COPROZERCONIDAE, A NEW FAMILY OF ZERCONOID MITES FROM NORTH AMERICA (ACARI: MESOSTIGMATA: ZERCONOIDEA)

BY Maria L. MORAZA* and Evert E. LINDQUIST**

ACARI
ZERCONOIDEA
TAXONOMY
CAVES
WOOD RATS

SUMMARY: A new family of mesostigmatic mites, Coprozerconidae, is described on the basis of material collected from feces of the wood rat, *Neotoma floridana magister* Baird, in a cave in Kentucky, U.S.A. *Coprozercon* n. gen. is described as the type genus of the family, based on material representing the type species, *Coprozercon scopaeus* n. sp. The characteristics and relationships of this family among others of the cohort Epicriina are discussed, including a rationale for Coprozerconidae as the sister group of Zerconidae. The tocospermous genus *Halozercon* Wiśniewski, Karg and Hirschmann, 1992, is transferred from the podospermous family Halolaelapidae to the tocospermous family Zerconidae.

ACARI
ZERCONOIDEA
TAXONOMIA
CUEVAS
RATA DE BOSQUE

RESUMEN: Se describe una nueva familia de ácaros Mesostigmata, Coprozerconidae, basada en material procedente de heces de la rata de bosque, *Neotoma floridana magister* Baird, de una cueva de Kentucky, E.U.A. *Coprozercon* gen. n. se describe como género tipo de esta familia, basandose en el material que representa a la especie tipo, *Coprozercon scopaeus* sp. n. Se discuten las características de esta familia con relación a las demás de la cohorte Epicriina, incluyendo una discusión de Coprozerconidae como el "grupo-hermanado" de Zerconidae. Se traslada el género *Halozercon* Wiśniewski, Karg y Hirschmann, 1992, desde la familia podoespermica Halolaelapidae a la familia tocoespermica Zerconidae.

INTRODUCTION

In the acarine order Mesostigmata, or Gamasida, members of the cohort Epicriina *sensu* JOHNSTON (1982), or "division" Epicriides *sensu* EVANS & TILL (1979), are relatively well known taxonomically but poorly known ecologically (KARG, 1993). Their diversity is centered in the Northern Hemisphere, where they occur primarily in edaphic habitats (JOHNSTON, 1982; KARG, 1993). Epicriina is a relatively early derivative free-living group, and associations with insects and other arthropods in restricted habitats have not been reported.

Cladistically and hierarchically, the Epicriina is currently in a state of flux. It was treated as a division (equivalent to a cohort) with three families, Epicriidae, Zerconidae and Arctacaridae, by EVANS & TILL (1979), and as a cohort with the two families Epicriidae and Zerconidae (with Arctacaridae placed in its own cohort) by JOHNSTON (1982). Earlier, EVANS (1955) had considered the Epicriina to consist of two superfamilies, Epicrioidea with only one family, Epicriidae, and Zerconoidea with two families, Zerconi-

dae and Arctacaridae. However, EVANS (1992) placed each of these three families in its own suborder, among six other tocospermous suborders of Mesostigmata, without considering phylogenetic relationships between them. Of these families, Zerconidae is by far the most disparate and speciose, with some 37 genera and nearly 100 species described. Epicriidae includes three genera and about 10 species described, while Arctacaridae includes but one genus and three species. Although phoresy is not known for any species in this cohort, we suspect that the deutonymph of the new taxon treated herein may be phoretic, for reasons presented in the discussion.

The hierarchic concepts of KARG (1965, 1993), which included Epicriidae among otherwise podospermous families in Phytoseioidea and Zerconidae among otherwise podospermous families in Ascoidea, is not accepted here. His classification implies independent derivation of the complexity of structures involved with podospermy, including the male spermatodactyl and the female bilateral sperm access systems, several times. The classification of KRANTZ (1978), in following KARG and additionally in placing Arctacaridae in yet another group, Parasitoidea, that includes some podospermous families such as Veigaiidae, is unacceptable for the same reason.

The present paper deals with the description of a new family of Zerconoidea for which material representing but one new species and genus has been studied. The recognition of attributes that may be diagnostic at the familial level, as distinct from the generic and in turn specific levels, is clearly problematical for such monobasic taxa. In this case we have been guided to a considerable extent by the attributes used by various other authors to distinguish between families of Gamasida other than Uropodina and Trigynaspida, and by the attributes used by authors to distinguish the many genera of Zerconidae currently recognized. The genus-group characters in Zerconidae include the following adult attributes (HALAŠKOVÁ, 1977, 1979): number of setae on peritrematal shield; relative length and shape of "peritrematal" setae $r1$ and $r3$ ($p1$ and $p2$ in most papers on Zerconidae); shape of posterior margin of peritrematal shield, and its connection with ventrianal shield; length and curvature of peritreme; sternal setae $st1$ on jugularia or on sternal shield; absence versus presence, number and arrangement of adgenital gland pores, $gv2$; presence/absence of adgenital platelets; presence/absence of small sclerites between genital and ventrianal shields; shape of ventrianal shield; number of setae on anterior margin of ventrianal shield; arrangement of opisthonotal setae, and number of setae on lateral margins of opisthonotal shield; presence/absence of transverse row of sclerotized fossae near posterior margin of opisthonotal shield; consolidation of opisthonotal and podonotal shields; holotrichy versus neotrichy on idiosomal dorsum; shape of anterior margin of tectum. In our view, some of these character states may be trivial, species-level attributes, and they have led to the splitting of generic concepts in Zerconidae, from the three genera that were recognized by SELLNICK (1958) to the 37 genera that are recognized currently. Except for the study of ATHIAS-HENRIOT (1976) on *Syskenozercon* Athias-Henriot, the polarities of many of these character states have not been considered. As a re-evaluation of generic groupings in Zerconidae is outside the scope of this study, however, we have provisionally accepted them as they stand.

MATERIAL AND METHODS

Mites were extracted, using Berlese-Tullgren funnels, from samples of feces of a wood rat, *Neotoma floridana magister* Baird, from a cave (see remarks following description of the new species for details). Specimens were mounted individually in Hoyer's medium and sealed with Glpt insulating varnish on microslides. Morphological observations, measurements, and illustrations were made using compound microscopes equipped with differential interference contrast and phase-contrast optical systems. All measurements, given as micrometers, were made with stage-calibrated eyepiece micrometers. Idiosomal setal notation follows LINDQUIST & EVANS (1965), with modifications for the posterior region as given by LINDQUIST (1994) and LINDQUIST & MORAZA (1999); leg chaetotaxy follows EVANS (1963, 1965), with modifications for tarsi II–IV as given by EVANS (1969). Distinctions between porelike structures of the idiosoma as either gland pores (solenostomes) or poroids (lyrifissures), are based on morphological

observations of ATHIAS-HENRIOT (1969a, 1969b), substantiated subsequently by physiological findings of KRANTZ & REDMOND (1987). Notation for these structures, as adenotaxy and poroidotaxy, respectively, follows JOHNSTON & MORAZA (1991); using this notation, the prominent two pairs of opisthonotal gland pores $gdZ3$ and $gdZ4$ are homologous with those denoted as $Po3$ and $Po4$ by SELLNICK (1958) and subsequent authors for zerconid mites.

Measurements of structures, expressed as ranges, were made as follows, unless noted otherwise. *Dorsal body length*: midline length from anterior margin between setae $j1$ to the caudal margin between setae $JV5$; *anterior and posterior (when present) dorsal shield lengths*: taken at midline from anterior to posterior margins of each shield; *ventrianal or anal shield length*: midline length from anterior margin to posterior edge of cribrum (which may be folded under); *ventrianal or anal shield width*: taken at greatest width (usually at level of anterior margin of anal opening). *Leg lengths*: from base of coxa to apex of tarsus excluding the pretarsus.

COPROZERCONIDAE new family

Type genus: *Coprozercon* new genus. Family monotypic, based on adult female and male and deutonymphal material representing one genus and one species.

Diagnosis. Adults of this family resemble those of other families of Epicriina *sensu* JOHNSTON (1982) (i.e., Epicriidae Berlese 1887, Zerconidae Berlese 1892) as follows. In adults of both sexes: palpi with five free segments, and palptarsal claw two-tined; peritremes reduced in length, not extending above bases of legs I; coxa II with anterodorsal spinelike projection; coxa IV retaining alveolar vestige of seta *av;* and legs I to IV with similar complement of setae on femora, genua and tibiae, including 10 setae on genua III and IV (*pv* present) and 9 on tibia III (*pl-2* present). In the adult female: setae *st4* off sternal shield; and epigynial portion of genital shield small, lacking expanded hyaline rim anteriorly. In the adult male: chelicerae formed much as in female, with movable digit lacking spermatodactyl; genital orifice

mid-sternal (though relatively anteriorly placed in Coprozerconidae) on sternogenital shield; and leg II not modified for mating. They further resemble those of Zerconidae, in distinction to Epicriidae, as follows. In both sexes: dorsal body setation holotrichous; tritosternum with well-developed laciniae; peritremes well developed in deutonymph, though reduced in adults; and tarsi II to IV with dorsal lyrifissure well removed distad circumsegmental fissure so that together they do not circumscribe a dorsal platelet bearing setae *ad3* and *pd3*. In the adult female: genital shield not enlarged, bearing only genital pair of setae, *st-5*. In the adult male (and deutonymph of both sexes): idiosoma covered by two well-developed, subequal podonotal and opisthonotal shields; anteriormost pair of marginal setae, *r1*, present; humeral pair of setae, *r3*, displaced ventrolaterally and inserted on peritremetal shield; and caudoventral pair of setae, *JV5*, displaced onto opisthonotal shield so as to appear like an extra pair of dorsal setae, "*J6*" or "*Z6*".

Members of Coprozerconidae are distinguished from those of Zerconidae and Epicriidae by the following characters. Idiosomal dorsum of adult female with podonotal shield reduced laterally, such that marginal *r*-setae inserted on soft cuticle rather than on its margins, and with opisthonotal shield absent (not even pygidial or mesonotal remnants evident); that of male and deutonymph with two fully developed shields which bear most of the marginal setae anteriorly (except *r3*) and posteriorly; opisthonotal shield of male with lateral margins extended posteroventrally to capture insertions of several ventral setae (*JV4*, *JV5*, sometimes *ZV4*), yet not consolidated caudally with ventrianal shield (in contrast with Zerconidae). Opisthonotum lacking transverse row of four, often sclerotized, depressions (or fossae) near posterior margin, which is characteristic of deutonymphs and adults of most members of Zerconidae. Peritrematal shield greatly reduced in adults of both sexes (though well developed in deutonymph), this shield a small fragment alongside coxa IV. Sternogenital region with normal five pairs of setae but lacking sternal poroids (lyrifissures); gland pores *gv1* present on posterior margin of sternal shield of female, but not evident on male and deutonymph. Male genital orifice located within sternogenital shield but rela-

tively far forward between setae *st1* and *st2* at midlevel of coxae II, orifice covered by single valve or platelet which lacks eugenital setae. Euanal setae and their alveolar vestiges absent. Tarsi II–IV each with 16 setae in adult, lacking one of two ventral sets *av-1, pv-1* and *av-2, pv-2*, though both sets present in deutonymph.

Description of adults. Idiosomal dorsum. Female idiosoma (Fig. 1) with reduced podonotal shield and unsclerotized opisthonotum (no mesonotal or pygidial plates evident); podonotum holotrichous, with setae idionymic, most of them, except *r*-marginals, on podonotal shield; opisthonotum holotrichous or slightly hypertrichous, with setae idionymic, all on unsclerotized cuticle. Male idiosoma (Fig. 21) with two subequally sized dorsal shields; podonotal shield expanded laterally and posteriorly to include all podonotal setae and porelike structures on soft cuticle in female; opisthonotal shield separate from ventrianal shield, but expanded caudoventrally to include one or more of posterior *JV* and *ZV* setae.

Idiosomal venter. Tritosternum with slender, elongate trapezoidal base and well-developed laciniae (Fig. 4). Sternal poroids (lyrifissures *ist1–ist3*) absent, genital poroids *iv5* present on soft cuticle, and gland pores *gv1* present but on female only. Female with sternal setae *st1–st3* and gland pores *gv1* on sternal shield; genital shield small, lacking expanded hyaline rim anteriorly, with genital setae *st5* on its lateral margins (Fig. 3). Male with sternal setae *st1–st5* on sternogenital shield, and with genital orifice located between setae *st1* and *st2* at midlevel of coxae II, this orifice covered by single valve which lacks eugenital setae (Fig. 22). Peritrematal shielding greatly reduced, without associated porelike structures evident; peritremes much reduced in length from those on deutonymph, extending only to level of coxae IV. Anal valves with lateral poroids present and euanal setae absent (Fig. 5), and postanal cribrum present (Figs. 3, 22).

Gnathosoma. Anterior margin of tectum with denticulate medial projection (Fig. 10). Subcheliceral plate with a pair of paralabral processes (Fig. 11). Chelicerae three-segmented, with well-developed, dentate fixed and movable chelae; fixed chela with simple pilus dentilis; dorsal cheliceral seta in dorso-lateral position behind dorsal lyrifissure; arthrodial process at base of movable chela simple (Fig. 6); movable chela of male lacking spermatodactyl. Subcapitulum with 4 pairs of setae, pair *h2* inserted laterad pair *h3* (Fig. 7). Anterior extremity of hypostome with pair of corniculi arising from its dorsolateral walls, and with one pair of internal malae; salivary stylets absent. Palpal segmentation normal, tibia not coalesced with tarsus; palptarsal apotele 2-tined; palpal setation holotrichous, its chaetotactic formula, *sensu* EVANS (1964), 2-5-6-14-15; palpgenu with dorsobasal lyrifissure (Fig. 8).

Legs (Figs. 17–20, 26). Tarsus I with paired claws and round-lobed pulvillus; tarsi II to IV with pretarsi bearing paired claws and round-lobed pulvillus. No sexual dimorphism in form of leg segments and their setae. Tarsi II to IV with 16 setae, 3-4/2,3/1-3, including apical dorsal set *ad-1, pd-1* which resemble setalike processes, and lacking ventral set *av-2, pv-2*; tarsi II–IV lacking ventral intercalary sclerite and setae *av-4, pv-4* in region of circumsegmental fissure; tarsus IV with dorsal lyrifissure well removed distad circumsegmental fissure so that together they do not circumscribe a dorsal platelet bearing setae *ad3* and *pd3*. Setation of coxae of legs I-II-III-IV, respectively, 2-2-2-1, coxa IV with alveolar vestige of second seta, *av*; setation of trochanters, 6-5-5-5. Chaetotactic formulae for femoral, genual, tibial setae of legs I-II-III-IV, respectively: femora I (2-3/2,2/2-2), II (2-3/1,2/2-1), III (1-2/1,2/0-0), IV (1-2/1,1/0-1); genua I (2-3/2,3/1-2), II (2-3/1,2/1-2), III (2-2/1,2/1-2), IV (2-2/1,3/1-1); tibiae I (2-3/2,3/2-2), II (2-2/1,2/1-2), III (2-1/1,2/1-2), IV (2-1/1,3/1-2). Leg I with four ventral setae on femur, three ventral setae on genu, and four ventral setae on tibia; femur II with two setae, *al-2* and *pv-2* (denoted *v-3* in EVANS, 1963), on basifemoral section, and lacking setae *pd-3* and *pl-2* on telofemoral section; femur III with seta *pd-2* but lacking *pl-1* (possibly an instance of homologue *pl-1* displaced to *pd-2* position); tibia IV with seta *pd-3*.

Deutonymphal characteristics (Figs. 23–25). Idiosomal dorsum with two, well-developed dorsal shields; peritrematal shields with setae *r3*, gland pores *gdr4*, and long peritremes extending to anterior region of podonotal shield; opisthonotal shield separate from anal or ventrianal shield caudally. Dorsal chaetotaxy, poroidotaxy and adenotaxy similar to

adult. Idiosomal venter with weakly sclerotized shielding; sternogenital porelike structures absent, poroids *iv5* on soft cuticle. Opisthogastric chaetotaxy and adenotaxy similar to adult. Gnathosoma as described for adult. Legs as described for adult except tarsi II to IV each with 18 setae, including both of ventral sets *av-1, pv-1* and *av-2, pv-2*.

Distribution and habitats. We have examined a total of 30 specimens representing one species of this family from wood rat feces found in Little Beauty Cave, Mammoth Cave National Park, Edmanson County, Kentucky, USA.

Etymology. See under description of genus.

Remarks. The cohort Epicriina has not been the subject of any adequate cladistic analysis, and its component families have generally not been defined apomorphically. Discordant views persist even in placement of the family Zerconidae in the Epicriina, with KARG (1965, 1993), followed by KRANTZ (1978) and KRANTZ & AINSCOUGH (1990), classifying Zerconidae in the superfamily Ascoidea in the cohort Gamasina. Arguments against KARG's view are given in our general discussion, below. A cladistic analysis of the Epicriides *sensu* EVANS & TILL (1979), or the Epicriina *sensu* JOHNSTON (1982), and their constituent families is beyond the scope of our study, though the following remarks and concluding general discussion are presented in a tentatively cladistic context.

Adults and deutonymphs of Coprozerconidae share a variety of characteristics with those of Zerconidae, as follows. (1) The peritrematal length is reduced in the adult from the normal, elongated state in the deutonymph. (2) The humeral pair of setae, *r3*, is in a lateroventral position, and they are often referred to as "peritrematal" or "peltidial" setae in the literature on Zerconidae (LINDQUIST & MORAZA, 1999). (3) The deutonymph and adult male have separate but well developed podonotal and opisthonotal plates. (4) Setae *s6* are inserted on the posterolateral corners of the podonotal shield. (5) Opisthonotal gland pores *gdZ3* and *gdZ5* are prominent. (6) A pair of caudoventral setae, *JV5*, is captured on the opisthonotal shield so as to appear like an extra pair of "dorsal" setae (LINDQUIST & MORAZA, 1999). (7) Sternal gland pore *gv1* is present in the adult female. (8) The basal pair of subcapitular setae is barbed. (9) The palptar-

sal apotele is two-tined. (10) Leg I has a pair of well developed tarsal claws. (11) An unpaired dorsal seta, *md*, is present proximally on tarsus I. (12) Coxa IV has an alveolar vestige of a second seta, *av*. Several of these character states (1, 2, 4, 5, 6) are apomorphic, the second and sixth, and perhaps the fifth, uniquely so; the first and fourth are independently apomorphic in the podospermous superfamily Rhodacaroidea. These apomorphies argue for a sister group relationship at some level between the new taxon and Zerconidae.

Coprozerconidae is characterized by several attributes that appear to be uniquely apomorphic to it among the described taxa of the cohort Epicriina. Although the deutonymph and adult male have fully developed podonotal and opisthonotal shields, the adult female has a somewhat reduced podonotal shield and lacks all remnants of an opisthonotal shield. In the adult male, the location of the genital opening closely behind setae *st1*, though sternal, is anterior to that found elsewhere in Epicriina. Sternal poroids *iv1–iv3* are absent. Tarsi II to IV lack one of the two pseudosymmetric pairs of ventral setae, *av-1, pv-1* and *av-2, pv-2* in adults though both pairs are present in the deutonymph. The deutonymph has a distinct ventral shield that is separate from the anal shield.

Among the variety of characteristics used by many authors to diagnose Zerconidae itself, the following attributes appear to be apomorphic within the Epicriina: (a) dorsal shield divided into two well developed plates in deutonymph and adult; (b) strongly serrated lateral margins of podonotal and opisthonotal shields in adult; (c) caudal fusion of opisthonotal and ventrianal shields in deutonymph and adult; (d) expansive peritrematal shields in adult; (e) expansive ventrianal shield usually encompassing metapodal plates and bearing all of opisthogastric setae present in adult female; (f) opisthonotal shield usually with transverse row of four sclerotized fossae near its posterior margin. As attributes (b), (e) and (f) are not characteristic of the apparently earliest derivative known genus, *Syskenozercon* Athias-Henriot, and (b) and (f) are also not characteristic of another early derivative genus, *Halozercon* Wiśniewski, Karg & Hirschmann, they should not be used as defining

apomorphies of Zerconidae[1]. The genus *Aleksozercon* Petrova is characterized in part by an entire dorsal shield in adults (PETROVA, 1978); however, in other respects this appears to be a more recent derivative taxon in Zerconidae, such that we view the entire dorsal shield as a secondarily derived attribute within this family.

Within Zerconidae, there is no subset grouping of genera that shares any of the derivative attributes of the new taxon. Therefore, *Coprozercon* should not be classified as a subfamily or as some other subset within Zerconidae but, rather, as the sister family of Zerconidae based on the shared apomorphic characteristics noted above. Relationships between Zerconidae + Coprozerconidae and other putative families of the cohort Epicriina are problematical. These are considered under the final discussion of this paper.

Coprozercon new genus

Type species: *Coprozercon scopaeus* new species. Genus based on adult female, male and deutonymphal material representing one species.

Diagnosis. Opisthonotum with gland pores $gdZ3$ and $gdZ5$ (termed $Po3$ and $Po4$ in much of literature on Zerconidae) prominent, enclosed by circular platelets on soft cuticle of adult female, and enclosed by somewhat larger, protruding circular areas superimposed on opisthonotal shield of deutonymph and adult male. Lateral margins of sternal shield of female and sternogenital shield of male emarginated between setae st-2 and st-3. Female with pair of metasternal platelets bearing setae $st4$. Adults lacking endopodal and exopodal sclerites alongside coxae I to III. Adgenital platelets absent; adgenital gland pores $gv2$ single, on female only.

Description of adults. Adults of small size (idiosomal length 190–270 mm) relative to most Zerconidae (260–750 mm), and with character states of family as described above, but restricted and augmented as follows:

Idiosomal dorsum (Figs. 1, 21). Female podonotum with 23 pairs of setae, including 14 to 16 pairs ($j2$–$j6$, $z2$–$z6$, $s1$, $s3$–$s5$, sometimes $j1$, $z1$) on somewhat reduced podonotal shield proper, and 7 to 9 pairs ($r1$–$r5$, $s2$, $s6$, sometimes $j1$, $z1$) on soft marginal cuticle alongside this shield; podonotum lacking setae $r6$; opisthonotum with 22 or more pairs of setae ($J1$–$J5$, $Z1$–$Z5$, $S1$–$S5$, $R1$–$R7$ plus sometimes with unpaired Jx-setae), all on soft striated cuticle. Dorsal and lateral porelike structures of female include: 7 pairs of poroids ($idj1$, $idj3$, $idj6$, $idz3$, $idz6$, $ids4$, $ids6$) and 6 pairs of gland pores ($gdj2$, $gdj4$, $gdz5$, $gdz6$, $gds4$, $gdr4$) on podonotum, of which several pairs on soft cuticle due to reduced area of podonotal shield; 11 pairs of poroids ($idJ1$, $idJ2$, $idJ4$, $idJ5$, $idZ3$, $idS1$, $idS2$, $idS3$, $idS4$, $idR3$, $idR5$) and 2 pairs of gland pores ($gdZ3$, $gdZ5$) on soft cuticle of opisthonotum; gland pores $gdZ3$ and $gdZ5$ prominent, each on small circular scutellae; opisthonotal sigillae readily discernible on soft cuticle. Male with all podonotal setae, poroids and gland pores on podonotal shield, including setae $r3$ and gland pores $gdr4$ on marginal ventral extensions of this shield, but excepting poroids $idz6$, $ids6$ and gland pores $gdz6$ which are on anterior margin of opisthonotal shield; with all opisthonotal setae, poroids and gland pores on opisthonotal shield, which are expanded lateroventrally so as to also capture several ventral setae ($JV4$, $JV5$, sometimes $ZV4$) and poroids ($ivo2$, $ivo4$); gland pores $gdZ3$ and $gdZ5$ large, each on circular protuberant area.

Idiosomal venter (Figs. 3, 22). Both sexes with sternal and genital shielding weakly sclerotized; adgenital platelets absent; endopodal strips absent alongside coxae II–IV except for short strip behind coxae IV in male. Female with pair of metasternal platelets bearing setae $st4$, and with single pair of adgenital gland pores $gv2$ on soft cuticle immediately behind bases of legs IV; these pores absent in deutonymph and male. Exopodal shielding absent and peritrematal shielding reduced, scarcely larger in area than reduced peritreme and stigma. Female opisthogaster with 9 pairs of setae ($JV1$–$JV5$, $ZV1$–$ZV4$) and 5

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1. The genus *Halozercon* was proposed for a species of mite, *H. karacholana* Wiśniewski, Karg & Hirschmann, whose females and males lack structures indicative of podospermy. In males, the chelicerae lack a spermatodactyl and the genital aperture is mid-sternal. Females apparently lack a pair of solenostomes near the bases of legs III or IV. Therefore, this genus should not be placed in Halolaelapidae, as proposed by WIŚNIEWSKI *et al.* (1992), or in any other family of podospermous Gamasina. *Halozercon* is here transferred to the tocospermous family Zerconidae, as a relatively early-derivative genus related to *Syskenozercon*, based on several of the apomorphies common to these genera that were noted by WIŚNIEWSKI *et al.* (1992).

pairs of poroids (*ivo1–ivo4, ivp*) inserted on soft cuticle, and with setae *JV3* aligned longitudinally with *JV1-JV2*; male opisthogaster with 3 or 4 pairs of setae (*JV1, ZV1, ZV2,* sometimes *ZV4*) and 2 or 3 pairs of poroids (*ivo1, ivp,* sometimes *ivo3*) on soft cuticle. Metapodal shielding not captured by ventrianal shielding in either sex, but formed as a pair of small free platelets near poroids *ivo2* on soft cuticle in female and apparently captured along with these poroids by ventral extension of opisthonotal plate in male. Female with opisthogastric shielding reduced to inversely subtriangular anal shield bearing 3 circumanal setae and gland pores *gv3*; male with small ventrianal shield bearing several pairs of ventral setae in addition to circumanal setae and gland pores *gv3*; para-anal setae in both sexes subequal in size with postanal seta, and inserted at level of posterior margin of anal opening.

Gnathosoma (Figs. 6–12). Tectum a single, narrow, denticulate projection. Fixed digit of chelicera with minute pilus dentilis and row of several teeth; movable chela dentate. Corniculi simple, well developed; internal malae slender, acuminate. Subcapitulum with basalmost pair of setae barbed, other three pairs smooth. Deutosternum with smooth anterior margin and usually 5 transverse rows of denticles, without longitudinal linear cells between rows of denticles. Palpal chaetotaxy as stated for family; palptrochanter with distal anterolateral pointed process.

Legs (Figs. 17–20, 26). Legs I–IV with paired claws well developed, inserted on well developed pretarsi. Tarsus I with lanceolate-tipped sensilla conspicuous but not elongate. Tarsi II–IV with vestige of ventral intercalary sclerite in circumsegmental fissure. Tarsi II–IV with apical setal processes *ad-1, pd-1* as long as pretarsi. Leg setae of moderate length, none modified as macrosetae; leg chaetotactic formulae as stated for family.

Deutonymphal characteristics. Idiosomal dorsum (Fig. 23). Idiosoma with subequally sized podonotal and opisthonotal shields, these separated by transverse strip of striated soft cuticle; peritrematal shield on either side united with podonotal shield anteriorly. Podonotal and opisthonotal chaetotaxy and poroidotaxy as in adult. Podonotal shield well sclerotized as in adult male, with 22 pairs of setae (*j1–j6, z1–z6,*

s1–s6, r1, r2, r4, r5). Opisthonotal shield well sclerotized as in adult male, with about 20 pairs of setae much as in male except some *R*-marginal setae and poroids *idR3, idR5* on soft marginal cuticle; gland pores *gdZ3* and *gdZ5* large, on prominent circular protuberant areas as in male.

Idiosomal venter (Fig. 24). Tritosternum and podosomal chaetotaxy and poroidotaxy as in adult; gland pores *gv1* absent as in male. Sternogenital shielding with 4 pairs of sternal setae (*st1–st4*) and genital setae (*st5*). Endopodal and exopodal strips absent. Peritrematal shields continuous alongside coxae II–IV; peritremes long, extending anteriorly to level above bases of legs I. Opisthogastric chaetotaxy, poroidotaxy and adenotaxy as in adult, except poroids *ivp* not discernible; opisthogaster with separate ventral shield bearing several pairs of ventral setae and anal shield bearing 3 circumanal setae and gland pores *gv3*; anal valves as in adult. Several ventral setae and poroids on soft cuticle around ventral and anal shields. One pair of metapodal platelets free on soft cuticle behind legs IV.

Gnathosoma and Legs (Fig. 25). As described for adult, except tarsi II–IV with both sets of ventral setae, *av-1, pv-1,* and *av-2, pv-2,* present.

Etymology. The name for this genus is a combination of the word "copro", meaning dung or fecal, and "zercon", a proper name, according to BERLESE (1892), used by many authors to form names for genera of mesostigmatic mites. The name is masculine in gender, and is intended to refer to the habitat in which these mites are found.

Coprozercon scopaeus sp. nov.
Figs. 1–26

Diagnosis. Dorsal setae of idiosoma nearly all of similarly moderate length (about 20–25 μm, except for shorter *j1* and *z1*) and somewhat thick form, with small basal spur. Opisthonotum with two unpaired, adelonymic (*sensu* HAMMEN, 1975) *J*-setae on soft cuticle in adult female, and on opisthonotal shield in deutonymph and adult male. Dorsal shielding lightly reticulated in adult female, but more strongly reticulated in adult male and deutonymph. Peritremes abbreviated in adults, about as long as diameter of

FIGS. 1–5: *Coprozercon scopaeus* n. gen. et sp., adult female.

1. — Body dorsum, with complete notation for setae and porelike structures; notation follows that of LINDQUIST & MORAZA (1999) for Zerconidae. 2. — Enlarged view of a posterodorsal body seta, showing detail of basal spurlike process and barbs along shaft. 3. — Body venter, with notation for opisthogastric setae and porelike structures; notation follows that of LINDQUIST & MORAZA (1999) for Zerconidae. 4. — Tritosternum. 5. — Enlarged view of anal opening.

stigma; peritremes elongate, extending to level of setae *s1*, in deutonymph.

Description. With character states of genus as described above, but restricted and augmented as follows:

ADULT FEMALE. *Idiosomal dorsum* (Fig. 1). Idiosomal length 260–270 μm (3 specimens); idiosomal width at level of posterior margin of podonotal shield including soft marginal cuticle in undistorted specimens 145–170 μm; podonotal shield length 130–135 μm, width 127–130 μm at level of setae *s5*; opisthosomal length from bases of setae *J1* to bases of setae *Z5*, 114–122 μm. Podonotum with 23 pairs of setae, including 14 to 16 pairs (*j2–j6, z2–z6,s1, s3–s5,* sometimes *j1, z1*) on podonotal shield, and 7–9 pairs (*s2, s6, r1–r5,* sometimes *j1, z1*) on soft marginal cuticle, *r3* in lateroventral position; setae *j1* (12–14 μm) and *z1* (10–11 μm) shorter than other setae, these of similarly moderate length (18–24 μm, nearly as long as longitudinal intervals between their bases) and thick, slightly curved form, with small basal spur (Fig. 2). Podonotal shield lightly reticulated, with fine striae and puncta within some reticula (ornamentation not shown in Fig. 1), and with irregularly sinuous lateral margins. Opisthonotum covered with striated soft cuticle, lacking any remnant of opisthonotal shield; with 22 pairs of setae (*J1–J5, Z1–Z5, S1–S5, R1–R7*) plus 2 unpaired extra setae (*Jx*), all of similar length (20–27 μm), thickness, and curved, basally spurred form to podonotal setae; *Jx* setae located along midline, one between bases of *J1*, one between bases of *Z3* and *J4*. Dorsal and lateral idiosomal porelike structures, positioned as in Fig. 1, include: 4 pairs of poroids (*idj1, idj3, idz3, ids4*) and 4 pairs of gland pores (*gdj2, gdj4, gdz5, gds4*) on podonotal shield, 3 pairs of poroids (*idj6, idz6, ids6*) and 2 pairs of gland pores (*gdr4, gdz6*) on soft podonotal cuticle, and 11 pairs of poroids (*idJ1–idJ5, idS1–idS4, idR3, idR5*) and 2 pairs of gland pores (*gdZ3, gdZ5*) on soft opisthonotal cuticle; pores *gdZ3* and *gdZ5* each on small, subcircular, sclerotized platelets about 6–7 μm in diameter.

Idiosomal venter (Fig. 3). Tritosternum with elongate trapezoidal base (length 12 μm), and paired laciniae which are free from each other along entire length (16–17 μm), each ending in arista (Fig. 4).

Presternal region lacking platelets or ornamented cuticle. Sternal shield weakly sclerotized, unornamented, length 59–67 μm, width 37–39 μm, with lateral margins indented at level between setae *st1* and *st2*, and more deeply so between setae *st2* and *st3*; length setae *st1–st3* 12 μm; gland pores *gv1* on slightly convex posterior margin of shield. Metasternal platelets weakly sclerotized; setae *st4* slightly shorter (10 μm) than other sternal setae. Genital shield subpentagonal, unornamented, small, its length (35–36 μm) slightly greater than its width (32–33 μm); anterior margin of shield narrowed, convex; posterior margin truncated; genital setae (length 10–12 μm) on lateral edges of this shield; genital poroids *iv5* on soft cuticle laterad genital shield. Peritreme length 15 μm including stigmata, peritreme itself subequally as long as diameter of stigma; abbreviated peritrematal plates with posterior margins pointed, and lacking porelike structures. Metapodal platelets slender, length 21 μm. Opisthogaster with 10 pairs of setae and 5 pairs of poroids (*ivo1–ivo4, ivp*) on soft striated cuticle; area between genital and anal shields with 6 pairs of simple, slender setae, of which *JV1, JV2, ZV1, ZV2* slightly shorter (10–12 μm) than *JV3, ZV3* (13–15 μm); area laterad anal shield with 3 pairs of longer (18–23 μm), thicker setae (*ZV4, JV4, JV5*), these similar in form to dorsal setae; poroids *ivo2* near *ivo3* laterad setae *ZV2*, *ivo4* posterolaterad setae *ZV4*, and *ivp* laterad setae *JV5*. Anal shield inversely subtriangular, unornamented, subequally as wide (56–61 μm) as long (56–58 μm), its anterior margin flat or slightly concave; para-anal setae (15 μm) nearly as long as postanal seta (16–17 μm); gland pores *gv3* on lateral edges of shield at level of anterior margin of anal opening; anal valve length 17 μm; cribrum restricted to triangular area of shield behind postanal seta.

Gnathosoma (Figs. 6–11). Tectum with broad, smooth, nearly flat anterolateral margins and slender, coarsely denticulate medial projection (Fig. 10). Subcheliceral plate with pair of deeply fringed paralabral processes arising from its dorsoproximal surface (Fig. 11). Fixed digit of chelicera with minute pilus dentilis proximad 2 well spaced, subdistal teeth; movable chela with 2 teeth similar in size and position to those of fixed digit, plus a smaller, offset third tooth between them; dorsal cheliceral seta prominent
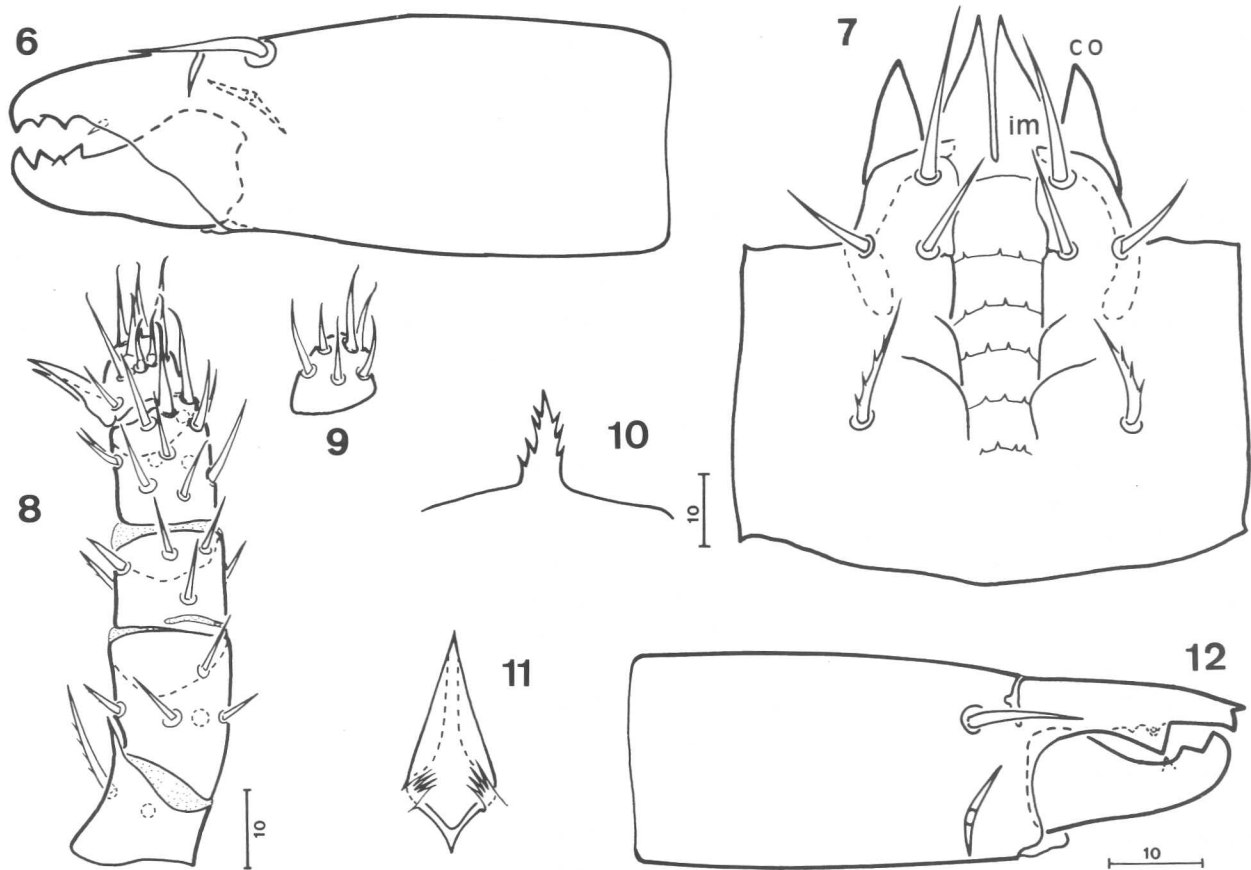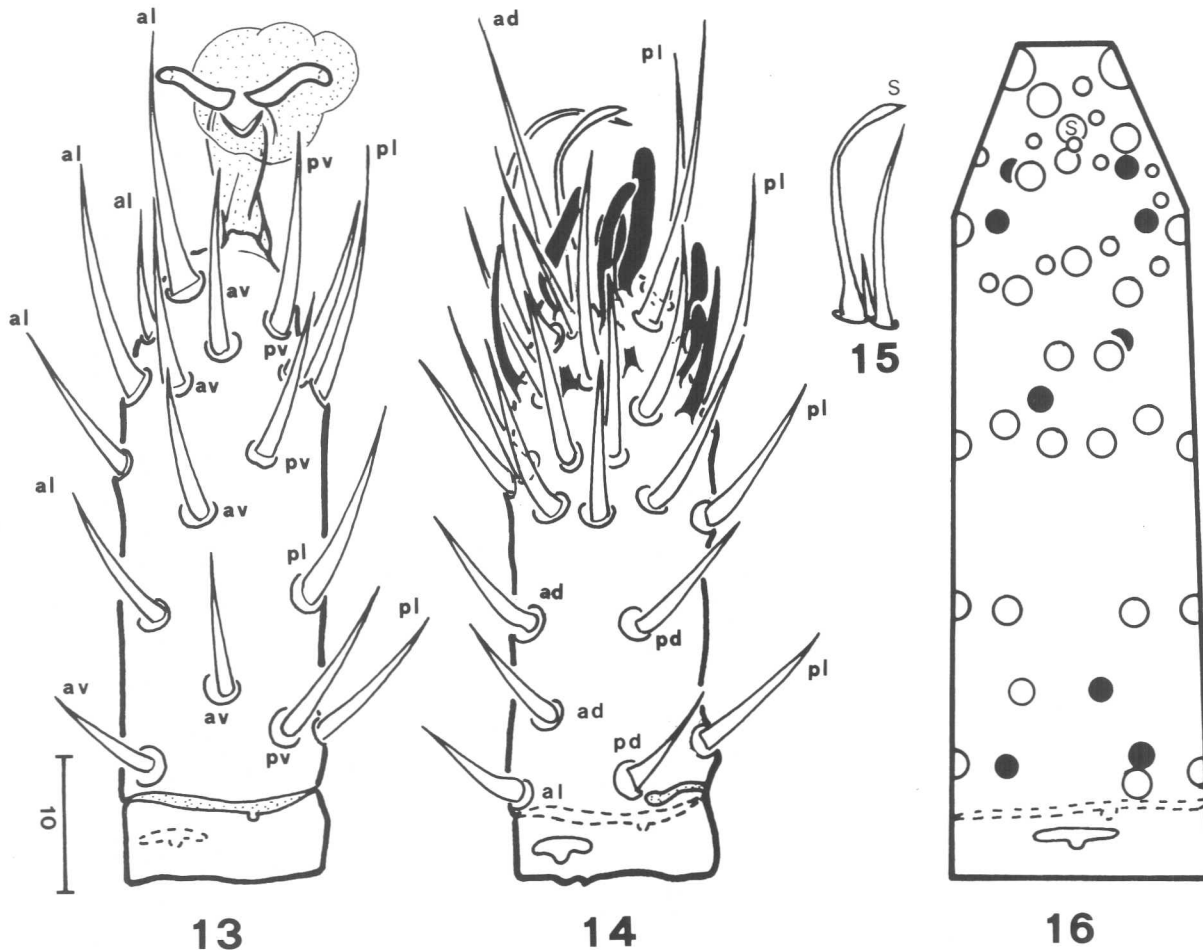
FIGS. 6–12: *Coprozercon scopaeus* n. gen. et sp., adult.

6. — Chelicera, lateral paraxial aspect, female. 7. — Subcapitulum, ventral aspect. 8. — Palpus, dorsal aspect. 9. — Palptarsus, ventral aspect. 10. — Tectum, dorsal aspect. 11. — Subcheliceral plate, showing paralabral processes, dorsal aspect. 12. — Chelicera, lateral paraxial aspect, male. Abbreviations: *co*, corniculus; *im*, internal mala.

(length 10 μm), inserted well proximad dorsal lyrifissure; antiaxial lyrifissure well developed; margin of hyaline envelope at base of movable chela smooth (Fig. 6). Corniculi well spaced, parallel; internal malae with lateral margins smooth, with broadly acute apices extending beyond tips of corniculi. Deutosternal groove of subcapitulum with smooth anterior margin hardly discernible between bases of anterior pair of subcapitular setae, and with 5 moderately broad rows of denticles, each with 3–5 denticles but anterior 2 rows sometimes edentate; rows gradually narrowing posteriorly (Fig. 7). Posteriormost pair of subcapitular setae barbed, similar in length to smooth second and third pairs of setae; anteriormost pair of setae smooth, nearly twice as long as other

pairs. Palpal length 68–70 μm; palpal chaetotaxy as described for family; palptrochanter with apical spinelike process paraxially, and with seta *v-2* barbed, longer (15–16 μm) than seta *v-1*; palpfemur with seta *al* slightly barbed, and pointed apically; palpgenu with seta *al-1* smooth, stouter than other genual setae, and with *al-2* slightly barbed (Fig. 8).

Legs (Figs. 13–20, 26). Excluding ambulacra, lengths of leg I 178–200 μm, leg II 103–137 μm, leg III 91–117 μm, leg IV 122–156 μm. Coxa I with 1 gland pore ventroproximally and ridge of serrated processes on anterolateral distal margin; coxa II with pointed spinelike process distally on anterodorsal margin, and with distal margin serrated behind condyle (Fig. 18); coxae III and IV with dorsodistal
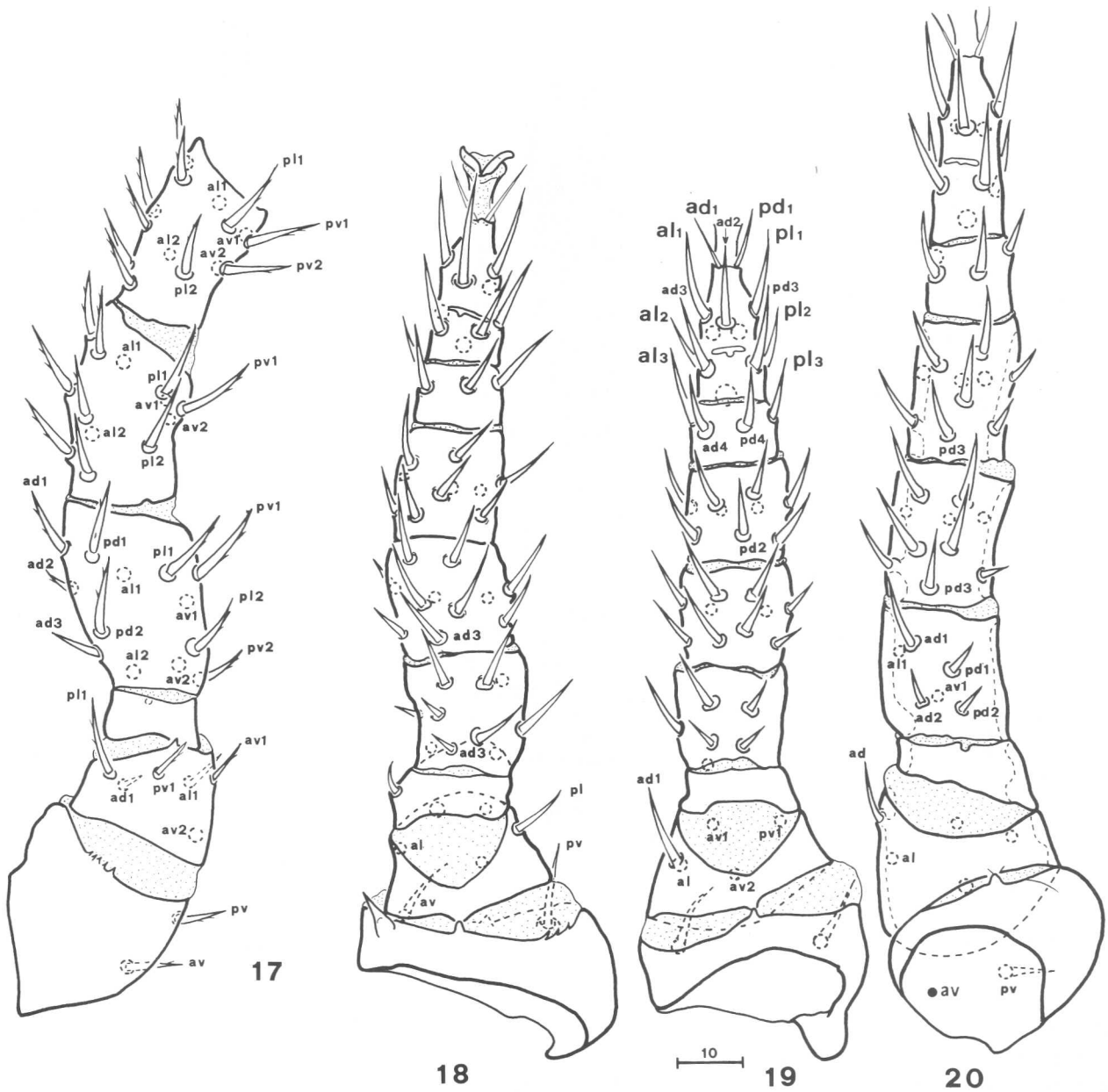
FIGS. 13–16: *Coprozercon scopaeus* n. gen. et sp., tarsus of leg I, adult.

13. — Ventral aspect. 14. — Dorsal aspect, excluding pretarsus; sensilla with porose walls shown in black. 15. — Separate detail of lanceolate-tipped seta *s* and adjacent setae. 16. — Diagrammatic view, circles indicating position of bases of setae and sensilla; ventral setae indicated by black, dorsal and lateral setae by open, circles.

margins smooth; coxa IV with alveolar vestige of second seta, *av*, minute (Fig. 20). Pretarsi of legs I–IV with well-developed, evenly curved claws (Figs. 13, 18). Tarsus I with 49 setae, including (as denoted in Figs. 13, 14) 6 anterolaterals, 5 posterolaterals, 5 anteroventrals, 4 posteroventrals and 29 other setae and sensillae dorsally and apically; configuration of dorsodistal cluster of sensillae as shown in Fig. 14; lanceolate-tipped sensilla *s* of moderate length (15 μm), moderately expanded distally (Fig. 15). Tarsi II–IV each with apical setal processes *ad-1* and *pd-1* moderately long (10–12 μm), smooth, slender, and with pretarsi moderately short (5–7 μm), their

paired claws short (5–7 μm). Setation of trochanters of legs I–IV, respectively, 6-5-5-5; that of femora, 13-11-6-6; that of genua, 13-11-10-10; that of tibiae, 14-10-9-10 (Figs. 17–20); leg chaetotactic formulae normal for family Coprozerconidae as presented above. Most leg setae slightly thickened and barbed on segments distad trochanters; none of leg setae elongated or enlarged as macrosetae.

ADULT MALE. *Idiosomal dorsum* (Fig. 21). Dorsal shields together 192–227 μm long (7 specimens), moderately sclerotized, entire surface of both shields reticulated, with fine striae and puncta within reti-

FIGS. 17-20: *Coprozercon scopaeus* n. gen. et sp., legs I to IV, adult. 17. — Leg I excluding tarsus, posterolateral aspect. 18. — Leg II, dorsal aspect. 19. — Leg III, excluding pretarsus, dorsal aspect. 20. — Leg IV, excluding pretarsus, dorsal aspect.

cula. Podonotal shield 110–120 μm long, 128–142 μm wide at level of setae *j5*, with straight posterior margin; this shield more expansive laterally than in female and deutonymph, bearing all 23 pairs of setae, 7 pairs of poroids and 6 pairs of gland pores of podonotum, though excluding poroids *idz6, ids6* and

gland pores *gdz6* which are on anterior margin of opisthonotal shield. Opisthonotal shield 98–110 μm long, 125–132 μm wide at level of setae *J2*, more expansive laterally than in deutonymph, bearing 25 pairs of setae including all 22 pairs (plus 2 unpaired *Jx*) of opisthonotal setae, 11 pairs of poroids and 3

pairs of gland pores, plus 2 or 3 pairs of ventral setae (*JV4, JV5,* sometimes *ZV4*) and 2 or 3 pairs of ventral poroids (*ivo2, ivo4,* sometimes *ivo3*) on its lateroventral extensions (Fig. 22). Size and form of dorsal setae, position of *Jx* setae, and position of porelike structures as in adult female; podonotal gland pores *gdz5* on small, rounded or conical protuberances behind setae *z5*; opisthonotal gland pores *gdZ3, gdZ5* prominent, on circular areas of about 13–15 μm diameter which protrude about 7 μm above surrounding surface of shield.

Idiosomal venter (Fig. 22). Tritosternum and presternal area as in adult female. Sternogenital shield weakly sclerotized, narrow, length 90–95 μm, greatest width between setae *st2* and *st3* 35–37 μm; anterior edge of genital opening only 3 μm behind level of setae *st1*; lateral margins of shield deeply emarginated at level of genital opening and more shallowly emarginated at level between setae *st2* and *st3*; setae *st1–st4* length 10–11 μm, genital setae *st5* shorter (7–8 μm); genital poroids *iv5* on soft cuticle flanking posterior margin of sternogenital shield. Narrow strip of endopodal plating present behind legs IV. Peritrematal structures abbreviated as in adult female. Opisthogaster with 3 pairs of setae (*JV1, ZV1, ZV2*) and 1 or 2 pairs of poroids (*ivo1,* sometimes *ivo3*) on soft cuticle flanking anterolateral margins of ventrianal shield (*ivo3* sometimes asymmetrically captured on ventral margin of podonotal shield). Ventrianal shield moderately well sclerotized, lightly ornamented with transverse lines and fine puncta, subpentagonal with rounded anterolateral angles, length (76–79 μm) about 1.4 times greatest width (54–55 μm) at level of gland pores *gv3*; this shield with 3 pairs of ventral setae (*JV2, JV3, ZV3*) in addition to circumanal setae and pores *gv3*. Opisthogastric setae similar in form and size (or slightly smaller) to their homologues on adult female. Anal valves and cribrum as in adult female.

Gnathosoma. Tectum, subcapitulum and palpi as in adult female, except a basalmost sixth row of deutosternal denticles present in some individuals. Cheliceral structures as in adult female except fixed chela with apex more slender, nearly straight (rather than hooked), extending slightly beyond tip of movable chela, and with apical tooth so as to appear bifid;

movable chela with two teeth, lacking small third tooth of female (Fig. 12).

Legs. Excluding ambulacra, lengths of leg I 172–185 μm, leg II 122–128 μm, leg III 112–120 μm, leg IV 154–157 μm. Form, setation and other structures of legs, including alveolar vestige of second seta, *av*, on coxae IV, as in adult female.

DEUTONYMPH. *Idiosomal dorsum* (Fig. 23). Idiosoma elliptical, covered by two subequally sized shields which are as well sclerotized, though not as expansive, and similarly ornamented as in adult male; idiosomal length, measured from bases of setae *j1* to those of *JV5*, 211–248 μm (12 specimens). Podonotal shield length 112–122 μm, width at level of setae *r4* 121–134 μm, with straight posterior margin; shield bearing all 23 pairs of podonotal setae including setae *r3* which, with gland pores *gdr4*, on lateral peritrematal extensions of shield; setae *r4, r5, s6* on well delineated, narrow marginal rim of shield. Opisthonotal shield length 98–120 μm, width at level of setae *R1* 107–122 μm, with rounded posterior margin; shield reticulated over most of surface, and with delineated narrow marginal rim, in contrast to adult male; setae *S1, R1, R3, R5, R7* inserted on this rim; podonotal shield bearing 20 pairs of setae plus 2 unpaired *Jx* setae, 10 pairs of poroids, and 3 pairs of gland pores. Setae *R2, R4, R6* and poroids *idR3, idR5* on soft lateral cuticle. Size and form of dorsal setae, position of *Jx* setae, and position of porelike structures as in adult male; gland pores *gdZ3, gdZ5* on conspicuous circular areas of similar size and protrusion as in male.

Idiosomal venter (Fig. 24). Sternogenital shield weakly sclerotized, unornamented, with irregularly sinuated lateral margins, interrupted behind setae *st4*, such that genital region a separate plate; setae *st1–st4* on sternal portion, *st5* on genital portion of that shielding; genital poroids *iv5* on soft cuticle flanking posterior margin of genital plate. Peritrematal shields well developed, with elongate peritremes reaching onto dorsolateral surface at level between setae *r1* and *s1*. Metapodal plates comma-shaped, positioned anterad poroids *ivo2*. Opisthogaster with lightly sclerotized, subtrapezoidal ventral shield, nearly smooth or faintly transversely lineate, bearing 3 pairs of setae, *JV2, JV3, ZV3*, and sometimes asymmetrically one
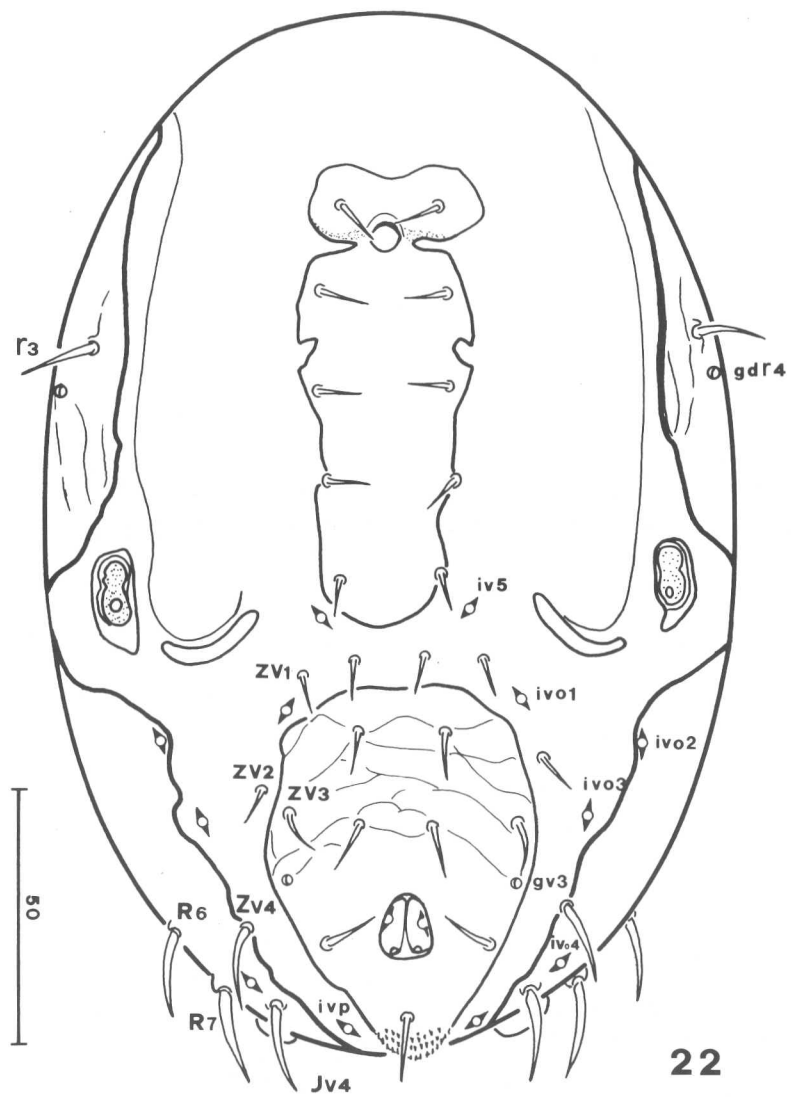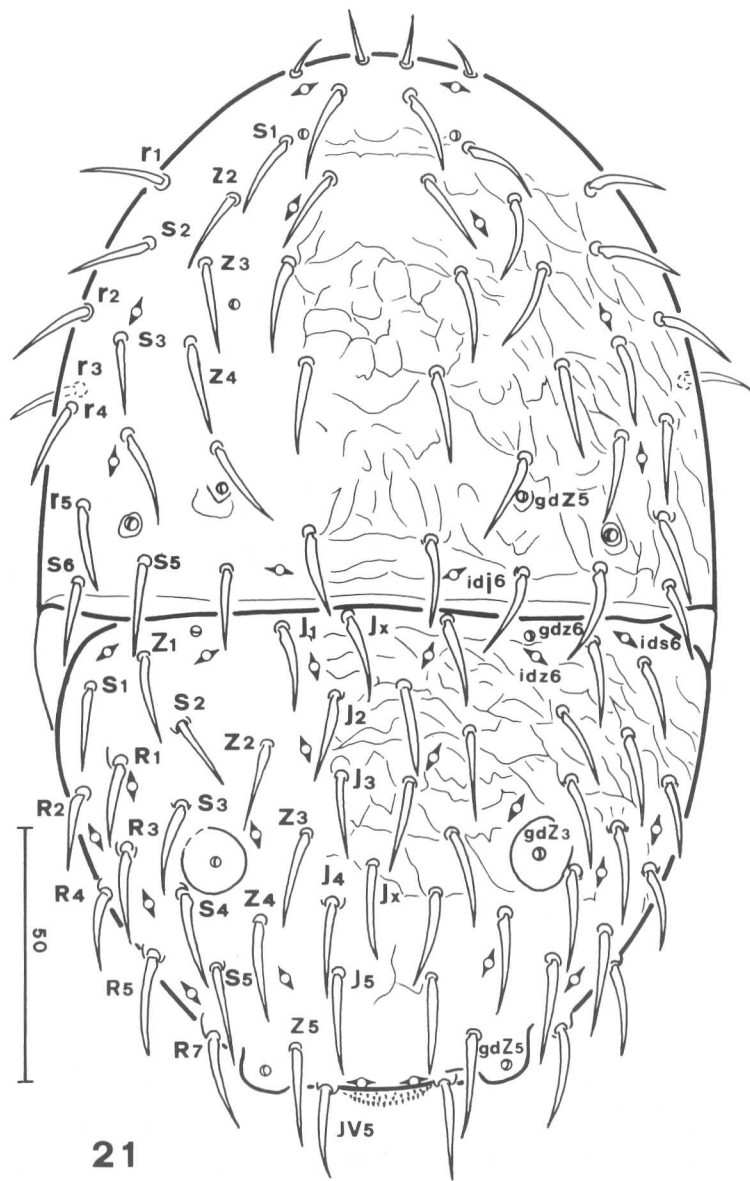
FIGS. 21-22: *Coprozercon scopaeus* n. gen. et sp., adult male, body dorsum (21) and venter (22).
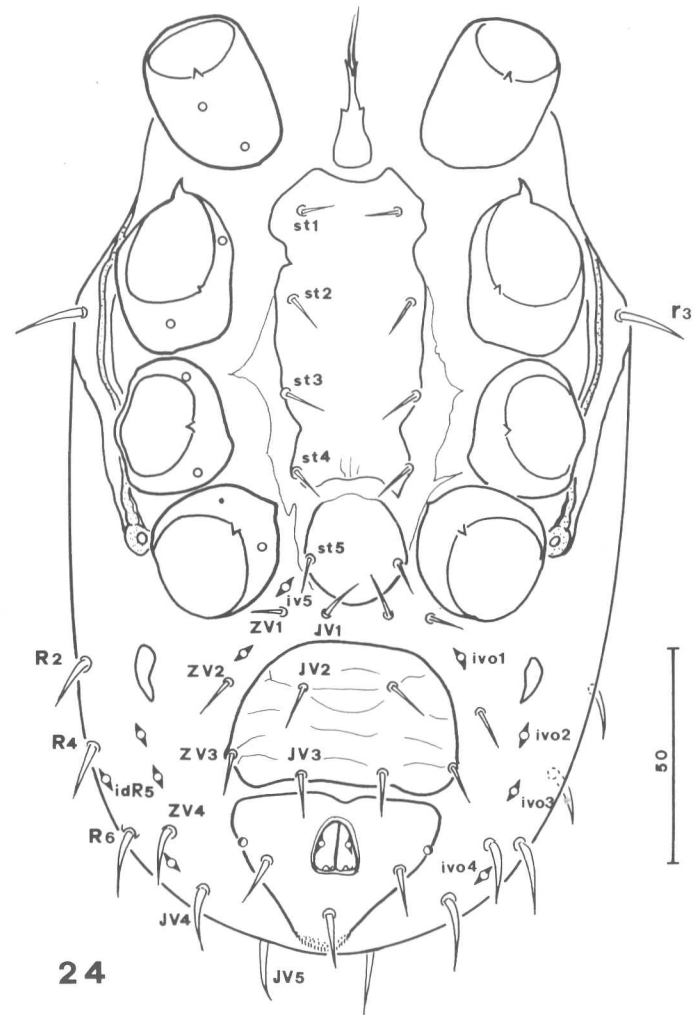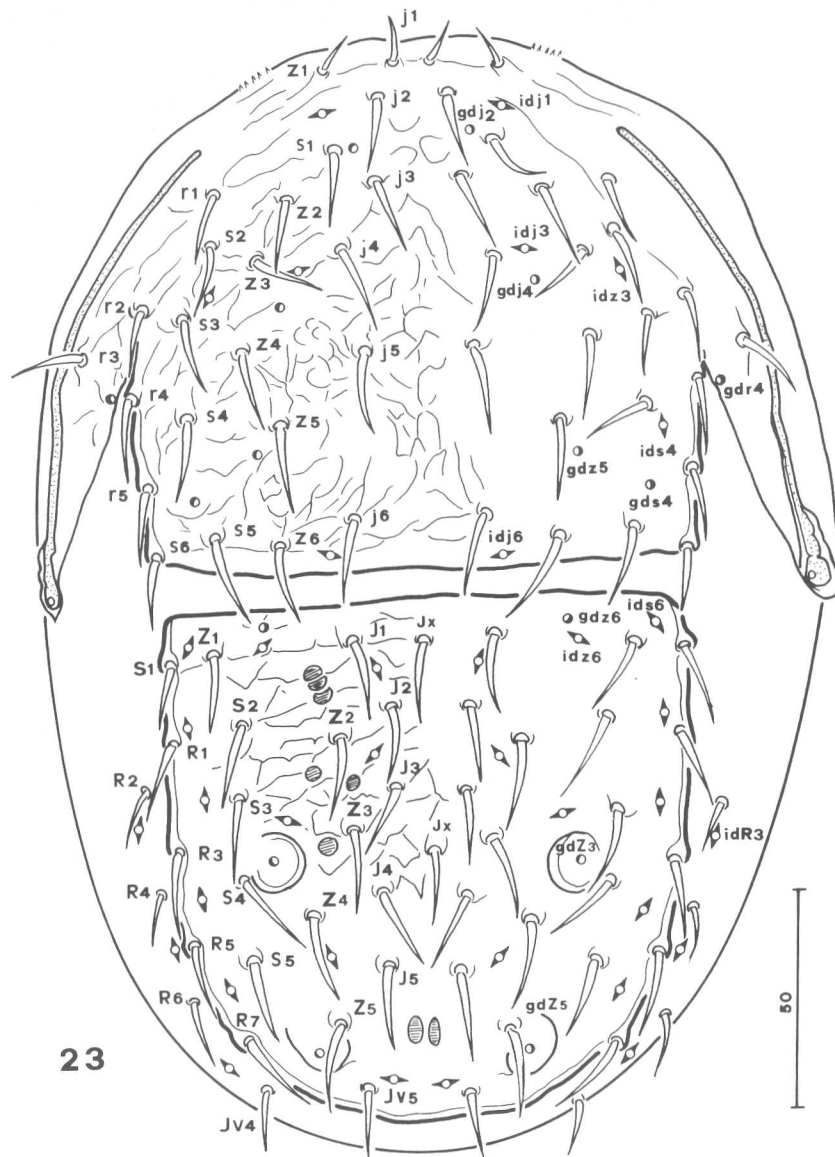
FIGS. 23-24: *Coprozercon scopaeus* n. gen. et sp., deutonymph, body dorsum (23) and venter (24), with notation for setae and porelike structures; notation follows that of LINDQUIST & MORAZA (1999) for Zerconidae.

of setae *ZV2*; with separate, inversely subtriangular, unornamented anal shield bearing circumanal setae and gland pores *gv3*; these shields nearly contiguous, and of similar width; ventral shield length at midlevel (28–33 μm) about 0.6 its width (51–61 μm) at level of setae *ZV3*; anal shield length 34–36 μm, anterior width 47–48 μm; anal valves and cribrum as in adult. Soft cuticle with 5 pairs of ventral setae (*JV1, ZV1, ZV2, ZV4, JV4*) and 4 pairs of poroids (*ivo1–ivo4*) flanking ventral and anal shields. Opisthogastric setae similar in form and size (though slightly smaller) to their homologues on adult.

Gnathosoma. Tectum formed as in adult. Chelicerae as in adult female. Other structures of gnathosoma, including setation of subcapitulum and palpi, as in adult.

Legs. Excluding ambulacra, lengths of leg I 177–195 μm, leg II 124–139 μm, leg III 115–129 μm, leg IV 150–161 μm. Form, setation, and other structures of legs, including presence of alveolar vestige of second seta, *av*, on coxa IV, as in adult except tarsi II–IV with 18 setae, including both sets of ventral setae, *av-1, pv-1* and *av-2, pv-2* (Fig. 25).

PROTONYMPH AND LARVA. Unknown.

TYPES. Holotype, adult female, U.S.A., Kentucky, Edmanson County, Mammoth Caves National Park, Little Beauty Cave, 31 August 1987, W. C. WELBOURN & M. E. CASANUEVA, ex fecal dump of wood rat, *Neotoma floridana magister* Baird; deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville. Paratypes: 2 adult females, 8 adult males, 19 deutonymphs, with data same as for holotype; of these, 2 females, 4 males, 9 deutonymphs deposited in the Canadian National Collection of Insects and Arachnids, type No. 22,268, maintained by Biological Resources Program, Agriculture Canada, Ottawa, Ontario; remainder deposited in Florida State Collection of Arthropods, as above.

ETYMOLOGY. The specific epithet, *scopaeus*, is a latinized version of the Greek word "skopaios", meaning dwarf and referring to the diminutive size of these mites.
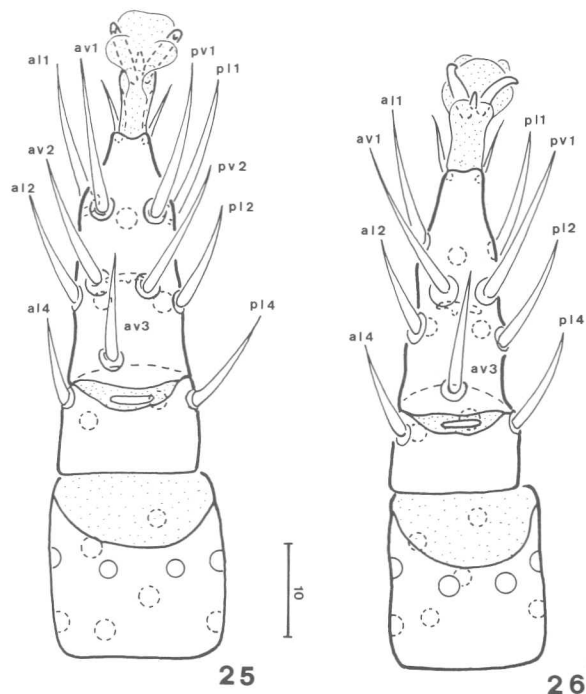
25 **26**

FIGS. 25–26: *Coprozercon scopaeus* n. gen. et sp., leg II, ventral aspect.

25. —Deutonymph, showing presence of two ventral sets of setae, *av-1, pv-1* and *av-2, pv-2*. 26. —Adult, showing presence of one ventral set of setae, *av-1, pv-1* and its shift in position in absence of second ventral set, *av-2, pv-2*.

REMARKS. All known mites of the families Zerconidae and Epicriidae have a free-living way of life in a variety of terrestrial and, to a limited extent, arboreal habitats. This new taxon is the first known example of an extant epicriine species that may be restricted to a cavernicolous habitat. Other than having perhaps less heavily sclerotized idiosomal shields than most zerconids, adults and deutonymphs of *Coprozercon scopaeus* do not exhibit any apparent troglomorphisms, as distinct from edaphomorphisms, *sensu* ZACHARDA (1980). *Paleozercon cavernicolus* Błaszak *et al.* is known only from fossil specimens found embedded in calcium deposits of a stalagmite near a cave entrance (BŁASZAK *et al.*, 1995), but its restriction to cave systems is problematical. *Zercon triangularis* Koch is recorded from caves in Europe (WOLF, 1938), but this widespread species is not restricted to caves.

The subspecies of wood rat with which *Coprozercon scopaeus* is associated nests in caves and rock slide

crevasses in Appalachian areas of Pennsylvania south to Tennessee (HALL & KELSON, 1959). The rats are active all year, primarily within cave systems, and they frequently defecate in the same places, or dumps, some distance from their nests. An individual rat may have several fecal dumps up to a meter or more apart, and these are actively used for extended periods of time, until the rat dies or moves out of a cave. The dumps thus provide a relatively stable organic resource for colonization by a variety of small arthropods, including various mites, collembolans, and a few insects such as staphylinid beetles, silphid beetles and sciarid flies (W. C. WELBOURN, personal communications, June 1993 and May 1997), and probably also by nematodes. The mites in this case were collected from a fecal dump in a moist area about 20 meters from the cave entrance and about 7 meters from the wood rat's nest. The fecal pile was about 20–25 cm high, with fecal pellets of various ages. Due to sampling restrictions, it could not be determined whether *C. scopaeus* occurred in the wood rat's nest.

Associations, including phoresy, with insects or other arthropods have not been recorded for epicriine mites. Where phoresy has been documented among tocospermous families of Gamasina, it is restricted to the deutonymph, much as it is among the families of Uropodina. Phoretic deutonymphs are generally well sclerotized, for protection against mechanical damage from their carriers and against desiccation while exposed on their carrier (ATHIAS-BINCHE, 1991). Also, they often have structural modifications, such as the circular, adhesive design of the anal shield among families of Sejina and Uropodina, for affixing themselves to their carriers. One might anticipate that *Coprozercon scopaeus* would benefit from a phoretic association with the wood rats or vagile insects to move from one patchy, temporary organic resource to another in cave systems, but we have no documentation for this. Perhaps significantly, the dorsal shields of its deutonymph are as well ornamented and sclerotized as in the adult male, and more strongly so than in the adult female, whereas in zerconids these shields are generally less ornamented and sclerotized in deutonymphs than in adults. But otherwise, there are no anal, setal or other structural modifications indicative of phoresy evident in the deutonymph of *C. scopaeus*.

The sexually dimorphic loss of the opisthonotal shield in the adult female of *Coprozercon* is otherwise not known among genera of Zerconidae and Epicriidae. Adults of *C. scopaeus* are small mites (idiosomal lengths of females 260–270 μm, of males 192–227 μm) compared to many other taxa of Gamasida. Perhaps a reduced opisthonotal shield in the female allows for more expansion of the soft opisthosomal cuticle when containing a relatively large egg. The greatest linear dimension, 132 μm, of an apparently fully formed egg in one specimen of *C. scopaeus* is about one half of that female's idiosomal length, and about equal to her opisthosomal length. However, adult females of a considerable variety of Zerconidae are similarly small, with their idiosomal length in the range of 265–365 μm, e.g., *Eurozercon pacificus* Halašková 267–280 μm, and *Aquilonozercon desuetus* Halašková 284–288 μm (HALAŠKOVÁ, 1979); yet these mites do not show any reduction of their opisthonotal shield (the egg sizes in such small zerconids has not been recorded). A somewhat comparable, sexually dimorphic reduction in opisthosomal shielding is found among species of *Arctacarus* Evans, though in this case a single holonotal shield is involved. The need, or function, of reduced opisthonotal shielding in *Arctacarus* does not seem to relate to the size of the egg in proportion to that of the maternal female. The females are large mites, with idiosomal lengths of 820–1000 μm (EVANS, 1955; BREGETOVA, 1977) and of 1030–1125 μm among specimens at hand in the Canadian National Collection. The greatest linear dimension of a fully formed egg in gravid females of *Arctacarus* at hand is only from 0.39 to 0.42 of the idiosomal length of the females.

In *Coprozercon scopaeus*, tarsi II to IV lack one of the two pseudosymmetric pairs of ventral setae, *av-1*, *pv-1* and *av-2*, *pv-2* in adults, even though both pairs are present in the deutonymph. This regressive deficiency is an adult deficiency of what most probably are larval setae on tarsi II and III, and protonymphal setae on tarsus IV, based on the general ontogenetic patterns of setation of tarsi II to IV throughout the Mesostigmata (EVANS, 1963, 1965, 1969, 1972). We are not aware of this condition having been reported for any other taxon in the Mesostigmata, and we have not observed it among any taxa of Zerconidae, Epicriidae and Arctacaridae. However, the number of

setae on tarsi II–IV is often examined cursorily, and such a deficiency, whether larval or postlarval, could be easily overlooked.

DISCUSSION

As noted at the outset of this paper, the Epicriina, variously treated as a cohort, "division", or suborder, is a problematical grouping, and current classifications are discordant about the content of families in the group, as well as the relationships of the group to others of the same level. In our introduction, we summarily dismissed the most discordant classificatory view maintained for nearly thirty years by KARG (1965, 1971, 1993) and followed by KRANTZ (1978) and KRANTZ & AINSCOUGH (1990). We review that classification further here. To classify the Epicriidae in the otherwise podospermous superfamily Phytoseioidea, the Zerconidae in the otherwise podospermous superfamily Ascoidea, and the Arctacaridae in the otherwise podospermous or at least "neospermous" (*sensu* ALBERTI, 1988) Parasitoidea, as the above authors do, is to view the lack of a cheliceral spermatodactyl and the mid-sternal position of the genital aperture in the males of these tocospermous gamasine mites as "coincident occurrences of these unusual characters" amidst these superfamilies (KRANTZ & AINSCOUGH, 1990). These classifications imply that the morphological and behavioral attributes of podospermy have arisen independently at least four times within the Gamasina: once in each of the superfamilies Phytoseioidea, Ascoidea and Parasitoidea, and at least once among the other superfamilies Eviphidoidea, Rhodacaroidea and Dermanyssoidea. The mechanisms of podospermy are complex and include transfer of spermatophores by males from their presternally located genital orifice by means of a spermatodactyl on their modified movable cheliceral digits for injection into one of the pair of copulatory pores (solenostomes) of females, which is located usually between the bases of coxae III–IV (EVANS, 1992). It is both highly improbable and unparsimonious that such a complex of attributes for direct sperm transfer would arise independently several times among superfamilies in the same major lineage, Dermanyssina. Instead, we are in accord with the interpretation of ALBERTI (1988) that tocospermy, in particular "archispermy"—the transfer of spermatophores containing vacuolate spermatozoa by males from their midsternally located genital orifice by means of their cheliceral digits for injection into the primary genital orifice of females—is a plesiomorphic complex of attributes. Therefore, it is more parsimonious to exclude the families Zerconidae, Epicriidae and Arctacaridae from the otherwise podospermous superfamilies noted above. In this way, "neospermous" tocospermy may be hypothesized to have arisen once, in a more narrowly circumscribed group Parasitina *sensu* JOHNSTON (1982) and EVANS (1992), which includes but one superfamily Parasitoidea and family Parasitidae, and excludes Veigaiidae and Rhodacaridae. Similarly, as a next step, podospermy may be hypothesized to have arisen but once, in the group Dermanyssina, which includes five superfamilies, *sensu* JOHNSTON (1982) and tentatively accepted by EVANS (1992). The sister linkage of Parasitina and Dermanyssina as a group characterized synapomorphically by "neospermy" is supported by the males of this grouping having ribbon spermatozoa, both in Parasitina whose chelicerae are equipped with a spermatotreme, and in Dermanyssina whose chelicerae have a spermatodactyl, for transfer of spermatophores (ALBERTI, 1988).

The position of the male genital orifice, and the difference in form and dentition of the male chelicera in comparison with that of the female and deutonymph, in Coprozerconidae are noteworthy in this context of tocospermy versus podospermy. The genital orifice is hardly mid-sternal, in that it is located closely behind the level of sternal setae *st1*, rather than between the levels of setae *st2* and *st3* as in Zerconidae, Epicriidae and Arctacaridae. This position is nearly as anterior as that found in the relatively early derivative podospermous family Rhodacaridae of Gamasina. In contrast to the latter, however, the anterior margin of the genital aperture in Coprozerconidae is slightly posterior to the level of setae *st1*, rather than between these setae, and it is clearly posterad the anterior margin of the sternogenital shield, rather than on that margin. The more slender, straight, pointed form of the fixed chela in the male, than in the female and deutonymph, of Coprozerconidae may be an adaptation for transfer of spermato-

phores, in absence of a spermatodactyl. We have observed a similar difference in form of the male fixed chela from that of the female among species of Zerconidae and Epicriidae, though this does not seem to have been noted in the literature. In Arctacaridae, the male fixed chela remains hooked apically, much as in the female, but it is thicker and less dentate than in the female and deutonymph (EVANS, 1955, and our personal observations). Such subtle modifications of the male chelicerae in tocospermous families may be more prevalent than is currently recognized, and more careful descriptive attention should be given to this form of sexual dimorphism.

Exclusion of Coprozerconidae, Zerconidae, Epicriidae and Arctacaridae from the Parasitina and Dermanyssina leaves the relationships and classification of these families at a still unresolved, albeit earlier derivative, level. A sister-group relationship between Coprozerconidae and Zerconidae is hypothesized in the remarks following the description of the new family above. Based on definitive and diagnostic criteria available in widely accepted general literature (e.g., JOHNSTON, 1982; EVANS, 1992), these two families, along with Epicriidae and Arctacaridae, are excluded from the following, apparently sister-pairs of major groups: the more early derivative Sejina and Microgyniina, the Cercomegistina and Antennophorina of Trigynaspida, and the Uropodina and Diarthrophallina. As a result, this leaves Zerconidae + Coprozerconidae, Epicriidae, and Arctacaridae more or less together by default, though not necessarily by definition.

At the generic level, taxa of Zerconidae and Epicriidae were grouped together over a century ago by BERLESE (1892), and this grouping has persisted in some classifications as recently as EVANS & TILL (1979), who also included the more recently described family Arctacaridae (EVANS, 1955) in their "Division Epicriides". The diagnosis for this grouping, however, has been based solely on plesiomorphic attributes, as follow: chelicerae with no or little sexual dimorphism (i.e., the male movable chela lacking an elaborated structure for transfer of spermatophores); male genital orifice mid-sternal in position, located at a level usually between coxae II; male insemination of females by way of the female genital orifice; and tibia I with 4 ventral setae. Earlier, EVANS (1955) noted

some other shared attributes between Epicriidae, Zerconidae, and the then new family Arctacaridae: female genital shield with hyaline epigynial portion reduced to a narrow sclerotized rim (such that egg is not extruded along a "chute" as in Dermanyssina); male genital opening covered by two plates, the anterior of which bears a pair of setae (eugenital setae); and palpi with five free segments, with specialized seta on palptarsus two — or three-tined. To these, we add: the at least somewhat shortened peritremes in adults; the lack of metasternal platelets (setae $st4$ inserted on soft cuticle) in adult females; gland pores $gv2$ usually multiple and together on a pair of adgenital platelets (secondarily single and on soft cuticle, or absent in some genera); and three leg chaetotactic attributes of deutonymphs and adults, namely, genua III and IV each with 10 setae, including a second ventral seta, pv; tibia III with 9 setae, including a second posterolateral seta, $pl-2$. However, all but two of these attributes are evidently plesiomorphies, and most of them are not exclusive to these families. Of the other two attributes, the narrow, sclerotized anterior rim of the genital shield may be viewed as readily as a primitive absence of a hyaline epigynial extension rather than as a secondarily reduced structure. Based on out-group comparisons, the lack of metasternal platelets is probably a secondary loss, but also a homoplastic one, as these platelets are retained in *Coprozercon*. At present, therefore, there are no synapomorphic attributes that define an exclusive natural grouping for Epicriidae, Zerconidae (+ Coprozerconidae) and Arctacaridae.

Based on sharing the attributes of the presence of peritrematal plates with clearly developed (though somewhat shortened) peritremes, dorsal shielding without a specially characteristic ornamentation, and jugular plates absent in adults, EVANS (1955) grouped the Arctacaridae together with Zerconidae in a superfamily Zerconoidea, distinct from the Epicrioidea which contained but one family. However, the first two of these shared attributes are clearly plesiomorphies, in contrast to each of the alternative character states typical in both sexes of Epicrioidea, namely, peritrematal plates and peritremes absent, and stigmata enclosed in dorsal shield, the latter with a characteristic, coarsely tuberculate ornamentation. The third attribute, absence of jugular plates, does not

hold for all genera of Zerconidae, particularly the early derivative ones (see below). To these attributes we add the shared presence of gland pores *gv1* on the posterior margin of the sternal shield in adult females and sometimes on the sternogenital shield of deutonymphs and adult males (absent in *Coprozercon*). Based on out-group comparisons, however, the presence of these pores is plesiomorphic.

It is perhaps because of this lack of synapomorphic evidence to link the families Epicriidae, Zerconidae and Arctacaridae as a natural group that EVANS (1992) subsequently opted to treat each one in its own superfamily and, in turn, suborder! This alternative, however, leaves not only the relationships between these families unresolved, but those of other major groups of Mesostigmata unresolved as well.

A sister relationship between Epicriidae and Zerconidae in a cohort Epicriina that excluded Arctacaridae, was recognized by JOHNSTON (1982). The basis for this arrangement was not apparent from the diagnosis given by him for the cohort, as it was not made clear whether any of the given characteristics were thought to be exclusive to this cohort, and none of them evidently is. Here, we list and consider character states that may be used to argue for a sister relationship between Epicriidae and Zerconidae (+ Coprozerconidae).

1. Protonymph with pygidial shield expansive, as wide as podonotal shield, and bearing 10 to 15 pairs of setae, including *S2, S3* (if present) laterally. Protonymphs of Arctacaridae at hand lack any vestige of a pygidial shield, and in this respect resemble the condition described by KARG (1965) for Veigaiidae.

2. Protonymph with setae *J4* widely separated from each other relative to interval between setae *J1*.

3. Adults with sternal setae *st1* on jugular plates. Though typical of epicriid mites, this state is found also in a few zerconids, e.g., *Syskenozercon* (ATHIAS-HENRIOT, 1976), *Rafas* Błaszak (BŁASZAK, 1979), and *Halozercon* (WIŚNIEWSKI *et al.*, 1992). As *Syskenozercon* and *Halozercon* are evidently among the earliest derivative known genera of Zerconidae, this attribute may be a possible characteristic of the stem group of Zerconidae, in which the jugular plates subsequently became consolidated into one sternal shield.

4. Adults with expansive peritrematal, or "lateropeltidial", shields. These shields are largely coalesced with dorsal shielding in the podonotal region, so as to apparently capture the bases of some *r*-marginal setae. Arctacarid adults have normally developed, but not expansive, peritrematal shields that do not bear any marginal setae.

5. Adults with peritremes shortened from the length expressed in deutonymphs. This condition is not found in Arctacaridae.

6. Coxa II with acute spur on its distal anterodorsal margin. This spur is absent in Arctacaridae.

On the basis of these attributes, a reasonable case can be made for grouping Epicriidae together with Zerconidae and Coprozerconidae in Epicriina, and excluding Arctacaridae from that group. Apart from the third attribute, which may be a symplesiomorphy, the others are synapomorphic for these families among the non-uropodine, non-trigynaspidine and non-podospermous gamasine families of Mesostigmata. None of the five attributes is autapomorphic, however. A similarly expansive opisthonotal shield in the protonymph occurs among some members of Eviphididae (KARG, 1965), but this clearly is an independently derived, within-group attribute of that family within the podospermous superfamily Macrocheloidea. A relatively wide interval between setae *J4* in protonymphs occurs in a variety of podospermous families, in which this seems to have arisen several times. Whether the condition of the peritrematal shielding in adults is an expansion of the peritrematal shields or a reduction of previously larger marginal shields (as prevalent among families of Uropodina and Trigynaspida) is problematical. Enlarged peritrematal shields are derived independently in such podospermous families as Pachylaelapidae and Varroidae. Shortening of the peritremes from the deutonymph to the adult, though homoplastic, has been rarely noted in other groups of Gamasida. A similar reversal in ontogenetic lengthening of the peritreme is found among some species in the podospermous family Digamasellidae (LINDQUIST, 1975), and this may not have yet been noted in other families having species with abbreviated peritremes in adults, as their

deutonymphs have not been studied carefully. The presence of an anterodorsal spur on coxae II appears to be more commonly homoplastic; without undertaking a comprehensive search for this structure in a wide array of Gamasida, we have observed it, for example, in some genera of tocospermous Sejoidea (e.g., *Microsejus, Asternolaelaps*) though not others (*Microgynium, Sejus*), and in some genera of podospermous Rhodacaroidea (e.g., *Rhodacarus, Rhodacarellus*) though not others (*Panteniphis, Gamasellus, Digamasellus*).

Although we are persuaded by the case already presented above, that Coprozerconidae is the sister family of Zerconidae, an alternative argument could be made that the new family is, instead, the sister group of Epicriidae. This could be based on two synapomorphies, reduction of peritremes in the adult to little, if any, more than the stigmata, and ventrolateral extension of opisthonotal shielding in the male, to capture two or three pairs of the ventral *ZV* or *JV* setae. However, reduction in peritrematal length is not as extreme in *Coprozercon* as in genera of Epicriidae, and it is matched in Zerconidae by the condition found among species of *Metazercon* BŁASZAK (HALAŠKOVÁ, 1979), and nearly so among species of *Skeironozercon* (HALAŠKOVÁ, 1977) and *Monozercon* (BŁASZAK, 1984). Also, the ventrolateral extension of opisthonotal shielding is not a sexually dimorphic character in Epicriidae, and so is probably independently derived in that family.

In view of the above discussion, we conclude the following:

1. A sister group relationship between Zerconidae and *Coprozercon*, the latter in its own family, is phylogenetically justifiable.

2. These two families constitute the superfamily Zerconoidea in exclusion to any other families.

3. The Zerconoidea is the sister group of the family Epicriidae, the latter in its own superfamily in exclusion to any other families.

4. The Epicrioidea and Zerconoidea together constitute the Epicriina, in the sense of a "cohort" as used by KRANTZ (1978), or the Epicriides, in the sense of a "division" as used by EVANS & TILL (1979).

5. The Arctacaridae is excluded from the Epicriina, and its relationship with other superfamilies of tocospermous Gamasida remains uncertain, other than its not being a member of Uropodina or Trigynaspida. We anticipate that its most likely relationship is as the sister group of the superfamily Parasitoidea, or "Division Parasitides" *sensu* EVANS & TILL (1979), or Parasitina *sensu* EVANS (1992). In this respect it will be interesting to determine whether spermatozoa of Arctacaridae are of a more derivative spindle or ribbon form, as found by ALBERTI (1984, 1988, 1991) for Parasitina and Dermanyssina, or of a more plesiomorphic vacuolated form, as found by him for Epicriina (including Epicriidae and Zerconidae), Sejina, Uropodina, Ixodida, Holothyrida and Opilioacarida.

6. The relationship of Epicriina with other major groupings of Gamasida is similarly problematical, apart from its not being a member of Uropodina or Trigynaspida. We anticipate that its most likely relationships are either as a sister group to the Sejina, or as a sister group to the grouping {Arctacaridae + Parasitidae + Dermanyssina families}.

REFERENCES

ALBERTI (G.), 1984. — The contribution of comparative spermatology to problems of acarine systematics. — Pp. 479-490 *in* D. A. GRIFFITHS & C. E. BOWMAN (Eds.), Acarology VI. Vol. 1. Ellis Horwood, Chichester.

ALBERTI (G.), 1988. — Genital system of Gamasida and its bearing on phylogeny. — Pp. 197-204 *in* G. P. CHANNA

BASAVANNA & C. A. VIRAKTAMATH (Eds.), Progress in Acarology. Vol. 1. Oxford & IBH Publishing, New Delhi.

ALBERTI (G.) 1991. — Spermatology in the Acari: systematic and functional implications. — Pp. 77-105 *in* R. SCHUSTER & P. W. MURPHY (Eds.), The Acari: Reproduction, development and life-history strategies. Chapman & Hall, London.

ATHIAS-BINCHE (F.), 1991. — Ecology and evolution of phoresy in mites. — Pp. 27-41 *in* F. DUSBÁBEK & V. BUKVA (Eds.), Modern Acarology. Vol. 1. Academia, Prague & SPB Academic Publishing, The Hague.

ATHIAS-HENRIOT (C.), 1969a. — Les organes cuticulaires sensoriels et glandulaires des Gamasides. Poroïdotaxie et adénotaxie. — Bull. Soc. zool. Fr., **94**: 485-492.

ATHIAS-HENRIOT (C.), 1969b. — Notes sur la morphologie externe des Gamasides (Acariens Anactinotriches). — Acarologia, **11**: 609-625.

ATHIAS-HENRIOT (C.), 1976. — *Syskenozercon kosiri* n. g., n. sp., Zerconidae dorsonéotriche des Alpes et de l'Himalaya (Arachnides, Gamasides). — Bull. Soc. zool. Fr., **101**: 433-444.

BERLESE (A.), 1887. — Acari, Myriopoda et Scorpiones hucusque in Italia Reperta. Ordo Mesostigmata (Gamasidae). Fasc. XLI, No. 5. — Typis Seminarii, Padua.

BERLESE (A.), 1892. — Acari, Myriopoda et Scorpiones hucusque in Italia Reperta. Ordo Mesostigmata (Gamasidae). Zerconidae Berlese 1892. — Pp. 74-79, pl. X. Typis Seminarii, Padua.

BŁASZAK (C.), 1976. — A revision of the family Zerconidae (Acari, Mesostigmata) (Systematic studies on family Zerconidae–I). — Acarologia, **17**: 553-569.

BŁASZAK (C.), 1979. — Tunisian Zerconidae (Acari: Gamasida). — Folia Entomol. Hung., **32**: 13-26.

BŁASZAK (C.), 1984. — Three new genera of zerconid mites (Acari, Mesostigmata, Zerconidae) from the United States of America with a key to the American genera. — Pols. Pismo Entomol., **53**: 587-601.

BŁASZAK (C.), COKENDOLPHER (J. C.) & POLYAK (V. J.), 1995. — *Paleozercon cavernicolus*, n.gen., n.sp., fossil mite from a cave in the southwestern U.S.A. (Acari, Gamasida: Zerconidae), with a key to nearctic genera of Zerconidae. — Internat. J. Acarol., **21**: 253-259.

BREGETOVA (N. G.), 1977. — Sem. Arctacaridae Evans, 1955. — Pp. 145-148 *in* M. S. GILYAROV (Ed.), Opredelitel' obitayushchikh v pochve kleshchei. Mesostigmata [A key to soil-inhabiting mites. Mesostigmata]. Izdatel'stvo "Nauka", Leningrad (In Russian).

EVANS (G. O.), 1955. — A collection of mesostigmatid mites from Alaska. — Bull. Brit. Mus. (Nat. Hist.), Zool., **2**: 287-307.

EVANS (G. O.), 1963. — Some observations on the chaetotaxy of the legs in the free-living Gamasina (Acari: Mesostigmata). — Bull. Brit. Mus. (Nat. Hist.), Zool., **10**: 275-303.

EVANS (G. O.), 1964. — Some observations on the chaetotaxy of the pedipalps in the Mesostigmata (Acari). — Ann. Mag. nat. Hist., Ser. 13, **6**: 513-527.

EVANS (G. O.), 1965. — The ontogenetic development of the chaetotaxy of the tarsi of legs II-IV in the Antennophorina (Acari: Mesostigmata). — Ann. Mag. nat. Hist., Ser. 13, **8**: 81-83.

EVANS (G. O.), 1972. — Leg chaetotaxy and the classification of the Uropodina (Acari: Mesostigmata). — J. Zool., London, **167**: 193-206.

EVANS (G. O.), 1969. — Observations on the ontogenetic development of the chaetotaxy of the tarsi of legs II-IV in the Mesostigmata (Acari). — Pp. 195-200 *in* G. O. EVANS (Ed.), Proc. 2nd Internat. Congr. Acarol., 1967. Akadémiai Kiadó, Budapest.

EVANS (G. O.), 1992. — Principles of Acarology. — C.A.B. International, Wallingford. xviii + 563 pp.

EVANS (G. O.) & TILL (W. M.), 1979. — Mesostigmatic mites of Britain and Ireland (Chelicerata: Acari-Parasitiformes). An introduction to their external morphology and classification. — Trans. zool. Soc. London, **35**: 139-270.

HALAŠKOVÁ (V.), 1977. — A revision of the genera of the family Zerconidae (Acari: Gamasides) and descriptions of new taxa from several areas of Nearctic Region. — Studie Českoslov. Akad. Věd, No. 7. 75 pp.

HALAŠKOVÁ (V.), 1979. — Taxonomic studies on Zerconidae (Acari: Mesostigmata) from the Korean People's Democratic Republic. — Acta Sci. Nat. Brno, **13**(3): 1-41.

HALL (E. R.) & KELSON (K. R.), 1959. — The mammals of North America. Vol. 2. Ronald Press, New York. Pp. i-viii, 547-1083.

HAMMEN (L. van der), 1975. — L'évolution des Acariens, et les modèles de l'évolution des Arachnides. — Acarologia, **16**: 377-381.

JOHNSTON (D. E.), 1982. — Acari. Parasitiformes. — Pp. 111-117 *in* S. B. PARKER (Ed.), Synopsis and classification of living organisms. Vol. 2. McGraw-Hill, New York.

JOHNSTON (D. E.) & MORAZA (M. L.), 1991. — The idiosomal adenotaxy and poroidotaxy of Zerconidae (Mesostigmata: Zerconina). — Pp. 349-356 *in* F. DUSBÁBEK & V. BUKVA (Eds.), Modern acarology. Vol. 2. Academia, Prague.

KARG (W.), 1965. — Larvalsystematische und phylogenetische Untersuchung sowie Revision der Systems der Gamasina Leach 1915 (Acarina: Parasitiformes). — Mitt. zool. Mus. Berlin, **41**: 193-340.

KARG (W.), 1971. — Zur Kenntnis der Epicriidae Berlese, 1885 (Acarina, Anactinochaeta). — Zool. Anz., **186**: 105-114.

KARG (W.), 1993. — Acari (Acarina), Milben. Parasitiformes (Anactinochaeta), Cohors Gamasina Leach, Raubmilben. — Tierwelt Deutschlands, Teil 59. 523 pp.

KRANTZ (G. W.), 1978. — A manual of acarology. 2nd edition. — Oregon State University Bookstores, Corvallis. 509 pp.

KRANTZ (G. W.) & AINSCOUGH (B. D.), 1990. — Acarina: Mesostigmata (Gamasida). — Pp. 583-665 *in* D. L. DINDAL (Ed.), Soil Biology Guide. J. Wiley & Sons, New York.

KRANTZ (G. W.) & REDMOND (B. L.), 1987. — Identification of glandular and poroidal idiosomal systems in *Macrocheles perglaber* F. & P. (Acari: Macrochelidae). — Exp. appl. Acarol., **3**: 243-253.

LINDQUIST (E. E.), 1975. — *Digamasellus* Berlese, 1905, and *Dendrolaelaps* Halbert, 1915, with descriptions of new taxa of Digamasellidae (Acarina: Mesostigmata). — Can. Entomol., **107**: 1-43.

LINDQUIST (E. E.), 1994. — Some observations on the chaetotaxy of the caudal body region of gamasine mites (Acari: Mesostigmata), with a modified notation for some ventrolateral body setae. — Acarologia, **35**: 323-326.

LINDQUIST (E. E.) & EVANS (G. O.), 1965. — Taxonomic concepts in the Ascidae, with a modified setal nomenclature for the idiosoma of the Gamasina (Acarina: Mesostigmata). — Mem. entomol. Soc. Canada, No. 47. 64 pp.

LINDQUIST (E. E.) & MORAZA (M. L.), 1999. — Observations on homologies of idiosomal setae in Zerconidae (Acari: Mesostigmata), with modified notation for some posterior body setae. – Acarologia, **39** [1998] : 203-226.

PETROVA (A. D.), 1978. — Novyi rod i novyi vid kleshchei-tserkonid (Parasitiformes, Gamasoidea, Zerconidae) s tsel'nym dorsal'nym shchitom [A new genus and species of zerconid mites with entire dorsal shield]. — Entomol. Obozr., **57**: 218-220 (In Russian). [1979 English translation in Entomol. Rev., **57**: 153-154.]

SELLNICK (M.), 1958. — Die Familie Zerconidae Berlese. — Acta zool. Acad. Sci. Hung., **3**: 313-368.

WIŚNIEWSKI (J.), KARG (W.) & HIRSCHMANN (W.), 1992. — Gangsystematik der Parasitiformes, Teil 547. Die Adultengattung *Halozercon* nov. gen., Typenart *Halozercon karacholana* nov. spec. aus Sibirien (Halolaelapidae, Ascoidea, Gamasina). — Acarologie, Nürnberg, **39**: 180-186.

WOLF (B.), 1938. — Animalium cavernarum catalogus. — W. Junk, 's-Gravenhage, Vol. 3. 918 pp.

ZACHARDA (M.), 1980. — Soil mites of the family Rhagidiidae (Actinedida: Eupodoidea). Morphology, systematics, ecology. — Acta Univ. Carol., Biol., **1978** (5-6): 489-785.