

Copyright © 2013 Magnolia Press





http://dx.doi.org/10.11646/zootaxa.3750.2.2 http://zoobank.org/urn:lsid:zoobank.org:pub:FB4B18B4-BA1E-4E04-9A2B-E2B63FF4E4B0

A new genus and species of Discozerconidae (Acari: Mesostigmata) from carabid beetles (Coleoptera: Carabidae) in New Zealand

OWEN D. SEEMAN¹ & MICHELLE R. BAKER²

¹Queensland Museum, PO Box 3300, South Brisbane, Queensland, 4101, Australia. owen.seeman@qm.qld.gov.au ²Griffith School of Environment, Griffith University Nathan Campus, 170 Kessels Rd, Nathan, Queensland, 4111, Australia

Abstract

Berzercon ferdinandi gen. nov., sp. nov. (Acari: Mesostigmata: Discozerconidae) is described from carabid beetles in New Zealand. As in all Discozerconidae, *Berzercon* has large ventrally-directed opisthogastric suckers. However it is distinctive in its long marginal setae, tripartite gnathotectum, fused palp tibia and tarsus, the female's large dome-shaped genital shield and the male's highly modified hypostomal seta h_1 . This new species also represents the first Heterozerconina from an insect host.

Key words: Heterozerconina, Sejida, taxonomy, species relationships, leg chaetotaxy

Introduction

Mites in the cohort Heterozerconina (Acari: Mesostigmata) are remarkable for their large opisthogastric suckers that allow them to adhere to their smooth, cylindrical hosts: centipedes (Discozerconidae) or millipedes, snakes and worm-lizards (Heterozerconidae). Only adult mites have suckers and associate with hosts. Their diet is unknown, although blood was found in the gut of Amheterozercon amphisbaenae (Flechtmann & Johnston), suggesting that parasitism occurs in species associated with reptiles (Flechtmann & Johnston 1990). Immature life stages are described only for Narceoheterozercon ohioensis Gerdeman & Klompen 2003 and an undescribed Brazilian species (Krantz & de Moraes 2011). The immature stages are free-living and N. ohioensis is predacious (Gerdeman et al. 2000; Gerdeman & Garcia 2009 (2010); Krantz & de Moraes 2011). The cohort-level relationships are unresolved. Johnston in Norton et al. (1993) suggested a sister-group relationship with the Trigynaspida, but Klompen (2000) and Lekveishvili & Klompen (2004) presented DNA evidence showing that the Heterozerconina are highly modified members of the cohort Sejina. Although these data are the best available evidence for classifying the Heterozerconina, Lindquist et al. (2009) continued to treat the group as its own separate cohort pending further evidence regarding the placement of these two enigmatic families. This treatment is followed here. The Heterozerconidae is a small family of 20 described species (Fain 1989; Klompen et al. 2013). The most remarkable synapomorphy of the family is the independent evolution of podospermy and a secondary sperm access system. Podospermy is best known in the Parasitina and Dermanyssina and, in both groups, involves the modification of the moveable digit for sperm transfer. Podospermy probably also occurs in some Antennophorina (e.g., Diplogyniidae), where males have modified cheliceral excrescences on the moveable digit, presumably to assist in transfer of the spermatophore (e.g., Seeman 2012). In contrast, male Heterozerconidae have a coiled spermatodactyl, but on the fixed digit of the chelicera (Di Palma et al. 2008). Female Heterozerconidae also possess a unique secondary sperm access system (Gerdeman et al. 2000).

The Discozerconidae comprises just three species: the type species, *Discozercon mirabilis* Berlese, collected from *Scolopendra subspinipes* Leach in Java (Berlese 1910); *Discozercon derricki* Domrow from scolopendrid centipedes in Australia (Domrow 1956); and *Discomegistus pectinatus* Trägårdh from *Scolopendra gigantea* L. in Trinidad (Trägårdh 1911). Unlike the Heterozerconidae, male discozerconids lack a coiled spermatodactyl, although *Discomegistus* does have a sexually dimorphic fixed digit (Trägårdh 1911), perhaps representing a precursor to the heterozerconid spermatodactyl. Female *Dz. derricki* lack a secondary sperm access system (pers. obs.), but whether this system is present in *Dz. mirabilis* and *Dm. pectinatus* is unknown.

The Discozerconidae all have similar opisthogastric suckers: they are large, directed ventrally and connected to soft cuticle. In contrast, those of the Heterozerconidae are connected to the anterior wall of a deep groove, and thus are directed posterolaterally (Gerdeman & Alberti 2007). Although the two families are closely related (Lekveishvili & Klompen 2004), these markedly different suckers caused Domrow (1956) to speculate that they have arisen independently. The existence of an undescribed Heterozerconidae without suckers (Lindquist *et al.* 2009; Klompen, pers. comm.) supports this opinion.

Herein, we describe a new species of Discozerconidae from New Zealand, collected from carabid beetles, a new class of host for the Heterozerconina. The new species bears little resemblance to *Discozercon*, and even less to *Discomegistus*, and therefore a new genus is erected to accommodate it.

Materials and methods

Mites were collected from live carabid beetles or from residues of pitfall traps that had captured carabid beetles. Mites were preserved in 80% ethanol. Specimens for light microscopy were cleared in Nesbitt's solution, mounted in Hoyer's medium, and examined under phase contrast (x200) or DIC (x400, x1000) with a Nikon Eclipse 80i microscope. Measurements are presented in micrometres and are presented as the measurement of the holotype first, followed by the range of all specimens. Most measurements were rounded to the nearest 10 for values > 1000 and nearest 5 for values < 1000; very small structures were measured to the nearest micrometre under oil immersion. Specimens for scanning electron microscopy were dried by placing them in an increasing series of ethanol concentrations to 100%, followed by drying in Hexamethyldisilazane (HMDS). They were then sputter-coated with gold and examined with a HitachiTM TM-1000.

Results

Discozerconidae Berlese, 1910

Diagnosis. Heterozerconina with: male chelicera without coiled spermatodactyl on fixed digit; female without secondary sperm access system; opisthogaster with pair of suckers directed ventrally, not in socket, arising from soft cuticle; metapodal shields separate from sternal and ventrianal shields.

Berzercon Seeman & Baker gen. nov.

Diagnosis. Male and female: Dorsal setae minute; marginal setae r2-R2 long; numerous shorter blade-like marginal setae fringing posterior margin between R2-R2. Presternal shield unpaired. Sternal shield fused with endopodal shield, bearing setae st1-4. Ventrianal shield long, thin, bearing one pair of ventral setae, postanal seta, and para-anal setae; ventrianal shield flanked by broad rectangular shield; metapodal shields fused in their anterolateral corner with peritrematal shield. Gnathosoma with strong corniculi; gnathotectum tripartite, with weak keel; palp tibia and tarsus fused; palp femur with lateral finely porose area. Moveable digit of chelicera with one simple excrescence; chelicerae with lateral membranous process. Pretarsi I–IV without claws; tarsi I–IV with apical flanges. Female: genital shield dome-shaped, reaching almost to anterior margin of sternal shield, with lateral sclerotised margin and medial spatulate process; genital opening not apparent; hypostomal seta h1 thick. Male: genital opening at anterior margin of sternal shield; hypostomal seta h1 highly modified.

Etymology. The genus name is constructed to sound like *berserk*, derived from Old Norse (*ber*-bear; *serkr*-coat), and in English meaning wild, frenzied and crazy. The suffix *-zercon* is commonly used in the Mesostigmata, especially Heterozerconina. Here, the genus name is meant to reflect the exceptional appearance of this beautiful mite.

Remarks. The new genus has several characteristics not present in other Discozerconidae: the long marginal setae, a tripartite gnathotectum, a fused palp tibia and tarsus, the arrangement of ventral shields and the male's highly modified seta h1. It does, however, share some characteristics with *Discozercon*: the long, thin ventrianal

shield; the bare shields flanking the ventrianal shield (posterior to the suckers); unmodified male chelicerae; and the anteriorly-positioned female genital shield. These characters suggest a closer relationship to *Discozercon* than *Discomegistus*, with which *Berzercon* shares the fusion of the endopodal shields with the sternogenital shield only.

Berzercon ferdinandi Seeman & Baker sp. nov.

Figures 1-22

Type material. Holotype: Female, New Zealand, Wairarapa, Mt Holdsworth, 11.iv.2004, A.M. Paterson, ex *Megadromus* sp. (Carabidae). Deposited in Landcare Research, Auckland, New Zealand. Paratypes: 3 males, same data as holotype; 1 female, 2 males, same data as holotype except ex *Mecodema* sp. (Carabidae), 15.xi.2002; 1 female, same data as holotype, except ex *Plocamostethus* sp. (Carabidae), 15.xi.2012. 2 females, 1 male, New Zealand, Waikato, Maungatautari (South Cell, outside CR4, transect 1, pitfall trap G), Jan–Feb 2009, C.H. Watts. 3 females, 3 males, New Zealand, Waikato, Limestone Downs (Contact Energy Waikato Wind Farm, block C, track CO15-CO13, trap D), 22 Dec 2009 – 13 Jan 2010.

Paratype deposition: 3 females, 5 males, Landcare Research, Auckland, New Zealand; 1 female, 1 male, Canterbury Museum, Christchurch, New Zealand; 2 females, 2 males, Queensland Museum, South Brisbane, Australia; 1 female, 1 male, Ohio State University, USA (OSAL0104614 (M) and OSAL0104613 (F)).



FIGURE 1. Berzercon ferdinandi sp. nov., adult female, ventral idiosoma.



FIGURES 2-3. Berzercon ferdinandi sp. nov., adult female. 2, ventral gnathosoma; 3, chelicera.

Other material: 1 female, 1 male gold-coated on SEM stub (QM). 1 females, 3 males, OSU (unmounted).

Collection notes: The sample from Maungatautari had seven species of carabid beetles: *Mecodema oconnori* (n = 1), *Parabaris atratus* (n = 10), *Ctenognathus* sp. (n = 2), *Dicrochile* sp. (n = 2), *Aulacopodus calathoides* (n = 1), *Holcaspis mordax* (n = 1) and *Molopsida polita* (n = 1). The sample from Limestone Downs had six species of carabid beetles: *Aulacopodus calathoides* (n = 1), *Ctenognathus bidens* (n = 8), *Ctenognathus lucifugus* (n = 4), *Dicrochile* sp. (n = 1), *Holcaspis mordax* (n = 4) and *Mecodema crenaticolle* (n = 2).

Description. *Female* (n = 8; Figures 1–11)

Dorsum (see male Fig. 12). Dorsal idiosoma length 1500 (1150-1500), width 1350 (1010-1350), with approximately 84 loosely paired minute setae.

Venter (Figs 1, 8–10). Tritosternum length 310 (270–310), laciniae separate, length 245 (225–245). Presternal shield entire, length 70 (50–70), width 255 (200–255), reticulate. Sternal and endopodal shields fused; cuticle reticulate medially, becoming smooth laterally. Genital shield dome-shaped, fused posteriorly at level of coxa III, extends anteriorly almost to anterior margin of sternal shield; genital shield reticulate. Sternogenital shield length 665 (525–665), width 570 (475–570). Genital shield length 215 (205–235), width 310 (275–310). Four pairs of intercoxal setae: *st1* lightly barbed, 65 (35–75), *st2* lightly barbed 70 (35–70), *st3* smooth, 75 (40–75), *st5* smooth 45 (35–45); setae *st1–3* flank genital shield; setae *st5* posterior to genital shield. Two pairs of lyrifissures, *stp1* anterolaterad *st2*, *stp2* anteriad *st3*. Genital shield with one pair of pores. Internal genital structure present, tongue-shaped, length 160 (140–165), width 35 (25–40).

Opisthogaster with one pair of large suckers (Figs 1, 10), length 380 (275–380), width 280 (235–280). Four pairs of lightly barbed setae anterior to suckers, in soft cuticle, most medial setae length 65 (35–65), other setae 95–105 (70–95). One pair of medial post-sternal setae, in soft cuticle, length 80 (45–80). Ventrianal shield elongate, finely reticulate, length 265 (245–325), width 170 (135–170), cribrum present. Anterior ventrianal setae with

barbed tip, 65 (50–65); para-anal setae lightly barbed, 115 (80–115); postanal seta lightly barbed, 45 (35–45). Paired ventral shields posteriad suckers, reticulate, one pair of pores in anterolaterad margin, length 110 (95–110), width 275 (195–290). Metapodal shields reticulate, bearing three pairs of smooth to lightly barbed setae 115–135 (90–135) and two pairs of pores laterad setae; anteriorly fused to exopodal shield. Ventral marginal shield present, bearing short flattened marginal setae. All areas of soft cuticle with faint reticulation.



FIGURES 4–7. *Berzercon ferdinandi* sp. nov., adult female. 4, leg I; 5, leg II; 6, leg III; 7, leg IV. Leg setae are partially labelled to aid orientation; see description for formulae.

Exopodal, post-stigmatal, peritrematal and lateral marginal shields fused, but with lines of fusion present; shields reticulate, becoming weaker anteriorly. Stigmata at posterior level of coxa III, peritreme short, length 175 (150–180), extending to posterior level of coxa II. Porose areas posterolaterad stigmata, laterad peritreme, anteriad peritreme, and anterior to coxa I.

Marginal setae r2-R2 long, barbed, with flattened serrate tips, r2 245 (185–245), r3 140 (110–140), r4 > 160 (180–200), r5 325 (270–335), r6 195 (135–195), R1 > 335 (325–360), R2 320 (265–320). Marginal setae posterior to R2 hypertrichous, 35–46 setae; all setae broad, flattened, with 3-pointed tips; 5–6 longer setae (90–110 long) interspersed amongst shorter setae (60–75 long).



FIGURES 8–11. *Berzercon ferdinandi* **sp. nov.**, adult female, scanning electron micrographs. 8, venter (scale bar = 500 μ m); 9, sternogenital shield (scale bar = 200 μ m); 10, opisthogaster (scale bar = 300 μ m); 11, ventral gnathosoma (scale bar = 200 μ m).

Gnathosoma (Figs 2, 11). Gnathotectum tripartite (see male Fig. 15), length 345 (295–345), middle process longest; weak keel present, extending to tip of middle process. Hypostomal setae h1 thick, barbed at tip, length 120 (105–135); setae h2 barbed, length 110 (95–110); setae h3 smooth, length 55 (40–55). Palpcoxal setae barbed, length 105 (80–110). Deutosternum reticulate, with ca. 13 rows of denticles laterad gutter; deutosternal gutter with ca. 8 irregular rows of denticles. Corniculi large, curved, horn-like, length 175 (170–190). Internal malae long, divided mid-way into a ribbon-like process and a thicker process with one edge ciliated. Palps four-segmented, tibia and tarsus fused. Palp apotele two-pronged. Setal counts 2-5-6-20. Most adaxial setae barbed. Trochanter with small distal adaxial process. Femur with large abaxial area of darker, densely porose cuticle; seta al short, thickened. Genu with three smooth, thin setae clustered. Tibiotarsus tip with six blunt-tipped sensory setae.

Chelicerae (Fig. 3). Fixed digit length 400 (315–400), with 13–18 small and two larger teeth; pilus dentilus blade-like, length 12 (10–12); cheliceral seta arises laterally, smooth, length 45–55. Moveable digit length 230 (190–230), with 6–10 small teeth, proximal tooth largest; single smooth excrescence arises ca. one-third distance from base of moveable digit, excrescence length 55 (40–55). Interdigital membrane (*sensu* Fain 1989) arising adaxially at base of digits, length 45–55.

Legs (Figs. 4–7). Tarsus I with acrotarsus. Pretarsi without claws, membranous. Tarsal tips with small membranous flanges. Setal counts: coxae 2-2-2-1; trochanters 6-5-5-5; femora 11-11-8-7; genua 12-9-10-11; tibiae 12-10-10; tarsi 43-18-18. Setal formulae for femora: I 2,2/1,3/1,2; II 1,2/2,3/2,1; III 1,2/1,2/2,0; IV 1,2/1,2/1,0. Setal formulae for genua: I 2,3/1,3/1,2; II 2,2/1,2/0,2; IV 2,3/1,3/0, 2. Setal formulae for tibiae: I 2,3/1,3/1,2; II-IV 2,2/1,2/1,2. Chaetotaxy presented on figures. Tarsus I with acrotarsus bearing ca. 17 setae; dense cluster of setae on dorsal side of tarsal tip and acrotarsus (see male Fig. 21); legs with some setae thickened, but most noticeably FeI *av1* and TaI *av3*; tarsi II-IV *ad1*, *pd1* with spatulate tips (see male Fig. 22).



FIGURE 12. Berzercon ferdinandi sp. nov., adult male, dorsal idiosoma.

Dorsum (Fig. 12). Similar to female. Dorsal idiosoma length 1110–1460, width 1350. *Venter* (Figs 13, 17–19. Tritosternum length 260–290, laciniae length 190–230. Presternal shield entire, length

Male (n = 9; Figures 12–22)

45–50, width 165–205. Sternal and endopodal shields fused; cuticle reticulate medially, becoming smooth laterally. Genital opening just behind margin of sternal shield, length 85–105, width 90–130. Sternal shield length 500–670, width 425–590. Four pairs of intercoxal setae: *st1* lightly barbed, 35–65, *st2* smooth, 40–60, *st3* smooth, 35–65, *st5* smooth 35–50. Two pairs of lyrifissures, *stp1* anterolaterad *st2*, *stp2* anteriad *st3*. Marginal setae *r2* 140–195, *r3* 75–140, *r4* 145–205, *r5* 255–350, *r6* 115–165, *R1* 270–330, *R2* 225–270.



FIGURE 13. Berzercon ferdinandi sp. nov., adult male, venter.

Opisthogaster similar to female. Sucker length 250–325, width 235–295. Four pairs of lightly barbed setae anterior to suckers, in soft cuticle, most medial setae length 35–55, other setae 70–90. One pair of medial post-sternal setae, in soft cuticle, length 50–60. Ventrianal shield elongate, finely reticulate, length 235–295, width 130–170, cribrum present. Anterior ventrianal setae smooth, 45–65; para-anal setae lightly barbed, 80–100; postanal seta lightly barbed, 30–50. Metapodal setae lightly barbed 90–130.

Gnathosoma (Figs 14–15). Gnathotectum tripartite, length 260–340, middle process longest; weak keel present, extending to tip of middle process. Hypostomal setae h1 modified, tip shaped like a fish-tail, base with medial process, length of seta 75–115; setae h2 smooth, 55–65; setae h3 bulbous, length 15–21, width 8–12. Palpcoxal setae barbed, length 105–125. Deutosternum, corniculi, internal malae similar to female. Palps similar to female.

Chelicerae (Fig. 16). Similar to female. Fixed digit length 295–355, with 10–14 small and two larger teeth. Moveable digit length 180–220, excrescence length 45–58.

Legs (Figs 21–22). Similar to female, no spurs or stronger setae.



FIGURES 14–16. Berzercon ferdinandi sp. nov., adult male, 14, ventral gnathosoma; 15, gnathotectum; 16, chelicera.

Etymology. This new species is named for Ferdinand the Bull, the main character of Munro Leaf's 1936 book, and loosely refers to the mite's large curved horn-like corniculi.

Remarks. We have treated all the material as the same species because we lack strong morphological evidence to separate them. However, the specimens exhibited a large size range, with the largest mites being from Mt Holdsworth (female 1420–1500; male 1260–1460) and the smallest from Limestone Downs (female 1150–1280;

male 1110–1260). Apart from these ambiguous size differences, no other features separated collections from different host species and sites. Additionally, each of the three collection sites, confined to the North Island, are distant to one another: Limestone Downs (northwest coastal) and Maungatautari (central north) are somewhat close together, but Mt Holdsworth is in the central-south. Consequently it seems surprising that these mites, whose hosts are flightless carabid beetles and occur in isolated habitats, seem to represent the same species.



FIGURES 17–22. *Berzercon ferdinandi* **sp. nov.**, adult male, scanning electron micrographs. 17, venter (scale bar = 1000 μ m); 18, sternogenital shield (scale bar = 200 μ m); 19, opisthogaster (scale bar = 200 μ m); 20, hypostome, right hand side (scale bar = 30 μ m); 21, acrotarsus and pretarsus I (scale bar = 50 μ m); 22, tarsus IV, arrows point to spatulate setae (scale bar = 100 μ m).

A noteworthy feature of *B. ferdinandi* is the presence of a keel on the gnathotectum, typically present only in the trigynaspid cohort Antennophorina. The keeled gnathotectum is expressed strongly in some antennophorine superfamilies (e.g., Megisthanoidea, Celaenopsoidea) but weakly in others and is sometimes absent (e.g., most Parantennulidae) (Kim 2004). The keel of *B. ferdinandi* is weak, visible as a long thin line, as seen in Fedrizzioidea, Aenictequoidea, Antennophoroidea and some Paramegistidae.

The presence of a keel may represent convergence, as a similar keel-like structure occurs in *Pyriphis* (Ologamasidae) (pers. obs.). However, a trigynaspid-heterozerconine sister-group relationship was suggested by Norton *et al.* (1993). Within the Trigynaspida, members of the Paramegistidae are associated with millipedes, lizards and snakes (e.g. Kim & Klompen 2002; Klompen & Austin 2007; Baker & Seeman 2008) and share at least a strikingly superficial resemblance. Many paramegistids are discoid, have smooth dorsal shields with numerous marginal setae, and extensive ventral shields, but these are probably independent adaptations to living on similar hosts. More curious are similarities between the chelicerae of the Paramegistidae and Heterozerconidae (and *Discomegistus*): both have a moveable digit with a fine row of cilia-like teeth and two interdigital membranes (one truly interdigital, the other on the fixed digit). Again, this probably reflects convergence in feeding habits on the same host taxon, but the likelihood of this being so is harder to dismiss due to the complex morphology of the chelicerae.

The modified hypostomal setae h1 of B. ferdinandi are also found in some sejid and trigynaspid taxa. In the Sejida setae h1 are often small and scale-like (e.g., Fig. 12.7D in Lindquist et al. 2009) but are not sexually dimorphic and bear little resemblance to the strong thick h1 setae of B. ferdinandi. In the Trigynaspida, *Promegistus* (Parantennuloidea: Promegistidae) have strikingly modified setae h1, being large and membranous in both sexes (pers. obs.), and many Ophiomegistus (Paramegistidae) and Antennophoridae have h1 much stronger than other hypostomal setae (e.g., Goff 1980; Wisniewski & Hirschmann 1992). Sexual dimorphism occurs in the hypostome and hypostomal setae of some Trigynaspida, most spectacularly in the Celaenopsidae, Euzerconidae, Schizogyniidae and Megacelaenopsidae (e.g., Kinn 1970; Funk 1974, 1980; Rosario 1988), but also less impressively in the Fedrizziidae (Seeman 2007). However these taxa are unlikely sister-groups of the Heterozerconina, being within well-established superfamilies (Celaenopsoidea and Fedrizzioidea, respectively). Instead, these partly illustrate the diversity of independently derived modifications found in male trigynaspid mites, presumably for transferring the spermatophore to the female's genital opening. Other examples are the Asternoseiidae (modified sternal setae, see Karg & Schorlemmer 2011, erroneously placed in Fedrizziidae), Saltiseiidae (modified gnathotecta; Walter 2000), Antennophoridae and Diplogyniidae (modified chelicerae; e.g., Wisniewski & Hirschmann 1992; Seeman 2012), and Fedrizziidae and Klinckowstroemiidae (modified presternal shields; e.g., Rosario 1988; Seeman 2007). Therefore, although the modified hypostomal setae of B. ferdinandi might provide a link with either the Sejida or Trigynaspida, the sexual dimorphism observed in these setae is likely to have evolved independently.

Acknowledgements

I am very grateful to Robert Cruickshank (Lincoln University, Christchurch), who first sent the mites, and to Stephen Thorpe (University of Auckland), who sent the specimens from Maungatautari, and to those who collected these specimens. Hans Klompen (Ohio State University), Jerry Krantz (Oregon State University), and Dave Walter (University of Alberta) all provided valuable discussion on this new mite, and Hans also provided much appreciated comments on the manuscript.

References

Baker, M.R. & Seeman, O.D. (2008) Mites and millipedes: a new *Neomegistus* (Acari: Mesostigmata: Paramegistidae) from Australia. *Systematic & Applied Acarology*, 13, 204–213.

Berlese, A. (1910) Brevi diagnosi di generi e specie nuovi di Acari. Redia, 6, 345-388.

Di Palma, A., Gerdeman, B.S. & Alberti, G. (2008) Fine structure and functional morphology of the spermatodactyl in males of Heterozerconidae (Gamasida). *International Journal of Acarology*, 34, 359–366. http://dx.doi.org/10.1080/17088180809434778

- Domrow, R. (1956) The family Discozerconidae (Acarina, Mesostigmata) in Australia. *Proceedings of the Linnean Society of New South Wales*, 81, 193–196.
- Fain, A. (1989) Notes on mites associated with Myriapoda. IV. New taxa in the Heterozerconidae (Acari, Mesostigmata). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Entomologie, 59, 145–156.
- Flechtmann, C.H.W. & Johnston, D. (1990) Zeterohercon, a new genus of Heterozerconidae (Acari: Mesostigmata) and the description of Zeterohercon amphisbaenae n. sp. from Brasil. International Journal of Acarology, 16, 143–148. http://dx.doi.org/10.1080/01647959008683526
- Funk, R.C. (1974) Megacelaenopsidae, a new family of Celaenopsoidea (Acari: Mesostigmata). Acarologia, 16, 382-393.
- Funk, R.C. (1980) Generic revision of the family Euzerconidae (Mesostigmata: Celaenopsoidea) with description of seven new genera. *International Journal of Acarology*, 6, 313–349.

http://dx.doi.org/10.1080/01647958008683236

- Gerdeman, B. & Alberti, G. (2007) First ultrastructural observations on the paired suckers of a heterozerconid mite (Heterozerconidae; Gamasida). In: Morales-Malacara, J.B., Behan-Pelletier, V., Ueckermann, E., Pérez, T.M., Estrada-Venegas, E.G. & Badii, M. (Eds.), Acarology XI: Proceedings of the International Congress. Instituto de Biología and Facultad de Ciencias, Universidad Nacional Autónoma de México; Sociedad Latinoamericana de Acarología. México, pp. 557–560.
- Gerdeman, B.S., Klompen, H. & Tanigoshi, L. (2000) Insights into the biology of a mite millipede association. *Fragmenta Faunistica, Warszawa*, 43 (Suppl.), 223–227.
- Gerdeman, B.S. & Klompen, H. (2003) A new North American heterozerconid, *Narceoheterozercon ohioensis* n.g., n. sp., with first description of immatures of Heterozerconidae (Acari: Mesostigmata). *International Journal of Acarology*, 29, 351–370.

http://dx.doi.org/10.1080/01647950308684352

- Gerdeman, B.S. & Garcia, R. (2009(2010)) Heterozerconidae: A comparison between a temperate and a tropical species. In: Sabelis, M.W. & Bruin, J. (Eds.), Trends in Acarology, Proceedings of the 12th International Congress. Springer Science, Dordrecht, pp. 93–96.
- Goff, M.L. (1980) The genus *ophiomegistus* (Acari: Paramegistidae), with descriptions of five new species, a new structure and a key to the species. *Journal of Medical Entomology*, 17, 398–410.
- Hunter, P.E. & Rosario, R.M.T. (1987) A new genus and species of Schizogyniidae (Acari: Trigynaspida: Celaenopsoidea). *International Journal of Acarology*, 13, 197–202.

http://dx.doi.org/10.1080/01647958708683767

Karg, W. & Schorlemmer, A. (2011) New insights into the systematics of Parasitiformes (Acarina) with new species from South America. Acarologia, 51, 3–29.

http://dx.doi.org/10.1051/acarologia/20111995

- Kim, C.-M. (2004) Trigynaspida (Acari: Mesostigmata): new diagnosis, classification, and phylogeny. *Acarologia*, 44, 157–194.
- Kim, C.-M. & Klompen, H. (2002) A new genus and species of Paramegistidae (Acari: Trigynaspida) associated with millipedes from Mexico. *Acarologia*, 42, 39–51.
- Kinn, D.N. (1970) A new genus of Celaenopsidae from California with a key to genera. *The Pan-Pacific Entomologist*, 46, 91–95.
- Klompen, H. (2000) A preliminary assessment of the utility of elongation factor-1? in elucidating relationships among basal Mesostigmata. *Experimental and Applied Acarology*, 24, 805–820.
- Klompen, H., Amin, M. & Gerdeman, B.S. (2013) A revision of the genus *Afroheterozercon* (Acari: Heterozerconidae). *Zootaxa*, 3626, 301–325.
 - http://dx.doi.org/10.11646/zootaxa.3626.3.1
- Klompen, H. & Austin, C.C. (2007) A new species of *Ophiomegistus* Banks (Acari: Paramegistidae) from Papua New Guinea. *Zootaxa*, 1387, 47–57.
- Krantz, G.W. & Moraes, G.J. de (2011) Discovery and description of nymphal stages of a heterozerconid mite (Acari: Mesostigmata: Heterozerconidae) from coastal forest litter in southeastern São Paulo State, Brazil. *In*: Moraes, G.J. de & Proctor, H. (Eds) *Acarology XIII: Proceedings of the International Congress. Zoosymposia*, 6, 24–33.
- Lekveishvili, M. & Klompen, H. (2004) Phylogeny of infraorder Sejina (Acari: Mesostigmata). Zootaxa, 629, 1-19.
- Lindquist, E.E., Krantz, G.W. & Walter, D.E. (2009) Order Mesostigmata. *In*: Walter, D.E. & Krantz, G.W. (Eds.), *A Manual of Acarolgy, Third Edition*. Texas Tech University Press, Lubbock, Texas. pp. 124–232.
- Norton, R.A., Kethley, J.B., Johnston, D.E. & OConnor, B.M. (1993) Phylogenetic perspectives on genetic systems and reproductive modes of mites. *In*: Wrensch, D. & Ebbert, M. (Eds.), *Evolution and Diversity of Sex Ratio in Insects and Mites*. Chapman & Hall, New York, pp. 8–99.
- Rosario, R.M.T. (1988) The genus *Antennurella* Berlese and descriptions of two new species of *Similantennurella* gen. nov. (Acarina: Trigynaspida: Klinckowstroemiidae). *Acarologia*, 29, 329–337.
- Seeman, O.D. (2007) Revision of the Fedrizziidae (Acari: Mesostigmata: Fedrizzioidea). Zootaxa, 1480, 1-55.
- Seeman, O.D. (2012) Diplogyniidae (Acari: Mesostigmata) associated with *Panesthia* cockroaches (Blattodea: Blaberidae). *Zootaxa*, 3163, 33–53.
- Trägårdh, I. (1911) Discomegistus, a new genus of myriopodophilous Parasitidae from Trinidad, with notes on the

Heterozerconinae. Arkiv für Zoologie, 7, 1–21.

- Walter, D.E. (2000) A jumping mesostigmatan mite, Saltiseius hunteri n. g., n. sp. (Acari: Mesostigmata: Trigynaspida: Salitiseiidae, n. fam.) from Australia. International Journal of Acarology, 26, 25–31. http://dx.doi.org/10.1080/01647950008683632
- Wisniewski, J. & Hirschmann, W. (2002) Gangsystematische studie von 3 neuen Antennophorus-arten aus Polen (Mesostigmata, Antennophorina). Acarologia, 33, 233–244.