palpal length 77–98; palp trochanter, femur, genu, tibia, tarsus setation, respectively: 0-4-5-12-11; anterolateral seta on genu and femur spatulate; dorsal setae *d-1*, *d-2* barbed on palpfemur.

Legs. Lengths of legs, excluding ambulacra, I (215–235), II (175–200), III (170–195). Pretarsi I (14–15) and II–III (10–11) with well developed, evenly curved claws; median lobe of pulvillus with rounded apical margin. Setation of legs I–II–III respectively, coxae: 2-2-2; trochanters: 4-4-4; femora: 10-7-5; genua: 8-6-6; tibiae: 8-7-7. Chaetotactic formulae, femora: 2-2/1, 2/1-2; 1-2/1, 2/0-1; 1-1/1, 2/0-0; genua: 1-2/1, 2/1-1; 1-2/0, 2/0-1; 1-2/0, 2/0-1; tibiae: 1-2/1, 2/1-1; 1-1/1, 2/1-1; 1-1/1, 2/1-1. Most of *ad*, *pd* and some *pl* setae barbed on femur, genu, tibia of legs I–III; other setae smooth. Tarsus I without notably elongated setae; sensillus *s* (21–23) slightly clavate-tipped, strongly recurved apically. Tarsi II–III (Figs. 13–14) with apical setal processes *ad-1*, *pd-1* well developed (10–12), and with setae *ad-3*, *pl-2* elongate (35–45), reaching nearly to base of pretarsus, untapered along most of length, curved whiplike apically; between these setae, *pd-3* of moderate length (25–26), slender, similar to those on basitarsus; other setae on telotarsi II–III short (9–12), stout, somewhat spine-like. Pretarsi II–III with prominent, simple paradactyli (11–12).

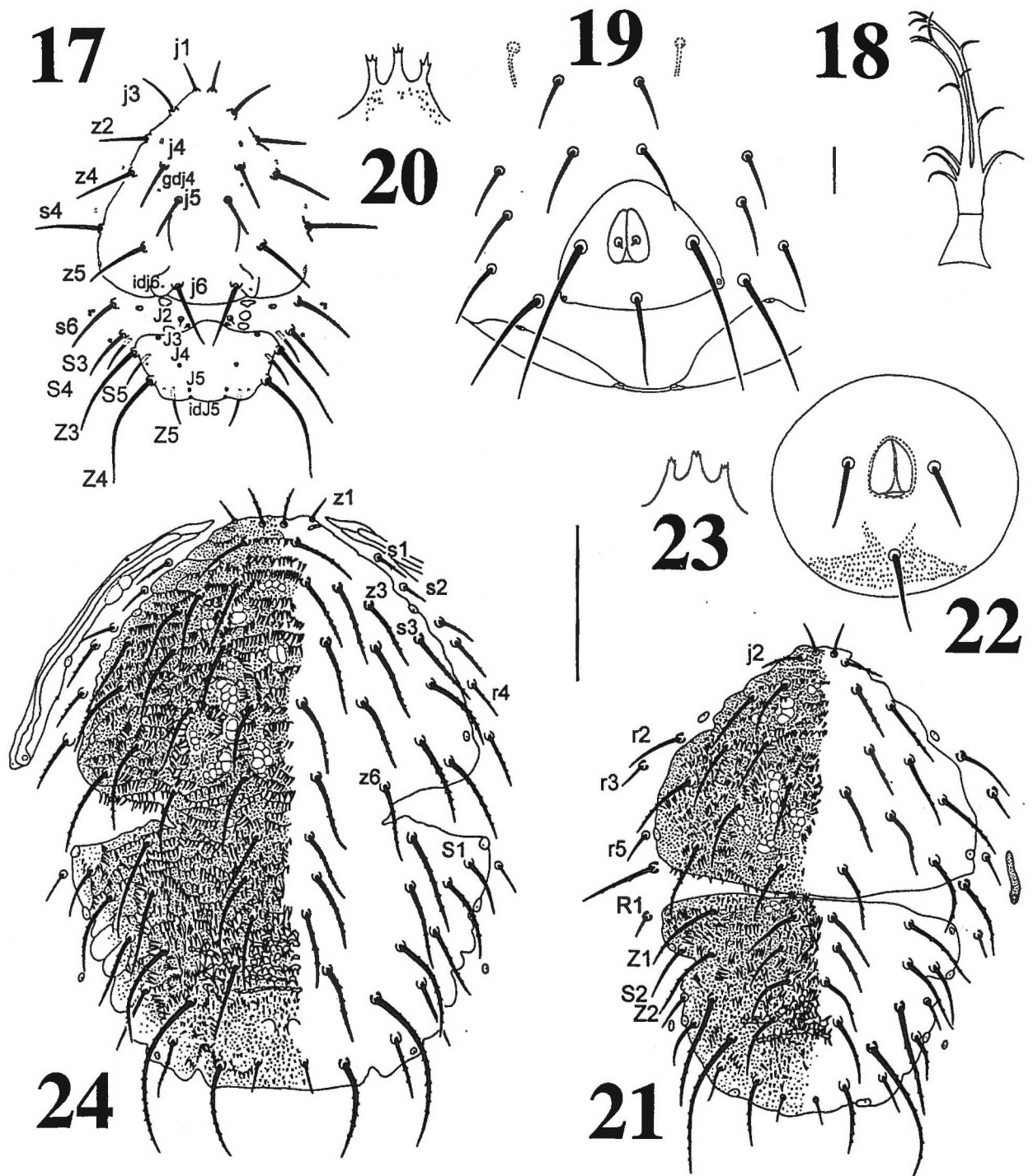
PROTONYMPH. *Idiosomal dorsum* (Fig. 21). Idiosoma (length 250–300) covered by two dorsal shields covered in dense spiculate-tuberculate ornamentation that occludes ready discernment of porelike structures. Anterior shield (length 145–160, greatest width 190–215), bearing 11 pairs of elongate, barbed setae, *j1-j6*, *z2*, *z4-z5*, *s4-s5*; *s6* in soft cuticle at shield corner; *r2*, *r3*, *r5* simple, in soft cuticle; poroids *idz3* in soft cuticle alongside notch in lateral margins of shield; setal lengths: *j1* (18–21), *j2* (25–28), *j3-j5* (35–40), *j6* (40–41), *z2*, *z4*, *z5* (38–43), *s4* (42–45), *s5* (45–49), *s6* (45–52), *r2* (35–36), *r3*, *r5* (20–24). Posterior shield (length 103–125, greatest width 160–195) with 14 pairs of mostly elongate, barbed setae: *J1-J5*,

Z1-Z5, *S2-S5*; setal lengths: *J1-J3* (25–35), *J4* (40–44), *J5* (15–16), *Z1*, *Z2* (50–54), *Z3* (60–73), *Z4* (75–88), *Z5* (40–42), *S2* (35–36), *S3* (20–22), *S4* (20–29), *S5* (20–24); shield notched behind *S2*; *R1* (8–14) in soft cuticle.

Idiosomal venter. Sternal shield faintly sclerotized, with 3 pairs of setae, *st1-st3* (17–20), and 2 pairs of poroids, *iv1-iv2*; setae *st5* (8–9) in soft cuticle. Opisthogaster with 4 pairs of setae, *JV1-JV2*, *JV5*, *ZV* in soft cuticle, *JV1* (17) longer than *JV2*, *JV5*, *ZV2* (10–11). Anal shield (Fig. 22) oval (length 50, width 60), with para-anal setae (16–18) subequal to postanal seta, euanal setae suppressed; with dense cribrum field behind and beside postanal seta; posterior margin of anal shield closely flanked by posterior margin of posterior dorsal shield. Peritreme short (30–35), reaching to insertion of *r5*.

Gnathosoma. Gnathotectum (Fig. 23) as in larva but tines less serrated, and dorsal surface smooth. Hypognathum with 4 pairs of simple setae, *h1*, *h2*, *pc* (22–25) longer than *h3* (15–17); other hypognathal structures as in larva. Fixed cheliceral digit (67–75) with row of 13–14 teeth, a tiny offset subapical tooth, and pilus dentilis (3); movable digit (27–33) with 3 teeth. Palpal length 90–100; palp trochanter, femur, genu, tibia, tarsus setation, respectively: 1-4-5-12-15; anterolateral seta on genu and femur spatulate; dorsal setae *d-1*, *d-2* smooth on palpfemur.

Legs. Lengths of legs, excluding ambulacra, I (225–240), II (175–200), III (170–195), IV (180–235). Pretarsal structures as in larva. Setation of legs I–II–III–IV respectively, coxae: 2-2-2-2; trochanters: 4-4-4-4; femora: 10-8-5-4; genua: 8-6-6-5; tibiae: 8-7-7-7. Chaetotactic formulae, femora: 2-2/1, 2/1-2; 1-2/1, 2/1-1; 1-1/1, 2/0-0; 1-1/0, 2/0-0; genua: 1-2/1, 2/1-1; 1-2/0, 2/0-1; 1-2/0, 2/0-1; 1-2/0, 2/0-0; tibiae: 1-2/1, 2/1-1; 1-1/1, 2/1-1; 1-1/1, 2/1-1; 1-1/1, 2/1-1. Most dorsal and lateral setae slightly barbed on femur, genu, tibia of legs I–IV; other setae smooth. Form of setae, pretarsus, claws on tarsus I as in larva. Tarsi II–IV (Figs. 10–12) with apical setal processes *ad-1*, *pd-1* (11–14), pretarsi (12–14), paradactyli (12–13) and claws as in larva. Tarsus II with only seta *pl-2* elongate (32–35), whiplike, reaching nearly to base of pretarsus; *ad-3* similar to *pd-3* in moderate length (21–25), slender, similar to basitarsal setae (20–24); other telotarsal setae, including mediodorsal *ad-2*



FIGS. 17-24. *Arrhenoseius gloriosus* n. sp. 17. — Idiosomal dorsum, larva. 18. — Tritosternum of larva. (19) Anal shield and adjacent opisthosomal setae, larva. 20. — Gnathotectum of larva. 21. — Idiosomal dorsum, protonymph. 22. — Anal shield of protonymph. 23. — Gnathotectum of protonymph. 24. — Idiosomal dorsum, deutonymph. Scale bars = 100 μ m (17, 21, 24); 10 μ m (28, 20, 23).

added on protonymph, short (7–12), stout, as in larva. Tarsus III with setae formed as on tarsus II except *pl-2* on telotarsus (7–10) and *pl-4* on basitarsus (9–12), short, stout. Tarsus IV with setae formed as on tarsus III except *al-2* longer (17) and slenderer, and ventrals *av-2*, *pv-2* moderately long (22–25), slender, like *ad-3*, *pd-3*, and *pd-4* longer (32).

DEUTONYMPH. *Idiosomal dorsum* (Fig. 24). Dorsum covered by shield (length 300–375, greatest width 250–270) with deep midlateral incisions extending to level of setae *z6*; shield covered in dense spiculate-tuberculate ornamentation except in posterior marginal scalloped areas, discernment of porelike structures occluded; spicules reduced in areas posterior to setae *Z4*. Anterior portion of shield bearing 16 pairs of setae, *j1-j6*, *z1-z6*, *s3-s6*, these barbed and mostly elongate, except *z1* short, smooth; 6 pairs of setae, *s1-2*, *r2-5*, in soft cuticle laterad shield, these slightly barbed except short *s2* smooth, none erect; setal lengths: *j1* (24), *j2* (38), *j3-j6* (45–50), *z1* (14), *z2* (50), *z3* (43), *z4* (52), *z5-z6* (41–46), *s1* (27), *s2* (15), *s3-s4* (51), *s5* (55), *s6* (60), *r2* (22), *r3* (30), *r4* (25), *r5* (35). Posterior portion of shield with 15 pairs of setae, *J1-J5*, *Z1-Z5*, *S1-S5*, these mostly elongate, barbed, except *S1* smooth, *J5* sparsely barbed basally; *R1* smooth, in soft cuticle laterad shield; setal lengths: *J1-J3* (43–46), *J4* (50), *J5* (22), *Z1* (62), *Z2* (53), *Z3* (62), *Z4* (100), *Z5* (59–61), *S1* (32), *S2* (51), *S3-S5* (39–41), *R1* (19).

Idiosomal venter. Sternogenital shield lightly sclerotized, smooth, except genital region lightly ornamented with oblique wavy lines; with 4 pairs of setae, *st1-st4* and 3 pairs of poroids, *iv1-iv3*; *st1-st3* (25–31) longer than *st4* (17); setae *st5* (21) and poroids *iv5* in soft cuticle. Opisthogaster soft cuticle with 8 pairs of setae on females (*JV1-JV5*, *ZV1-ZV3*), but with 5 pairs on males (lacking *JV4*, *ZV1*, *ZV3*); these setae of moderate length (13–21). Anal shield smooth, subquadrate (length ca 60–80, width ca 80–85), with para-anal setae (16) nearly as long as postanal seta (16–21), euanal setae suppressed; with pair of widely spaced gland pores *gv3* on lateral edges of shield at level of para-anal setae, and with broad (width 50) cribrum field behind postanal seta. Peritrematal shield lightly sclerotized, free from dorsal shield anteriorly, with poroid *ip1* at level of setae *r3*, gland pore *gp1* at level of *r4*, and poroid

ip2 on posterior extremity closely behind stigma; peritreme extending to level of insertion of *j2*.

Gnathosoma. Gnathotectum triramous, tines smooth, sharply pointed. Hypognathum as in protonymph, except 5th row of deutosternal denticles conspicuously narrower than 4th and 6th rows. Fixed cheliceral digit (75–85) with row of 14–15 teeth, otherwise as in protonymph; movable digit (30–35) with 3 teeth. Palpal length 115; palp trochanter, femur, genu, tibia, tarsus setation, respectively: 2-5-6-14-15; form of palpal setae as on protonymph, palp genu with *al-2* spatulate like *al-1*.

Legs. Lengths of legs, excluding ambulacra, I (295), II (250), III (230), IV (268). Setation of legs I–II–III–IV respectively, coxae: 2-2-2-2; trochanters: 6-5-5-5; femora: 12-11-6-6; genua: 13-11-9-9; tibiae: 13-10-8-9. Chaetotactic formulae, femora: 2-3/2,2/1-2; 2-3/1,2/2-1; 1-2/1,2/0-0; 1-2/1,1/0-1; genua: 2-3/2,3/1-2; 2-3/1,2/1-2; 2-2/1,2/1-1; 2-2/1,3/0-1; tibiae: 2-3/2,3/1-2; 2-2/1,2/1-2; 2-1/1,2/1-1; 2-1/1,3/1-1. All setae on legs I–IV smooth. Form of setae, pretarsus, claws on tarsus I as in protonymph. Tarsi II–IV with apical setal processes *ad-1*, *pd-1*, pretarsi (11–13) and claws as in protonymph; paradyctyli (10–11) relatively smaller than in protonymph. Tarsus II with setae formed much as in protonymph: only seta *pl-2* elongate (40), whiplike, reaching nearly to base of pretarsus; *ad-3* similar to *pd-3* in moderate length (28), and similar in slender form and length to medioventral seta *av-3* added on deutonymph and to basitarsal setae (25–26); other telotarsal setae short (8–15), stout. Tarsus III with setae formed as in protonymph; medioventral seta *av-3* added on deutonymph slender (26). Tarsus IV with setae formed much as in protonymph: *pd-3* (34) longer than *ad-3* (24); medioventral seta *av-3* (30) added on deutonymph and ventrals *av-2*, *pv-2* (28) moderately long, slender; basitarsus with *pl-4* short (10), stout, *pd-4* (40) conspicuously longer than *ad-4* and *al-4* (25).

Biology

Populations of *Arrhenoseius gloriosus* are present in subtropical rainforest litter in south east Queensland from the moist montane forests in the Border Ranges along the New South Wales border, at least as far north as the similar forests in the Conondale

Ranges in the Sunshine Coast hinterlands, and west to the dry rainforests of the Bunya Mountains. Most collections are from forest floor litter, but the mites also inhabit crows nest fern litter in the rainforest canopy at Lamington National Park. The larva and all subsequent instars are voracious predators of nematodes. Cultures were established from a collection from about the middle of its known range, on Mt Glorious north of Brisbane.

At a constant temperature of 25° C, *A. gloriosus* develops from egg to adult in 6–7 days, with males reaching maturity about a half day earlier than females. Female deutonymphs are guarded by males, which rest their front legs on the torpid nymphs or sit on their backs, and are mated immediately after eclosion. Females can live for 3–4 weeks after reaching maturity and lay an average of 1 egg per day during this period. Males will also court older, fully sclerotised females, riding their backs and eventually descending onto the female's venter and applying their mouthparts to the leg bases; however, these mating attempts apparently are futile. For females mated when recently emerged, progeny sex ratios are strongly female-biased ($65 \pm 2\%$ female); however, females that are not allowed access to males until they are fully sclerotised have only sons. Virgin females kept isolated from any contact with males lay fertile eggs, but these also develop only into males, indicating that males are probably haploid and that the genetic system in *A. gloriosus* is arrhenotoky.

REMARKS

What little is known of the biology of *Zercozeius spathuliger* is difficult to compare with the observations above for *A. gloriosus*. Based on observations of ATHIAS-HENRIOT (1967), some populations of *Z. spathuliger* seem to be thelytokous, while others may possibly be arrhenotokous rather than pseudoarrhenotokous, in view of the highly female-biased sex ratios that she noted.

Spiculate dorsal shield ornamentation has rarely been noted among mesostigmatic mites, and ascid mites in particular. We have observed a less dense spiculation on adults of an undescribed species of *Proctolaelaps* that inhabits *Cryptoporus* shelf fungi in

coniferous forests of northeastern California, a completely different habitat than that of *Arrhenoseius gloriosus*.

The absence of deutonymphal setae *JV4*, *ZV1*, *ZV3* on the adult male of *A. gloriosus* is noteworthy, as this may reflect either of two phenomena. If these setae are present on the deutonymphal male, then they must be suppressed subsequently in the adult. If they are absent on the deutonymphal male, then deutonymphs are sexually dimorphic in opisthogastric setation and they may be recognized as male or female. The arrhenotokous genetic mechanism in *A. gloriosus* makes it a useful animal to readily address this question. Our study of all-male progeny reared from an unmated female indicate that the male deutonymph lacks setae *JV4*, *ZV1*, *ZV3*, as in the male adult, indicating deutonymphal sexual dimorphism. In contrast with *A. gloriosus*, both male and female adults of *Z. spathuliger* retain the same full complement of opisthogastric setae that are present in the deutonymph.

DISCUSSION

Though unusual and evidently apomorphic, the protonymphal attribute of an expansive posterior dorsal shield in *Arrhenoseius* can not be compared effectively for phylogenetic analysis, as the protonymph of relatively few other taxa of Ascidae and related families are known or described. Similarly, the patterns of ontogenetic changes in setal form on tarsi II to IV in *Arrhenoseius* can not be assessed cladistically in the absence of comparable observations and data for other taxa. The latter points to a more general problem concerning the inadequacy and incompleteness of descriptions of taxa of Mesostigmata, especially as they concern changes in structures through ontogeny. For example, MORAZA & LINDQUIST (1999) noted the unusual absence of one of the pseudosymmetric pairs of ventral setae on tarsi II to IV in their newly-described zerconoid genus *Coprozercon*; but even more unexpected was their observation that this is a regressive deficiency, i.e., a suppression of setae that are present on the deutonymph. The uniqueness of that condition is uncertain in view of the lack of comparable data for many other taxa of

Gamasida. The following observations of ontogenetically abrupt changes in form of tarsal setae in *Arrhenoseius* may be another case in point.

Tarsi II and III of the larva of *Arrhenoseius gloriosus* are nearly identical in form of their setation: setae *ad-3* and *pl-2* are similarly elongated and whiplike; between them, *pd-3* is shorter and slender like the four basitarsal setae; and the other telotarsal setae are short and stout (Figs. 13, 14). On the protonymph, *ad-3* of tarsi II–III and *pl-2* of tarsus III are shortened and no longer whiplike, and tarsus III further differs from tarsus II in *pl-4* being short and stout; setation of tarsus IV resembles that of tarsus III except for *al-2* and especially *av-2* and *pv-2* being longer and slender on the telotarsus, and *pd-4* being longer on the basitarsus (Figs. 11–12). Apart from the normal addition of medioventral seta *av-3*, setation of tarsi II–IV on the deutonymph remains similar in form to that on the protonymph. By contrast, on the adult of both sexes, tarsus II reverts to the larval condition in having the same two setae, *ad-3* and *pl-2*, elongated and whiplike, with *pd-3* much shorter between them; tarsus III differs in having *ad-3* elongated, whiplike, as in the larva but *pl-2* short, spinelike, as in the protonymph; and tarsus IV expresses a new pattern in having *ad-3* and adjacent *pd-3* (instead of *pl-2*) elongated, whiplike, and having *av-2* and *pd-4* shorter but *pv-2* and *av-3* longer than in the deutonymph (Figs. 7–9). Such patterns of change in setal form, both among tarsi II to IV of the same instar and between tarsi II to IV of different instars, do not occur in *Zercozeius spathuliger* and have not been documented among other taxa in Ascidae or related families. There may be a wealth of new attributes of potential phylogenetic importance among such patterns.

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