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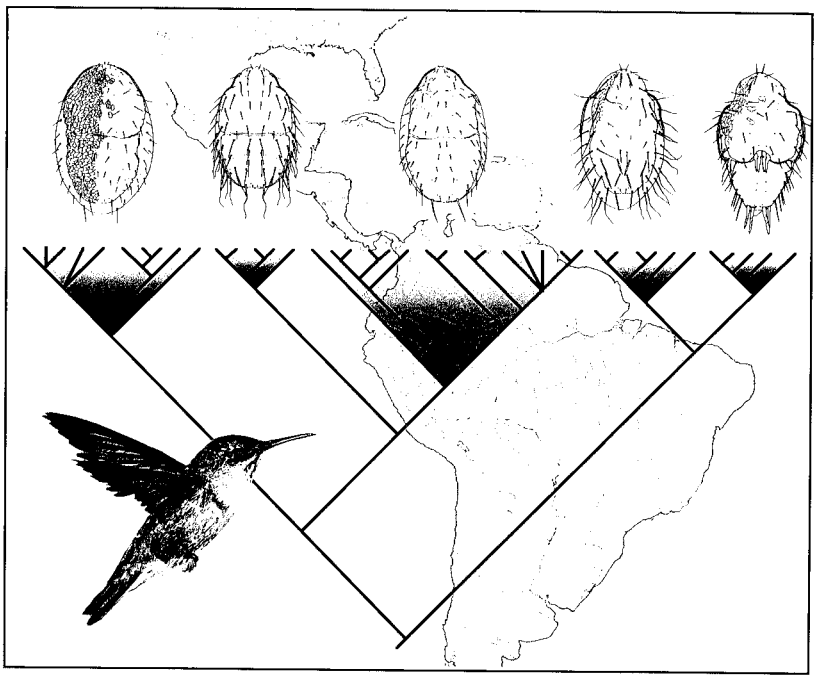
Systematics and Host Plant Affiliations of Hummingbird Flower Mites of the Genera *Tropicoseius* Baker & Yunker and *Rhinoseius* Baker & Yunker (Acari: Mesostigmata: Ascidae)

Piotr Naskrecki and Robert K. Colwell



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Front cover: (left to right) *Tropicoseius cervus* Naskrecki & Colwell, *T. erioxynon* Naskrecki & Colwell, *T. naeemi* Naskrecki & Colwell, *Rhinoseius luteyni* Naskrecki & Colwell, and *R. richardsoni* Hunter. Illustration by Piotr Naskrecki.

ISBN 0-938522-67-1

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Systematics and Host Plant Affiliations of Hummingbird Flower Mites of the Genera *Tropicoseius* Baker & Yunker and *Rhinoseius* Baker & Yunker (Acari: Mesostigmata: Ascidae)

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Published by the
ENTOMOLOGICAL SOCIETY OF AMERICA
Lanham, Maryland
1998

Contents

Abstract

A cladistic analysis and systematic revision of 2 primarily neotropical mite genera, *Tropicoseius* Baker & Yunker and *Rhinoseius* Baker & Yunker (Mesostigmata, Ascidae, Melicharini), are presented. The 2 genera and 5 of their species are redescribed, and 11 species of *Tropicoseius* and 1 species of *Rhinoseius* are described as new. A key to species of the 2 genera is given. The genera *Tropicoseius* and *Rhinoseius* form a monophyletic lineage, of which the sister group appears to be the genus *Xanthippe* Naskrecki and Colwell. Mites of the genera *Tropicoseius* and *Rhinoseius* feed and reproduce within the inflorescences of hummingbird-pollinated plants. Host plant specificity and fidelity is very high. A posteriori mapping of host plant affiliations on the cladogram reveals a striking pattern of origin and radiation for these mites, with 1 clade (*Rhinoseius*) in dicotyledonous groups of the tropical highlands, and a gradual evolutionary shift within the sister clade (*Tropicoseius*) to lowland habitats and monocotyledonous hosts.

KEY WORDS *Tropicoseius, Rhinoseius,* cladistic analysis, hummingbird flower mites, host plant affiliations

Introduction

Little is known of the phylogeny and ecology of most groups of wildland mites, especially those of tropical regions. The ecology and behavior of the lineages collectively known as hummingbird flower mites, however, have been studied in unusual depth over the past 25 yr (Colwell 1973, 1979b, 1983, 1985, 1986a, b, 1995; Colwell et al. 1974; Colwell and Naeem 1979, 1994; Wilson and Colwell 1981; Dobkin 1984, 1985, 1987, 1990; Heyneman 1985; Heyneman et al. 1991; Paciorek et al 1995; Colwell and Naskrecki, in press). All known species of hummingbird flower mites share an obligate affiliation with the flowers of hummingbird-pollinated plants, where they feed on nectar and pollen, and are transported between inflorescences in the nasal cavities of hummingbirds.

The term *hummingbird flower mite* was originally applied by Colwell (1973) to mites of the closely related genera *Rhinoseius* and *Tropicoseius* (Ascidae) (sensu Baker & Yunker 1964), based on a detailed study of 2 species (1 in each genus, as defined here) in the highlands of Costa Rica. That study confirmed Baker and Yunker's (1964) conjecture that mites of these genera probably were phoretic rather than parasitic on hummingbirds, feeding on plants visited by the birds.

Later, Fain et al. (1977a) described several new species of *Proctolaelaps* Berlese, 1926 (Ascidae) from hummingbird nares (as well as some additional *Rhinoseius* spp.). Based on detailed ecological studies (Colwell 1979b; 1986b), the term hummingbird flower mite was extended to these species and others, all in a possibly monophyletic lineage within *Proctolaelaps* that has converged on the same ecology and behavior as *Rhinoseius* and *Tropicoseius*. Additional species from hummingbird nares and flowers

have been described in the genus *Lasioseius* Berlese, 1916 (Fain et al. 1977a, Naeem et al. 1985, Ohmer et al. 1991), but their feeding habits remain unknown, and it is unclear if phoresy on hummingbirds is an essential component of their life history.

Many workers independently contributed to the task of describing and classifying hummingbird flower mites (reviewed by Fain [1992], with additional references in the species accounts of this monograph). Between 1964 and 1994, the number of described species in the genera *Rhinoseius* and *Tropicoseius* rose from 11 to 42 (not counting the 12 new species we describe here), whereas the number of described species of *Proctolaelaps* associated with hummingbirds and the flowers they pollinate increased from none to 12. Although some tentative groupings of species have been published (Fain et al. 1977b, Fain 1992), this revision is the first study to attempt a reconstruction of the phylogeny of hummingbird flower mites through formal cladistic analysis. This monograph treats the genera *Rhinoseius* and *Tropicoseius*. A companion study of the hummingbird–flower-affiliated *Proctolaelaps* is under way.

It has been apparent since the earliest ecological studies of hummingbird flower mites (Colwell 1973) that the mites are specialists on their plant hosts. Courtship, mating, and oviposition occur on the host plant (Colwell 1985; 1986a, b). The affiliation of hummingbird flower mites with their host plants is not only quite specific but characteristically exclusive (at least within localities), although some cases of consistent host sharing are known (Colwell 1979b; 1986). In contrast, the mites are quite opportunistic with regard to hummingbird carriers. The mites that any given individual hummingbird carries generally represent whatever mixture of flowers the bird is currently visiting(Colwell 1973; 1979b; 1986a). Thus, although important biogeographically, data on the hummingbird carriers of hummingbird flower mites turns out to be of little evolutionary interest.

Within a local community in the tropical lowlands, many hummingbird flower mite species are monophagous on plants that flower all year. Others exploit plants with limited flowering seasons, whether in the tropical lowlands or at higher elevations or higher latitudes, by shifting between host plants seasonally (Colwell and Naeem 1994). At least 1 species of *Tropicoseius* is a long-distance seasonal migrant as a passenger on migrating hummingbirds (Colwell and Naeem 1979). Some species of hummingbird flower mites that are monophagous locally inhabit related plant species or even unrelated ones in other localities. For example, in the well-studied Trinidad assemblage (Colwell 1986a, OConnor et al. 1997), *T. heliconiae* is known exclusively from *Heliconia psittacorum*, but there are records from 9 other species of *Heliconia* elsewhere (Table 5).

Hummingbirds (family Trochilidae), a strictly New World family of >300 species, breed from Alaska (Rufous Hummingbird, *Selaphorus rufus* [Gmelin]) to Tierra del Fuego (Green-backed Firecrown, *Sephanoides galeritus* [Lesson]) (Skutch 1973). At tropical latitudes, wet lowland rainforest typically supports 10–25 sympatric hummingbird species (Feinsinger and Colwell 1978, Colwell and Coddington 1994). Hummingbird species tend to replace one another along elevational gradients (from sea level to >5,000 m elevation in the Andes [Feinsinger et al. 1979]) with only 3–5 species typically in tropical highland assemblages. Endemic hummingbird species inhabit the Greater and Lesser Antilles and the Juan Fernández Archipelago (Colwell 1989).

Hummingbird flower mites are found throughout virtually the full geographical range of hummingbirds (and the plants they pollinate). Range limits for this group of mites, as currently known, are posted by *Tropicoseius chiriquensis* Baker & Yunker, 1964 (=*Rhinoseius epoecus* Colwell & Naeem, 1979) from sites in northern California, *Tropicoseius fuentesi* n. sp. from central Chile, *Tropicoseius erioxynon* n. sp. from the Ecuadorian altiplano, *Tropicoseius naeemi* n. sp. from Dominica, W. I, and *Tropicoseius rowelli* n. sp. from Jamaica. Variation in the species richness of sympatric assemblages of these mites parallels that of their host plants and hummingbird carriers (Colwell 1979b). In lowland rainforest of Trinidad, W. I., for example, 17 species of hummingbird flower mites coexist (8 species of *Tropicoseius* and 9 of *Proctolaelaps*) (OConnor et al. 1991, 1997), whereas only 2 species (*Tropicoseius colwelli* and *Rhinoseius richardsoni*) are found at 3,000 m elevation in Costa Rica (Colwell 1972). The host plant affiliations of the mites in these 2 assemblages have been constant for >2 decades (OConnor et al. 1991, 1997; R.K.C., unpublished data; see also the Material Examined sections of this monograph).

Several features of hummingbird flower mites make them unusually good subjects for both systematic and ecological studies. The high level of host plant specificity (1 or a very few host species per mite species, locally and simultaneously), consistent host plant fidelity (the same mite species in the same host species year after year), and the high frequency of host exclusivity (1 or rarely 2 mite species per host species locally) make it easy to obtain abundant specimens of most species in relatively species-pure collections (compared with soil mites in a Berlese funnel residue, for example). The conspicuous visibility of virtually all hummingbird-pollinated flowers further simplifies finding the mites in the field. In addition, the association of mites with flowers means that fluid collections of floral material in botanical collections provide an additional source of specimens. For this study, the floral collections of plant systematists W. J. Kress (Heliconiaceae), J. Luteyn (Ericaceae and Campanulaceae), P. E. Berry (Rapateaceae and Onagraceae), and B. Stein (Campanulaceae) proved to be a rich source of specimens and new species.

Finally, because these mites breed in flowers, both sexes and all instars typically are collected together from the host plants, greatly simplifying the tentative association of females and males (although correct as-

sociation must be confirmed by morphological evidence). Many mite species, including hummingbird flower mites (Wilson and Colwell 1981, Colwell and Naeem 1994), have female-biased sex ratios. Moreover, males of many species do not disperse phoretically and thus cannot be collected from specimens of their phoretic hosts (Athias-Binch 1991); hummingbird flower mites are an exception (Colwell and Naeem 1994). Thus, for many groups of mites, taxonomy must be based on female characters, even though males are often richer in apomorphies.

In contrast, the cladistic analysis in this study is based exclusively on species for which we were able to examine both sexes (and, in most cases, extensive series of specimens), as is apparent from lists of specimens examined. In addition to the 12 new species described in this monograph, we have described previously unknown sexes of 4 additional species and have fully redescribed 1 species. Many species of *Tropicoseius* and *Rhinoseius* have proven to be highly variable in morphology, sometimes with discrete morphs but more frequently display continuous variation in characters. In some specimens, bilateral asymmetry adds to the spectrum of morphological variation.

Materials and Methods

Because many people collected the material used for this study, details of collecting method vary and in some cases are not known. Generally, however, mites were found on living plants in the field by examining longitudinally sectioned flowers. When disturbed in this way, hummingbird flower mites are easily detected as they run rapidly over the floral tissue. Usually, both floral parts and mites were placed directly into 70–90% ethanol. In the case of very large flowers, mites were sometimes collected with a size 0000 artist's paintbrush and placed directly into ethanol instead. When the host plant was not known to the collector and voucher specimens were not collected for the host plant, the inclusion of floral parts with the mites virtually always allowed identification of the host plant at least to genus. (Botanists who aided in identifying plants are named in the acknowledgments.)

In the case of mites collected from museum collections of floral specimens, mites were collected from the preserving fluid (usually FAA) with a fine wire loop mounted on a needle holder and placed in 70–90% ethanol. Intact flowers were sectioned longitudinally when necessary. Host identifications in these collections relied on the museum records for the plant specimens.

With regard to mites from hummingbirds, Colwell and his collaborators collected all mites from mist-netted birds. Each bird was quickly removed from the net, not only for the safety and well-being of the bird, but to prevent the mites from escaping onto the threads of the net (they apparently sense the distress of the bird and rapidly leave the nares). Any visible mites were first suctioned from the surface of the bill and the feathers

around the base of the bill into a Bard-Parker Infant Suction Set aspirator (25 ml mucus trap with cap and catheter suction tube) (Bard-Parker, Rutherford, NJ) carrying ≈3 ml of 70–90% ethanol. Then the tip of the catheter was placed against (but not into) the nasal opening, gently lifting the operculum, and gentle suction was applied twice to each nasal opening (alternating sides). Temporary marks were placed on the bird's back (using dots of different colors of Liquid Paper [Liquid Paper, Boston, MA]), and the bird was released. The marks allowed individual identification of birds in case of recapture, permitting quantitative studies of phoresy. The mites and ethanol were then transferred to a vial, and the aspirator was thoroughly cleansed with ethanol before reuse.

Freshly collected mites or mites that had been stored in alcohol for a short time were placed directly into Hoyer's medium on microslides and sealed with GLPT (GC Electronics, Rockford, IL) insulating varnish. Mites that had been stored in ethanol for a considerably longer period of time (5–20 yr) were first immersed in lactic acid for 2–3 d, and subsequently mounted in Hoyer's medium on microslides. Specimens collected from flowers that previously had been preserved in a mixture of formaldehyde, acetic acid, and ethanol (FAA) for a number of years were usually badly affected by the medium and required considerably longer and more elaborate treatment. They characteristically had very dark coloration that effectively prevented light from penetrating the specimens and hindered their examination under a microscope. Such specimens were immersed in lactic acid and kept at a temperature of 50–55°C for up to 2 wk. Specimens that had still not yielded to clearing with lactic acid were subsequently treated with Nesbitt's fluid (chloral hydrate with hydrochloric acid) for up to 5 h. Such a drastic treatment was usually effective, and the specimens could be placed in Hoyer's medium and mounted on microslides. Some specimens, however, especially those that had been stored in FAA for >10 yr, had to be treated with 5% solution of KOH for up to 1 hr to remove the dark pigmentation. A number of specimens were collected from dried flowers from vials that originally had contained ethanol. These were first softened in 10% ethanol, then immersed in lactic acid for 1–2 d and placed in Hoyer's medium.

Systematic observations, measurements, and illustrations were made using a Zeiss compound microscope equipped with a differential interference contrast optical system and drawing tube. Measurements were taken using a stage-calibrated eyepiece micrometer. Most specimens (including all types) are individually mounted on microslides in Hoyer's medium. All primary types of newly described species and voucher specimens of redescribed species are deposited in the Canadian National Collection of Insects and Arachnids, Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Ottawa; additional paratypes are deposited in the Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs; the Institut Royal des Sciences Naturelles de Belgique, Brus-

sels; and, where feasible, in the national collections of the countries of origin.

Measurements are expressed as ranges of micrometers (μm). Dorsal shield length measures were taken as a midline length from anterior margin between setae *j1* to the caudal margin behind setae *J5*. Dorsal shield width measurements were taken at the level (indicated for each species) where the podonotal part of the dorsal shield was the widest. Symmetrical setae were measured on both sides of the body, and when their length differed, both values were recorded. Length of the spermatheca indicates the distance from the solenostome to its most distant discernible element. Length of the spermatodactyl indicates the distance from the base of the movable chela to the apex of the spermatodactyl.

In the descriptions and data matrices, the system of setal notation for legs follows that of Evans (1963); whereas the system of setal notation for the idiosoma is based on that of Lindquist and Evans (1965). The family concept of Ascidae and the tribe concept of Melicharini follow those of Lindquist and Evans (1965).

Type specimens of hummingbird flower mites described by previous authors and examined during this study were borrowed from the following institutions:

FMNH	Field Museum of Natural History, Chicago, IL
INBio	Institute Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, DC
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor, MI
USDA	Systematic Entomology Laboratory, USDA–ARS, Beltsville, MD
USPZ	Universidade de São Paulo, Escola Superior de Agricultura, Departamento Zoologia, Sao Paulo, Brazil

Cladistic Analysis

The following systematic treatment of the genera *Rhinoseius* Baker & Yunker, 1964, and *Tropicoseius* Baker & Yunker, 1964 (together these genera comprise *Rhinoseius* sensu Lindquist and Evans 1965) includes all species described and assigned to these genera by various authors through 1994 (for a detailed review of the taxonomic history see Fain 1992 and Wiese and Fain 1993). Up to the time of this monograph, 42 species had been described. Of these 42 species, 6 are synonymized below. In addition, we describe 12 species as new, giving a current total of 48 valid species.

To generate an hypothesis of the phylogenetic relationship among these species, we performed a cladistic analysis based on numerical parsimony. The cladistic analysis included 41 of the 48 species of *Rhinoseius* sensu stricto and *Tropicoseius* recognized in this study. Seven previously described species were excluded from the analysis because either only 1 sex of the species is known, or specimens were not available for examination at the time of the analysis.

In the cladistic analysis of the 41 ingroup species, 49 morphological characters were used (46 binary and 3 multistate characters). The data matrix included both male and female characters. Specifically, the characters used related to the size and arrangement of opisthosomal shields, dorsal and ventral opisthosomal chaetotaxy, leg chaetotaxy, certain elements of the gnathosoma (tectum, chelicerae, rostral setae, corniculi) as well as reproductive structures of both sexes (Table 1). Because one of the main goals of this study was to reconstruct a number of biological traits of the hummingbird flower mites, no characters relating to host plant affiliation, geo-

Table 1. Characters used in the analysis of *Rhinoseius* sensu Lindquist and Evans 1965 (Character states considered plesiomorphic are coded as "0", apomorphic character states are coded as "1" or "2")

Character	Plesiomorphic (0)	Apomorphic (1)	Apomorphic (2)
1. Opisthoventral setae *Zv1* (male)	on ventral or opisthoventral shield	on soft cuticle	
2. Ventrianal shield (male)(1)	shield large, with setae *Zv3*	shield small, setae *Zv3* on soft cuticle	
3. Ventrianal shield (male)(2)	shield undivided	shield transversely divided into separate anal and ventral shields	
4. Pair of posterior processes on ventrianal shield (male)	absent	present	
5. Metapodal plates (male)	merged with ventrianal shield	separate from ventrianal shield	
6. Opisthoventral setae (male)	normal	flagelliform	
7. Exopodal plates (male and female)	present	absent	
8. Genital shield (female)	anterior margin of shield rounded or tapered	anterior margin of shield truncated or with angular incision	
9. Genital setae (female)	on genital shield	on soft cuticle	
10. Anal shield (female)	narrower or equal in width to posterior part of genital shield	distinctly wider than posterior part of genital shield	
11. Dorsal shield (male)	entire, no lateral incisions	with lateral incisions	divided into separate podonotal and opisthonotal shields
12. Peritrematic plates (male and female)	normally developed	reduced around stigmas	
13. Setae *z1* (male and female)	present	absent	

Table 1. Continued

Character	Plesiomorphic (0)	Apomorphic (1)	Apomorphic (2)
14. Podonotal setae *s6* (male and female)	present	absent	
15. Opisthonotal setae *J*'s (male)	not modified	one or more pairs of *J*'s very stout, spinelike	
16. Opisthonotal setae *J1* (male)	simple	stout, spinelike	
17. Opisthonotal setae *J4* (male)	not modified	spinelike and moved anteriad	absent
18. Opisthonotal setae *J3* (female)	present	absent	
19. Opisthonotal setae *J5* (female)	not modified	modified to a bundle of microspinules	
20. Tectum (male and female)	rounded or crenulate (denticulate)	tapering to an acute point	
21. Rostral setae (male)	capitular setae longer, equal or subequal to anterior rostral setae	capitular setae half as long as anterior rostral setae	
22. Corniculi (male)	inner margins of corniculi parallel or convergent	inner margins of corniculi divergent	
23. Movable chela (female)	with one or more teeth	edentate	
24. Fixed chela (female)	multidentate (more than 10 teeth)	maximum tridentate	
25. Stylus on movable chela of chelicera (male)	absent	present	
26. Shape of spermatodactyl (male)(1)	directed anteriad, not as below	directed posteriad, broad, dagger-like, straight or incurved	
27. Length of spermatodactyl (male)	shorter or as long as IInd segment of chelicera	distinctly longer than IInd segment of chelicera	

Table 1. Continued

Character	Plesiomorphic (0)	Apomorphic (1)	Apomorphic (2)
28. Shape of spermatodactyl (male)(2)	without apical or subapical projection	arrow-shaped, with apical or subapical triangular projection	
29. Apex of spermatodactyl (male)	simple	highly modified, bifurcated	
30. *ad1* and *pd* on palpfemur (female)	smooth	serrated	
31. Coxa I (male and female)	without rows of denticles	with one or more rows of denticles	
32. *ad* on trochanter I (female)	smooth	serrated	
33. Setae *ad1, pd1* and *pd2* on femur I (female)	simple	thickened, spinelike	
34. *av1* on femur I (male)	simple	knob- or spinelike	
35. Leg II (male)	slender, genu longer than wide and at most twice as wide as that of leg I	very stout, genu always wider than long, at least three times as wide as that of leg I	
36. Seta *pv* of coxa II (male)	normal, not thickened	at least three times as thick and long as *av* on coxa II	
37. Seta *av1* of femur II (male)	simple or only slightly thickened	spinelike, blunt or acute	strongly enlarged, spurlike
38. Dorsal setae *pd1* and *ad1* of femur II (male)	smooth	barbed	
39. Seta *av1* of tibia II (male)	simple	thick, spine- or knoblike	
40. Seta *pv1* on tarsus II (male)	simple	enlarged, spine- or knoblike	

Table 1. Continued

Character	Plesiomorphic (0)	Apomorphic (1)	Apomorphic (2)
41. Seta *av2* on tarsus II (male)	not larger than *av3*	at least twice as large as *av3*	
42. Setation of tibia III (male and female)	8 setae present (*pl2* absent)	9 setae present	
43. Seta *pv1* on tarsus III (male)	simple	knoblike	
44. Seta *av2* on tarsus III (male)	simple	knoblike	
45. Seta *av3* on tarsus III (male)	simple	knoblike	
46. Coxa IV (male and female)	simple, without posterior spur	with posterior spur	
47. Setation of tibia IV (male and female)	10 setae present	9 setae present (*pl2* absent)	
48. Maturation pouch (female)	absent	present	
49. Infundibulum (female)	absent	present	

graphical or altitudinal distribution, or any ecological characteristics of the species were included in the data matrix.

The characters were polarized using 4 outgroup taxa representing 3 genera of Melicharini, the tribe that also includes the ingroup taxa. The specific outgroup taxa used were as follows: *Proctolaelaps belemensis* Fain, Hyland & Aitken, 1977; *Proctolaelaps vandenbergi* (Ryke, 1954); *Melichares agilis* Hering, 1838; and *Xanthippe clavisetosa* Naskrecki & Colwell, 1995. Based on the structure of the chelicerae, we believe that *Xanthippe* is probably the taxon most closely related to the ingroup. The monophyly of the ingroup, which is equal to the generic concept of *Rhinoseius* proposed by Lindquist and Evans (1965), is best supported by (1) the unique structure of the chelicerae, with the movable chela in both sexes devoid of basal multiple teeth (which are characteristic of all other Melicharini) and the fixed chela edentate in both sexes (there is at least 1 tooth on the movable

chela in other Melicharini); (2) free metapodal plates in males (homoplastic with some *Proctolaelaps* spp. and *Xanthippe hendersoni* Naskrecki & Colwell); and (3) an enlarged leg II in males, with setae *av* on femur II usually strongly enlarged.

The computations were conducted using PAUP 3.1.1 for Macintosh (Swofford 1993). MacClade 3.02 (Maddison and Maddison 1992) was used for the analysis of character distribution. Because the data matrix consisted of 45 taxa (Table 2), we were restricted to using heuristic methods of tree computation. (The exhaustive search algorithm is applicable to data matrices with no more than 11 taxa, and the branch-and-bound search algorithm permits no more than ≈20 taxa [Swofford 1993]). During the searches, all characters were weighted equally, and, because the evolution of multi–state characters could have followed several different paths, all were unordered. The search used the tree-bisection-reconnection (TBR) branch-swapping algorithm, kept all minimal trees (MULPARS option), and collapsed all branches of 0 length to yield polytomies. The ACCTRAN character-state optimization option (preference of reversals over parallel evolution) was used, and no topological constraints were enforced. Neither decay indices nor bootstrap values could be calculated because it is impossible to perform exhaustive searches in such a large data matrix, so a replacement technique had to be used. Therefore, we used the stepwise additions option, with 100 random replicates. This technique greatly reduces the chances of hitting local optima by randomly changing the sequence of taxa during the initial tree-building process. We repeated the searches using 2 additional branch-swapping algorithms: subtree pruning-regrafting and nearest-neighbor interchanges.

All searches resulted in 1 tree of identical topology and length 86, consistency index (CI) = 0.605, retention index (RI) = 0.918, rescaled consistency index (RC) = 0.555, and homoplasy index (HI) = 0.395 (Fig. 37).

The analysis resulted in a phylogenetic hypothesis of a basal split of the ingroup into 2 clades. This split is strongly supported by numerous synapomorphies (see generic descriptions below). The topology of the tree and distribution of apomorphies clearly support the monophyly, and consequently the reinstatement of the genus *Tropicoseius* Baker & Yunker, 1964, synonymized by Lindquist & Evans (1965) with *Rhinoseius* Baker & Yunker, 1964. In other words, this taxonomic change does not contradict the monophyletic basis for the generic concept of *Rhinoseius* proposed by Lindquist & Evans (1965), but rather amends it by dividing this taxon into 2 evolutionarily meaningful genera.

Within the genus *Tropicoseius,* we recognize 3 informal species groups—the *chiriquensis, braziliensis* and *wetmorei* groups. Two species groups are proposed within *Rhinoseius*—the *rafinskii* and *richardsoni*

Table 2. Data matrix for the analysis of *Rhinoseius* sensu Lindquist and Evans 1965

Species	Character coding 1111111111222222222233333333334444444444 1234567890123456789012345678901234567890123456789
**P. belemensis*	0000000000000000000000000110000000000000010000000
**P. vanderbergi*	0000000000000000000000000100000000001000010000000
**Melichares*	0100000000000000000000000000000000000000010000000
**Xanthippe*	0010000000100000000001010100000000001000010000000
ornatus	0100100000100000000000111000001000102001101110000
chiriquensis	0100100000100000000000111000001000102001101100000
rowelli	?1001000001000000000001110000010001020011011100 00
peregrinator	0100100000100000000000111000001000102001101110000
berryi	0100100000100000000000110000001000102011101100000
chazdonae	1100100000000000000000111000001000102011100100000
colwelli	1100100000100000000000111000001000102011101100000
kaliszewskii	0100100000100000000000111000001000102001101100000
steini	0100100000000000000000111000101000102011100100000
cervus	1100100000000000000000111000101000102011100100000
braziliensis	0100110000100000000100110010010100002111101100000
erioxynon	0100110000200000000100110010011100002011001100000
fuentesi	0100110000200000000100110010011100002111001101001
phoreticus	0100110000100000000100110010010100002111101101000
uniformis	0100110000100000000110110000000100002111001100000
bakeri	0100100000100000000110110000000001011011001100010
heliconiae	0100100000100000000110110000000001011011001100010
fidelis	0100100000100000000110110000000001011011001100010
naeemi	0100100000100000000110110000000001011011001100010
ochoai	0100100000100000000110110000000001011011001100010
bisacculatus	0100100000100000000110110000000001011011001100010
analis	0100000000100000000110110000000001011011001100010
fairchildi	0100100001100000000110110000000011011011001100010
colombiensis	0100100001100000000110110000000011011011001100010
erro	0100100000100000000110110000000001011011001100000
trinitatis	0100100000100000000110110000000001011011001100010
venezuelensis	0100100000100000000110110000000001011011001100010
klepticos	0100100000100000000110110000000001011011001100010
kressi	0100100000100000000110110000000001011011001100010
wetmorei	0100100000100000000110110000000001011011001100010
nadachowskyi	0110101110011110101001110101001000000000010001101
rafinskii	0110101110010110101001110101001000000000010000101
antioquiensis	0001111110210111211001110100001000001000010001101
caucaensis	0100101010110100011001110100001000002000010001 10?
androdon	0001101110210100011001110100001000001000010001101
richardsoni	0001111110211111211001110100001000001000010001101
haplophaedia	0000101110210100011001110100001000001010010001101
luteyni	0110101110010100011001110101001000000000010000101
ucumariensis	1110101110010100011001110101001000000000010000101
pastorae	1110111110010100001001110100001000002000010000101
tiptoni	0110101010010100001001110100001000002000010000101

*, outgroup taxa.

Table 3. Characters used in the analysis of the *wetmorei* species group (Character states considered plesiomorphic are coded as "0", apomorphic character states are coded as "1" or "2")

Character	Plesiomorphic (0)	Apomorphic (1)
1. Opisthoventral setae *Jv3* (male):	on shield	on soft cuticle
2. Opisthoventral setae (male)	setae on shield and on soft cuticle of similar length	setae on soft cuticle decidedly shorter than setae on shield
3. Setae of *R* series (male)	on dorsal shield	on soft cuticle
4. Distance between genital and anal shields (female)	distance longer than half of width of anal shield	distance shorter than half of width of anal shield
5. Anal shield (female)	shield distinctly longer than wide	shield roughly circular
6. Leg IV (female)	slender, genu at least twice as long as wide	stout, genu at most as long as wide
7. Shape of spermatodactyl (male)	spermatodactyl straight, apex not modified	spermatodactyl slender, weakly sinuate, apex modified
8. Mucro (female)	short, not reaching apex of movable chela	long, reaching or surpassing apex of movable chela
9. Apex of spermatodactyl (male)	even if modified, not as below	apex clearly bent and twisted
10. Maturation pouch (1)	not divided	divided into separate, proximal and distal elongate pouches
11. Maturation pouch (2)	if present, with smooth walls	walls striated
12. Maturation pouch (3)	distal part of pouch straight	distal part of pouch bent under right angle
13. Maturation pouch (4)	not elongate	very long, at least 8 times as long as wide
14. Maturation pouch (5)	not elongate	elongate but short, at most as long as one fifth of major duct

groups. The diagnosis and a list of species included for each group appear in the descriptive part of this paper.

A weak point of the resulting tree was an unresolved relationship among certain species within the *wetmorei* group. On the other hand, the monophyly of this group as a whole is well supported by the following 4

Table 4. Data matrix for the analysis of the *wetmorei* species group

Species	Character coding 1 1111 1234567890 1234
*phoreticus**	1000000000 0000
*uniformis**	0000000000 0000
erro	0000000000 0000
bakeri	0100001100 1010
heliconiae	?100000100 0101
fidelis	0100000100 0101
naeemi	1010001100 1010
ochoai	0100000101 0100
bisacculatus	0100000101 0100
analis	0000001110 0010
fairchildi	0000110100 0010
colombiensis	0000110100 0010
trinitatis	0011001110 0010
venezuelensis	0000001110 0010
klepticos	0000001110 0010
kressi	0011001110 0010
wetmorei	0000000100 0100

*, Outgroup taxa.

apomorphies: (1) shortened capitular setae, (2) knob like modification of seta *av1* on femur I in the male, (3) enlargement of seta *pv* on coxa II in the male, and (4) presence of a maturation pouch in the female inseminating apparatus. The polytomy resulted from the absence in our initial data matrix of those characters indicative of specific distinctness within this group, but otherwise was subject to homoplasy on the generic or higher level. These include characters such as the relative length and arrangement of setae, minor variations in the shape of the ventral shield, and characters of the female maturation pouch.

With the objective of resolving relationships among species of the *wetmorei* group, we performed a second analysis in which we used 14 such characters (Table 3), none of which had been used in the broader analysis. We polarized these 14 new characters using 2 species (*T. uniformis* and *T. phoreticus*) of the *braziliensis* group as outgroups. (The *braziliensis* group is the sister clade of the *wetmorei* group.) Because the data matrix for this second analysis consisted of only 15 ingroup and 2 outgroup taxa (Table 4), we were able to use the branch-and-bound search algorithm in PAUP, which guarantees finding the most parsimonious trees. As in the first analysis, the search used the tree-bisection-reconnection (TBR) branch-swapping algorithm, kept all minimal trees (MULPARS option), and collapsed

Table 5. Known host plants and bird carriers of all *Tropicoseius* and *Rhinoseius* species

Mite species	Plant host	Bird carrier
Genus *Tropicoseius*		
Group *chiriquensis*	Gentianaceae	*Campylopterus hemileucurus*
colwelli	*Symbolanthus pulcherrimus*	*Eugenes fulgens*
	Gesneriaceae	*Panterpe insignis*
	Columnea microcalyx	*Colibri thalassinus*
	Columnea sp.	
	Tropaeolaceae	
	Tropaeolum sp.	
	Amaryllidaceae	
	Bomarea sp.	
	Campanulaceae	
	Centropogon talamancensis	
	Centropogon cordifolius	
	Centropogon solanifolius	
	Centropogon valerii	
	Centropogon sp.	
	Rubiaceae	
	Hamelia patens	
	Bromeliaceae	
	Pitcairnia brittonia	
chazdonae	Campanulaceae	Not recorded
	Centropogon nutans	
	Centropogon granulosus	
	Centropogon curvatus	
	Centropogon gamosepalus	

Table 5. Continued

Mite species	Plant host	Bird carrier
	Centropogon umbrosus	
	Centropogon urubambae	
	Centropogon sp.	
	Rubiaceae	
	Palicourea sp.	
cervus	Campanulaceae	Not recorded
	Centropogon affinus	
	Centropogon densiflorus	
steini	Campanulaceae	Not recorded
	Centropogon gesneraeformis	
	Centropogon sp.	
	Siphocampylus sanguineus	
	Ericaceae	
	Ceratostema peruvianum	
kaliszewskii	Rapateaceae	Not recorded
	Kunhardtia rhodantha	
chiriquensis	Rubiaceae	*Amazilia edward*[h]
	Hamelia patens	*Amazilia versicolor*
	Lythraceae	*Amazilia saucerottei*[h]
	Cuphea sp.	*Amazilia tzacatl*[h]
	Campanulaceae	*Eugenes fulgens*
	Lobelia laxiflora	*Colibri thalassinus*
	Lobelia sp.	*Chlorostibon canivetii*
	Scrophulariaceae	*Hylocharis leucotis*
	Castilleja affinis	*Lampornis amethestinus*

Table 5. Continued

Mite species	Plant host	Bird carrier
	Castilleja chromosa	*Campylopterus* sp.
	Castilleja latifolia	
	Castilleja franciscana	
	Castilleja integrifolia	
	Castilleja sp.	
	Mimulus sp.	
	Liliaceae	
	Knifophia sp.	
	Aloe sp.	
	Gesneriaceae	
	Columnea sp.	
ornatus	Campanulaceae	*Phaethornis superciliosus*[h]
	Lobelia ?persicaefolia	*Phaethornis guy*[h]
	Lobelia ?flavescens	*Phaethornis syrmatophorus*[h]
		Androdon aequatorialis[h]
		Chlorostilbon mellisugus[h]
peregrinator	Bromeliaceae	Not recorded
	undetermined[i]	
rowelli	Gesneriaceae	Not recorded
	Columnea hirsuta	
	Besleria lutea	
	Campanulaceae	
	Lobelia martegon	
berryi	Onagraceae	Not recorded
	Fuchsia regia	

Table 5. Continued

Mite species	Plant host	Bird carrier
changensis	Not recorded	*Phaethornis guy*[a]
bellavistensis	Gesneriaceae	Not recorded
	undetermined[i]	
carlosalberti	Gesneriaceae	Not recorded
	undetermined[i]	
	Bromeliaceae	
	undetermined[i]	
Group *braziliensis*		
uniformis	Rubiaceae	*Phaethornis superciliosus*[c]
	Psychotria poeppigiana	*Glaucis hirsuta*[c]
	Costaceae	
	Costus cylindricus	
	Bromeliaceae	
	Aechmea fendleri	
	Cucurbitaceae	
	Psyguria triphylla	
erioxynon	Bromeliaceae	Not recorded
	Puya clava-hercules	
	Puya sp.	
	Amaryllidaceae	
	Bomarea sp.	
	Campanulaceae	
	cf. *Lobelia*	

Table 5. Continued

Mite species	Plant host	Bird carrier
fuentesi	Campanulaceae	*Patagona gigas*
	Lobelia salicifolia	
	Bromeliaceae	
	Puya violacea	
braziliensis	Bromeliaceae	Not recorded
	undetermined[a]	
	Ananas sp.[c]	
phoreticus	Bromeliaceae	*Chlorestes notatus*
	Pitcairnia integrifolia	*Glaucis hirsuta*
	undetermined	*Amazilia tobaci*[c]
Group *wetmorei*	Rubiaceae	*Phaethornis syrmatophorus*
erro	*Psychotria elata*	
	Psychotria poeppigiana	
	Psychotria sp.	
	Heliconiaceae	
	Heliconia sarapiquensis	
	Costaceae	
	Costus scaber	
	Costus sp.	
	Bromeliaceae	
	undetermined[a]	
	?Marantaceae	
	undetermined	
	?Ericaceae	
	undetermined	

Table 5. Continued

Mite species	Plant host	Bird carrier
eisenmanni	Not recorded	*Phaethornis guy*[a]
wetmorei	Heliconiaceae	*Campylopterus hemileucurus*
	Heliconia nutans	*Phaethornis guy*[a]
	Heliconia lankesteri rubra	
	Heliconia beckneri	
	Heliconia imbricata	
	Heliconia irrasa imbricata	
	Heliconia latispatha	
	Heliconia tortuosa	
	Heliconia diesiana	
	Heliconia sp.	
	Zingiberaceae	
	Renealmia cernua	
	Amaryllidaceae	
	Bomarea ovata	
	Rubiaceae	
	Psychotria poeppigiana	
	Bromeliaceae	
	undetermined	
	Acanthaceae	
	undetermined	
bisacculatus	Costaceae	*Glaucis hirsuta*[c]
	Costus spiralis	*Phaethornis guy*[c]
	Costus scaber	
	Heliconiaceae	
	Heliconia chartacea	

Table 5. Continued

Mite species	Plant host	Bird carrier
ochoai	Heliconiaceae	Not recorded
	Heliconia colgantea	
	Costaceae	
	Costus sp.	
fidelis	Costaceae	Not recorded
	Costus arabicus	
	Costus sp.	
heliconiae	Heliconiceae	*Phaethornis superciliosus*[a,f]
	Heliconia velloziana	*Phaethornis longuemareus*[c]
	Heliconia psittacorum	*Phaethornis yaruqui*[a,b]
	Heliconia richardiana	*Glaucis hirsuta*[c]
	Heliconia acuminata	*Amazilia candida*[f]
	Heliconia nickeriensis	*Amazilia tzacatl*[f]
	Heliconia chartacea	*Amazilia saucerrotei*
	Heliconia latispatha	*Campylopterus hemileucurus*
	Heliconia sarapiquensis	*Campylopterus largipennis*[c]
	Heliconia sp.[a]	*Chlorestes notatus*[c]
	Costaceae	*Thalurania furcata*[c]
	Costus sp.	
	Bromeliaceae	
	Gravisia aquilega	
	undetermined	
	Rapateaceae	
	Guacamaya superba	

Table 5. Continued

Mite species	Plant host	Bird carrier
bakeri	Bromeliaceae	*Chlorostilbon ricordii ricordii*[b]
	undetermined	*Amazilia rutilis*
		Cynanthus latirostris
		Campylopterus curvipennis
		Eulampis jugularis
naeemi	Heliconiaceae	Not recorded
	Heliconia sp.	
analis	Heliconiaceae	*Phaethornis superciliosus*[d]
	Heliconia lutea	
	Heliconia ?bihai	
trinitatis	Heliconiaceae	*Glaucis hirsuta*[c]
	Heliconia hirsuta	*Phaethornis guy*[c]
kressi	Heliconiaceae	Not recorded
	Heliconia vaginalis	
venezuelensis	Heliconiaceae	*Phaethornis superciliosus*[a,c]
	Heliconia ignescens	*Phaethornis guy*[c]
	Heliconia latispatha	*Amazilia chionopectus*[c]
	Heliconia stricta	*Glaucis hirsuta*[c]
	Heliconia chartacea	*Coereba flaveola* (Coerebidae)[c]
	Heliconia sp.[a]	
klepticos	Heliconiaceae	Not recorded
	Heliconia spathocincinata	
	Heliconia bihai	
	Heliconia standleyi	
	Heliconia marginata	

Table 5. Continued

Mite species	Plant host	Bird carrier
fairchildi	Heliconiaceae	*Campylopterus hemileucurus*
	Heliconia mutisiana	*Eutoxeres aquila*[d,h]
	Heliconia nariniensis	*Phaethornis guy*[a,d]
	Heliconia trichocarpa	*Threnetes ruckeri*[d]
	Heliconia rhodantha	
	Heliconia ramonensis var. *glabra*	
	Heliconia ramonensis ramonensis	
	Heliconia pogonantha var. *holerythra*	
	Heliconia ignescens	
	Heliconia reticulata	
	Heliconia obscura dichroma	
	Heliconia obscura fusca	
	Heliconia scarlatina	
	Heliconia dielsiana	
	Heliconia curtispatha	
	Heliconia sclerotricha	
	Heliconia angelica	
	Heliconia nigripraefixa	
	Heliconia chrysocraspeda aff.	
	Heliconia colgantea	
	Heliconia tortuosa	
	Heliconia longa	
	Heliconia sp.[h]	

Table 5. Continued

Mite species	Plant host	Bird carrier
colombiensis	Heliconiaceae	*Phaethornis syrmatophorus*[d]
	Heliconia curtispatha	*Phaethornis superciliosus*[d]
	Heliconia peteriana	*Phaethornis guy*[d]
	Heliconia pastazae	*Eutoxeres aquila*[d]
	Heliconia combinata	
	Heliconia sp.	
	Bignoniaceae	
	Pachyptera himenaea	
adsimilis	Not recorded	*Phaethornis syrmatophorus*[d]
perezgloriae	Not recorded	*Eutoxeres aquila*[i]
chlorestes	Not recorded	*Chlorestes notatus*[d]
Genus *Rhinoseius*	Gesneriaceae	*Phaethornis yaruqui*[h]
Group *rafinskii*	*Besleria robusta*	*Phaethornis guy*[a]
tiptoni	*Besleria* sp.	*Phaethornis syrmatophorus*[h]
	Columnea purpurata	*Aglaiocercus coelestis*[h]
	Columnea sp.	*Lampornis castaneoviridis*[a]
	Dalbergaria florida	
	Heliconiaceae	
	Heliconia trichocarpa	
pastorae	Gesneriaceae	Not recorded
	Alloplectus dielsii	
	Ericaceae	
	Ceratostema peruvianum	
	Bromeliaceae	
	undetermined[i]	

Table 5. Continued

Mite species	Plant host	Bird carrier
luteyni	Scrophulariaceae *Castilleja* sp. Ericaceae *Psammisia incana*	Not recorded
ucumariensis	Campanulaceae *Centropogon argutus* *Siphocampylus ecuadoriensis* *Siphocampylus giganteus* Ericaceae undetermined Gesneriaceae undetermined[f]	Not recorded
rafinskii	Ericaceae *Vaccinium corymbosum*[g] Liliaceae undetermined[g] Bromeliaceae *Puya* sp.[g]	Not recorded
nadachovskyi	Ericaceae *Plutarchia angulata* *Cavendishia ruiz-teranii* *Sphyrospermum buxifolium* *Macleania puberula* *Thibaudia floribunda* *Ceratostema reginaldi* undetermined[f]	Not recorded

Table 5. Continued

Mite species	Plant host	Bird carrier
Group *richardsoni* *caucaensis*	Not recorded	*Androdon aequatorialis*[h] *Amazilia rosenbergi*[h] *Phaethornis yaruqui*[h] *Ocreatus underwoodii*[h]
haplophaedia	Ericaceae *Cavendishia pseudospicata* *Macleania* cf. *ericae* *Macleania coccoloboides* x cf. *ericae* *Macleania stricta* *Anthopterus verticillatus* *Disterigma pentandrum*	*Haplophaedia lugens*[h]
androdon	Ericaceae *Cavendishia coccinea* *Cavendishia* sp.[h]	*Androdon aequatorialis*[d,h] *Amazilia rosenbergi*[h] *Phaethornis yaruqui*[h] *Thalurania colombica*[h]
richardsoni	Ericaceae *Macleania glabra* *Macleania sleumeriana* *Macleania* sp. *Cavendishia subamplexicaulis* *Cavendishia smithii* *Cavendishia ?cuatrecasasii* *Cavendishia* sp. *Symphysia floccosa* *Psammisia* sp. undetermined	*Eugenes fulgens* *Panterpe insignis* *Doryfera ludovicae*[h] *Coeligena wilsoni*[h] *Campylopterus hemileucurus*[c] *Lampornis castaneoviridis*[c]

Table 5. Continued

Mite species	Plant host	Bird carrier
	Campanulaceae	
	Centropogon gutierrezi	
	Rapateaceae	
	Guacamaya superba	
antioquiensis	Ericaceae	*Androdon aequatorialis*[c]
	Cavendishia palustris	*Chalybura urochrysia*[c]
	Cavendishia sp.[h]	*Phaethornis guy*[c]
		Aglaiocercus coelestis[h]

[a] Baker and Yunker 1964; [b] Dusbabek and Cerny 1970; [c] Fain, Hyland and Aitken 1977b; [d] Fain and Hyland 1980; [e] Fletchmann and Johnston 1978; [f] Hyland, Fain and Moorhouse 1978; [g] Micherdzinski and Lukoschus 1980; [h] Ohmer, Fain and Schuchmann 1991; [i] Wiese and Fain 1993.

all branches of 0 length to yield polytomies. The ACCTRAN character-state optimization was used, and no topological constraints were enforced.

The *wetmorei* group search yielded 1 tree of length 17, consistency index (CI) = 0.824, retention index (RI) = 0.917, rescaled consistency index (RC) = 0.755, and homoplasy index (HI) = 0.176 (Fig. 38). The tree still contains a tetratomous grouping of species, but because these 4 species differ from one another only in the presence of a single autapomorphic character state each, we could not investigate their relationships further. To estimate support for individual clades within the tree, we performed a bootstrap analysis (100 replicates; only groups of frequency >50% retained). The analysis showed high or moderate support for most branching points, with only the *bakeri-naeemi* clade collapsing (occurring in <50% replicates). The bootstrap values are presented in Fig. 38.

Discussion of Characters

Part I: Cladistic Analysis of *Rhinoseius* (sensu Lindquist and Evans 1965)

The following discussion presents our rationale for polarization of characters in the data matrix as well as speculations on the character and taxa evolution derived from the parsimony analysis. Note that porotaxy, comprising characters frequently used in systematic studies on Mesostigmata, is not discussed in this section and often is not illustrated in figures. The distribution and arrangement of opisthonotal pores could not be reliably observed in all specimens because of variation in preservation techniques and in the condition of specimens under study.

Numbers in parenthesis denote the number of the character as presented in Table 1; character states coded as "1" or "2" in the table are considered apomorphic (for example, "char. 3[1]" indicates character number 3, state 1).

Ventrianal Shield in Male (Characters 1–5). A large ventrianal shield covering most of the opisthosomal venter of the male probably represents the ancestral condition in Melicharini. Within the genera *Tropicoseius* and *Rhinoseius,* several independent tendencies toward reduction in the size of the shield can be observed. In species of *Tropicoseius,* the shield is constricted such that setae *Zv3* are on soft cuticle on either side of the shield (char. 2[1]). Several species of *Rhinoseius (antioquiensis, richardsoni, androdon, haplophaedia)* have large ventrianal shields that cover most of the opisthosomal venter and bear setae *Zv3.* The remaining species of this genus are characterized by the ventrianal shield divided into a small, transversely elongate ventral shield (which may or may not bear some setae of *Jv* and

Zv series), and a small anal shield bearing only the anal setae (char. 3[1]). A similar tendency toward reduction of the anterior part of the ventrianal shield can be observed in some species of *Tropicoseius*. In *T. colwelli* and *T. cervus*, the anterior part of the shield is reduced to various degrees, sometimes forming a separate platelet, and setae *Zv1* are always on soft cuticle (char. 1[1]). In *T. chazdonae*, the anterior part is completely reduced so that the remaining part of the shield forms the anal shield, and all opisthoventral setae, except the anals, are on soft cuticle (a similar condition is present in males of Eviphididae). In these 3 species, the tendency toward reduction in size of the ventrianal shield is correlated with the reduction of the posterior part of the sternal shield. The presence of characteristic cuticular processes on the posterior part of the ventrianal shield is a synapomorphy for *R. antioquiensis, R. richardsoni,* and *R. androdon* (character 4[1]).

With 1 exception, free metapodal plates are present in all species of both genera. Although free metapodal plates also are present in several species of *Proctolaelaps* (e.g., *P. kirmsei* Fain, Hyland & Aitken), their presence is probably an independently derived feature of both *Tropicoseius* and *Rhinoseius*. The reversal of this condition, in which the plates are merged with the ventrianal shield, can be observed in *T. analis*.

Opisthoventral Setae in Male (Character 6). Within *Tropicoseius*, very long, flagelliform opisthoventral setae are synapomorphic for all species of the *braziliensis* group. Within *Rhinoseius*, flagelliform setae apparently appeared independently in *R. pastorae, R. antioquiensis,* and *R. richardsoni*. In *T. braziliensis* and *T. erioxynon* as well as in *R. richardsoni*, individual specimens with short, unmodified opisthoventral setae also occur.

Exopodal Plates (Character 7). A complete reduction of exopodal plates is one of the synapomorphic features of all *Rhinoseius* species. In most species of this genus endopodal plates also are absent; they are present only in *R. haplophaedia*. Exopodal plates normally are developed in all *Tropicoseius* species, the typical condition for Melicharini.

Genital Shield (Characters 8–9). The genital shield in *Tropicoseius* and *Rhinoseius* consists of 2 parts, the anterior and posterior. The anterior part covers the genital opening. It is very weakly sclerotized and usually poorly discernible under an optical microscope (but easily seen on SEM photographs, Fig. 2c and d). In many specimens the anterior edge of the hyaline part can be confused easily with the posterior edge of the sternal shield. Probably for this reason, most of the figures that accompanied previous descriptions of the hummingbird flower mites depict it incorrectly or do not illustrate it at all. In all species of the genus *Tropicoseius*, the anterior part of the shield is either broadly rounded or tapered. Such a shape possibly represents the ancestral condition because it is present in all other Ascidae. In *Rhinoseius*, the anterior margin is distinctly incised, except for 2 cases *(R. tiptoni, R. caucaensis)* in which the shield is truncated but without the emargination. The latter 2 types of the shield probably represent derived conditions (char. 8[1]). The posterior part of the genital shield is well sclerotized and easily discernible in all species of both genera. A longitudinal ornamentation of the shield is often present. In *Tropicoseius*, the shield always bears a pair of genital setae, whereas in *Rhinoseius* species these setae are on soft cuticle adjacent to the shield. Such a reduction in the width of the shield is one of the apomorphic characters of the latter genus (char. 9[1]). There are, however, species of Melicharini (e.g., *Proctolaelaps cancellarius* Treat & Nederman) where a similar condition can be observed. The shape of this part of the shield is generally uniform in both genera, being slightly widened and broadly rounded behind the level of the genital setae. In some species of *Rhinoseius*, however, the posterior part of the shield is distinctly widened and its hind margin is truncated.

Anal Shield in Female (Character 10). Females of Melicharini, including the genera *Rhinoseius* and *Tropicoseius*, are characterized by a small anal shield, narrower than or as wide as the posterior part of the genital shield. Exceptionally, the shield extends anteriorly so that setae *Jv2* are on it. An anal shield that is clearly enlarged and wider than the posterior part of the genital shield is a synapomorphic feature of 2 closely related species of *Tropicoseius*—*T. colombiensis* (Fig. 2c) and *T. fairchildi*.

Dorsal Shield in Male (Character11). A dorsal shield completely divided into separate podonotal and opisthonotal shields is an apomorphic feature that appeared independently in both *Tropicoseius* and *Rhinoseius*. A possible explanation for the observed phenomenon is a heterochronic process, either neoteny or progenesis. Those *Rhinoseius* species that have the dorsal shield entirely divided (similar to their nymphal instars), additionally exhibit other features typical of juvenile instars of Ascidae, including shortened peritremes and reduced (or underdeveloped) peritrematic shields. Such a correlation suggests the effect of a neotenic process in which juvenile conditions of certain characters are expressed in reproductively mature individuals (paedomorphosis). On the other hand, more than half of the known species of the genus *Rhinoseius* are characterized by an entire dorsal shield in the adult males or, at most, with hardly marked, shallow incisions at the level of setae *j6*. These species also show shortened peritremes and poorly developed peritrematic shields. A similar phenomenon is observed within the genus *Tropicoseius*. Males of *T. erioxynon* and *T. fuentesi* have the dorsal shield completely divided, and the peritremes are somewhat shortened when compared with other species of the genus, although their peritrematic shields are developed normally. In species in which the dorsal shield is entire *(T. chazdonae, T. cervus, T. steini)* this condition is correlated with an extremely enlarged 2nd pair of legs, which can be 3 times as thick as the remaining pairs. This may suggest another heterochronic effect—acceleration. The occurrence of males with the dorsal shield having shallow lateral incisions and somewhat smaller 2nd legs in *T. steini*

supports this hypothesis. Except for *T. erioxynon* and *T. fuentesi,* females of all species in both genera have dorsal shields with narrow lateral incisions, a condition frequently observed in Ascidae and other Mesostigmata.

Fain (1992) suggested that the reduction in size of the dorsal shield in *Rhinoseius* (sensu lato) is related to their frequent exposure to the nasal mucosa of the bird carriers. He recognized 4 types (A–D) of shapes of dorsal shields within the genus, but noted that the character (i.e., type of shield) is unstable and subject to intraspecific variation. Apparently, the author confused a superficial line (transverse suture) connecting lateral incisions of the shield with the real, unsclerotized gap between podonotal and opisthonotal parts in species with the completely divided shield. In fact, the former shows intraspecific variation because the line is a simple folding of the dorsal shield and its presence probably depends on the degree of sclerotization of the shield (i.e., the age of an individual). Often, conspecific individuals collected from the same flower show various degrees of development of the suture—from complete absence, to presence only near the midline of the body, to the complete connection of lateral incisions. It must be noted, however, that some species (e.g., *T. chiriquensis, T. colombiensis*) show a more pronounced tendency to form the suture, whereas in others the suture occurs rarely or never (all *Rhinoseius* species).

Peritrematic Shields (Character 12). As noted above, reduced peritrematic shields possibly represent a paedomorphic and at the same time synapomorphic condition for all *Rhinoseius* species. All species of the genus lack the elongate, sclerotized extension of the peritrematic shield around the stigma that in other Melicharini, including *Tropicoseius,* usually bears 1 or 2 pores and is often connected to exopodal shields. The peritrematic shields in *Rhinoseius* species are reduced to narrow sclerotizations discernible dorsally, widest between the levels of setae *r3* and *r5,* but still connected anteriorly to the dorsal shield.

Setae of Opisthosomal Dorsum (Characters 13–19). One of the apomorphic characters of the genus *Rhinoseius* is the absence of podonotal setae *s6* in both sexes (char. 14[1]). Another synapomorphy for all its species is the modification of opisthonotal setae *J5* in females (and most males) into a bundle of microspinules (char. 19[1]). Strongly enlarged, spinelike setae on the opisthonotum in males were apparently derived independently twice within the genus (char. 15[1]). In *R. antioquiensis* and *R. richardsoni,* the enlarged setae are probably homologous with setae *J1* (char. 16[1])and *Z1* in females. In *R. nadachowskyi* and *R. rafinskii,* the number of hypertrophied setae is larger but setae *J1* are not modified. Setae *J3* are absent in females of all species of the *richardsoni* group and in *R. luteyni* and *R. ucumariensis* (char. 18[1]). It is not clear if the absence of these setae in the latter 2 species represents a parallelism or, less likely, a retention of a plesiomorphic character state characteristic of the common ancestor of the genus. Two species of the genus *(R. nadachowskyi* and *R. richardsoni)* independently lost podonotal setae *z1* (char. 13[1]). The modification of opisthonotal setae *J4* into spines and their displacement anteriad are synapomorphic for *R. antioquiensis* and *R. richardsoni* (char. 17[1]), whereas the absence of these setae is apomorphic for *R. nadachowskyi* and *R. rafinskii* (char. 17[2]). All remaining species of both genera have retained the plesiomorphic, unmodified condition.

Like some other taxa of Melicharini (e.g., many species of *Proctolaelaps*), species of the genus *Tropicoseius* lack only setae *z3,* with the exception of *T. erioxynon,* in which setae *S1* also are absent in most individuals of both sexes. This character, because it is autapomorphic for *T. erioxynon,* was not included in the data matrix.

Gnathosoma (Characters 21–30). In all species of *Rhinoseius,* the tectum (also called gnathotectum or epistome by some authors) (char. 20[1]) is short, either finely crenulate or smoothly rounded (more often in females than in males). Because a similar form of the tectum is present in many other taxa of Melicharini, this condition may be ancestral. A smoothly rounded tectum is typical for all species of the *chiriquensis* group. All species of the *braziliensis* and *wetmorei* groups have an elongated tectum tapering to a sharp point (only females of *T. fuentesi* have tecta rounded apically). Some species, especially those of the *braziliensis* group but also some of the *wetmorei* group, have the tectum finely serrated or bifurcated apically. This, however, is subject to intraspecific variation. In general, the tectum is shorter and somewhat wider in females than in males.

Males of all species of the *wetmorei* group and of *T. uniformis* are characterized by very short capitular setae of the gnathosomal venter (char. 21[1]). They are at most half as long as the anterior rostral setae, but in most cases are even shorter. The remaining species of the genus *Tropicoseius* and all *Rhinoseius* species have the capitular setae normally developed, usually about as long as the anterior rostral setae. This condition is commonly observed in other species of Melicharini and possibly represents the ancestral state.

One of the diagnostic features of the genus *Rhinoseius* is the structure of the male corniculi, which are distinctly outwardly curved and divergent (char. 22[1]). In most cases, their apices are slightly bilobed (Fig. 31c). Within Melicharini, this character is shared only with the closely related genus *Xanthippe* and most likely represents a derived condition. Corniculi of all species of *Tropicoseius* have a typically melicharine structure, with their inner margins straight or slightly concave. Females of Melicharini have the corniculi more slender and less widely separated than those in males, with inner margins either straight or slightly concave. Females of a few species of *Proctolaelaps* have the corniculi slightly bilobed apically; this appears to be a 2ndarily derived condition, associated with an enlarged anus and fungivory (E. E. Lindquist, personal communication).

Tropicoseius and *Rhinoseius* share a unique, apomorphic structure of the female chelicera, with greatly reduced dentition. The fixed digit of the female chela is usually bidentate (rarely tridentate) and devoid of the multiple, small teeth on its basal part that are present in all other Melicharini (including pollen- and nectar-feeding species of *Proctolaelaps*) (char. 24[1]). Only females of *Xanthippe* spp. have the fixed digit of a similar structure of the fixed digit, but differ in the structure of the movable chela. As noted earlier, the edentate movable chela in both sexes (char. 23[1]) is among the apomorphic characters that support monophyly of the lineage consisting of *Tropicoseius* and *Rhinoseius* (=*Rhinoseius* sensu Lindquist and Evans 1965). Species of the closely related genus *Xanthippe* have a single, prominent tooth on the movable chela, which is one of the autapomorphic characters for that genus.

Like other podospermic Mesostigmata, male *Tropicoseius* and *Rhinoseius* have a sperm injection appendage, the spermatodactyl (also called spermatostyle or spermatophoral process) on the movable chela of the chelicera. Its shape is highly species-specific but is usually consistent with a generalized structural type characteristic of a given genus. Within Melicharini, there are 2 basic types of the spermatodactyl. The 1st, present in some *Proctolaelaps* species, both known *Xanthippe* species, and all *Rhinoseius* species, is strongly bent at its very base so that the whole organ is directed posteroventrad, with no setalike stylus (char. 26[1]). The 2nd type, which possibly represents an ancestral condition, is present in many *Proctolaelaps* species, *Melichares* species, and all *Tropicoseius* species. This 2nd type of spermatodactyl is directed anteriad, although sometimes it is very long and bent or twisted distally (but never at its base). In *Tropicoseius* spp., a stylus usually is present (char. 25[1]), sometimes being quite long (relative to the length of the mucro present on the movable chela in females), reaching or surpassing the apex of the spermatodactyl. These differences in the structure of the male copulatory organs most likely are reflected in the mating behavior of the mites, but comparative observations are lacking.

Micherdzinski and Lukoschus (1980) noted the differences between these 2 types of spermatodactyl among hummingbird flower mites but could not detect a correlation with the types of female inseminating apparatus. We have determined, however, that a spermatodactyl directed posteroventrad always is associated with the more derived type of inseminating apparatus in the female (large infundibulum, reduced sperm ducts in the genus *Rhinoseius* and in most species of *Proctolaelaps*), whereas in species in which the female inseminating apparatus has retained the generalized, phytoseiid type structure (see below), the spermatodactyl is directed anteriad (genus *Tropicoseius*) and sometimes carries a stylus (most species of the *braziliensis* group).

Spermatodactyls with triangular, apical projections (char. 28[1]) are apomorphic for 4 closely related species of *Rhinoseius*—*R. nadachowskyi, R. rafinskii, R. ucumariensis,* and *R. luteyni.* Highly derived, apically bifurcated spermatodactyls are present in closely related *T. steini* and *T. cervus* of the *chiriquensis* group (char. 29[1]). A very long, bent or twisted spermatodactyl is one of the synapomorphic characters (char. 27[1]) that support the monophyly of a small clade consisting of *T. braziliensis, T. phoreticus, T. erioxynon,* and *T. fuentesi.* The same group of species shares the presence of barbed setae *ad1* and *pd1* on the palpfemur in females (char. 30[1]).

Legs (Characters 31–47). The presence of rows of small denticles, the number of which may vary from 1 to 4, on the ventral side of coxa I (char. 31[1]) probably represents a derived condition. The rows are present in all species of the *chiriquensis* group, all *Rhinoseius* species, and also in *T. erioxynon* and *T. fuentesi* within the *braziliensis* group. Serrated setae *ad* on trochanters I (char. 32[1]) is a synapomorphy of all species of the *braziliensis* group. With the exception of *T. erioxynon,* males in this species group also have barbed setae *pd1* and *ad1* on femora II, which most likely represent an apomorphic condition (char. 38[1]). Males of the *wetmorei* group share the presence of modified, knoblike setae *av1* on femur I (char. 34[1]). Within the group, females of *T. fairchildi* and *T. colombiensis* possess thickened, spinelike setae *ad1, pd1,* and *pd2* on femur I (char. 33[1]).

Leg II in males, when compared with that of females, is enlarged to various extent in both *Tropicoseius* and *Rhinoseius* species. Males of the *chiriquensis* group, however, show the most remarkable (probably derived) expression of this character. In all species of the group the 2nd pair of legs in males is at least 3 times as thick as the 1st pair, and the genu is always wider than long and strongly convex dorsally (char. 35[1], Fig. 1a). The 2nd leg is least enlarged in species of *Rhinoseius,* with the exception of *R. tiptoni,* in which it is almost as large as in most species of the sister genus. In some species of *Rhinoseius*—*R. antioquiensis, R. richardsoni* the 2nd leg in males is only slightly stouter than that of females.

Distinctly thickened seta *pv* on coxae II in males is synapomorphic for the species of the *wetmorei* group (char. 36[1]). In this group, this seta is at least 3 times as thick and long as seta *av.* In females, the difference in size of these setae is less pronounced but still easily discernible. In other species of the genus, as well as in other taxa of Melicharini, the setae of coxae II are not enlarged. Within the tribe, most species of both *Rhinoseius* and *Tropicoseius* are distinguished by the presence of enlarged seta *av1* on femur II in males. In its most derived state, this seta is modified into a large, spurlike structure (char. 37[2]). This character state seems to have arisen independently in *Tropicoseius* (species groups *chiriquensis* and *braziliensis*) and in basal species of *Rhinoseius.* Such a distribution of this state also may suggest spurlike setae represent the condition present in the common

ancestor of both genera. In species of the *wetmorei* group and most species of the *richardsoni* group, femoral seta *av1* is only slightly enlarged (approximately twice as thick as other setae of the article). In most cases, the seta is blunt, rarely pointed. A similarly modified seta is present in *Xanthippe* species and in some species of *Proctolaelaps*. In the *wetmorei* group (and in some species of *Rhinoseius*), the enlarged seta *av1* on femur II is correlated with the presence of a thickened, spinelike form of femoral seta *pv1*. Four species of *Rhinoseius*—*R. nadachowskyi, R. rafinskii, R. luteyni,* and *R. ucumariensis* have femoral seta *av1* of males unmodified or only slightly enlarged, resembling the condition typical for most Melicharini. Seta *av1* on tibia II in males is enlarged and knoblike in most *Tropicoseius* spp (char. 39[1]). This seta retains a plesiomorphic, unmodified condition in closely related *T. ornatus, T. rowelli, T. peregrinator, T. chiriquensis,* and *T. kaliszewskii*. The only species of *Rhinoseius* with tibial seta *av1* enlarged is *R. haplophaedia*. Knoblike seta *pv1* on tarsus II in males is synapomorphic for all *Tropicoseius* species (char. 40[1], Fig. 1a). Enlarged seta *av1* in this genus is shared only with *Xanthippe* species, whereas setae *av2* and *av3* of tarsus II are modified in all 3 genera. Tarsal *av2* on leg II is extremely enlarged (at least twice as large as *av3*) in males of the *chiriquensis* group and in *T. braziliensis* and *T. phoreticus* (char. 41[1]).

The modified, knoblike setae on tarsus III in males represent additional apomorphic features of the genus *Tropicoseius*. All species of the genus have seta *av2* modified (char. 44[1]); seta *pv1* is modified (char. 43[1]) in all species except *T. chazdonae, T. cervus,* and *T. steini,* whereas *av3* is knoblike only in *T. ornatus, T. rowelli,* and *T. peregrinator* (char. 45[1]) (Fig. 2 b–d). All these setae are unmodified in *Rhinoseius* species (Fig. 2a).

The genus *Tropicoseius* is characterized by the presence of 9 setae, including seta *pl2,* on tibia III (char. 42[1]). We consider this character state apomorphic for this genus because it possibly represents a reversal. Other Melicharini (except for a few species of *Proctolaelaps* and *Mucroseius*), including *Rhinoseius,* consistently lack seta *pl2* on this article. Lack of seta *pl2* on tibia IV is an apomorphic feature of *Rhinoseius* (char. 47[1]).

The presence of characteristic posterior spurs on coxa IV (char. 46[1]) is a synapomorphy that supports the monophyly of the *richardsoni* group within the genus *Rhinoseius*. This character state apparently appeared independently in *R. nadachowskyi* and 2 species of *Tropicoseius*—*T. phoreticus* and *T. fuentesi*. In the latter 2, however, the spurs are much smaller and less conspicuous than in *Rhinoseius* spp.

Female Inseminating Apparatus (Characters 48–49). There is no uniform, widely accepted terminology for the inseminating apparatus in females of Mesostigmata. Evans and Till (1979) recognized 2 types of female apparatus (sometimes referred to as Michael's organs) within the order—the laelapid type and the phytoseiid type. They indicated possible homologies among these 2 types by using similar terms for their components.

Because it is not possible, at present, to homologize the various elements of the laelapid and phytoseiid types, Evans (1992) later decided to abandon that terminology. Describing the phytoseiid–type, which closely resembles the inseminating apparatus present in the genera *Rhinoseius* and *Tropicoseius,* he used terms introduced by Athias-Henriot (1971) and Karg (1982) that do not imply homology with components of the laelapid type. Evans' (1992) terms differed from those applied by Fain et al. (1977b) to hummingbird flower mites of the genera *Proctolaelaps* and *Rhinoseius*; these authors adopted terminology previously used by Fain (1963) for endoparasitic Halarachnidae and Rhinonyssidae.

To avoid further confusion, the terminology used in this paper generally follows that of Evans (1992). Only 2 modifications are introduced to describe structures not depicted in his generalized diagram of the phytoseiid type of sperm access system in Dermanyssina. To describe a conspicuous chamber adjacent to the solenostome, we use the term *infundibulum,* because that term was applied to a similar and possibly homologous structure in the laelapid type (Fain et al. [1977b] consider it a greatly enlarged combined adductor canal and maturation pouch). Following Fain et al. (1977b), the tube-or bulblike widening often present in the distal part of the major duct is here called the maturation pouch (although its actual function remains unknown). It is possible that this structure is homologous to the atrium of the phytoseiid type.

The female inseminating apparatus in *Rhinoseius* species exhibits a rather uniform, simple, though possibly highly derived structure. The solenostome opens between the coxae of legs III and IV and leads to an enlarged, usually easily discerned chamber, the infundibulum. The enlarged infundibulum is one of the apomorphic characters of the genus (char. 49[1]). The major duct is relatively short, and other components of the apparatus are not discernible. In contrast, the inseminating apparatus in *Tropicoseius* species seems to be less modified from the generalized phytoseiid type. The infundibulum is absent (except for *T. erioxynon* where it is considerably smaller than in *Rhinoseius* species) and the major duct is long, often with a maturation pouch (char. 48[1]), the shape and size of which are greatly variable. The absence of the maturation pouch seems to be a plesiomorphic condition since it is absent in other Melicharini. Other parts of the apparatus (minor duct, calyx) are usually poorly visible.

Part II: Relationships Among Species of the *wetmorei* Species Group

Numbers in parenthesis denote the number of the character as presented in Table 1; character states coded as "1" in the table are considered apomorphic (for example, "char. 3[1]" indicates character number 3, state 1).

Opisthoventral Setae in Male (Characters 1 and 2). Within the ingroup, the consistent location of setae Jv3 on soft cuticle is apomorphic for *T. naeemi* (char. 1[1]). Some specimens of *T. heliconiae* may also have 1 or both of these setae on soft cuticle, but the ventrianal shield in this species is distinctly wider, and the setae, even if on the cuticle, are very close to the edge of the shield. A similar condition can be observed in many species of the *chiriquensis* group. In general, setae on the soft cuticle around the shield are similar in length to those on the shield. Distinctly shortened setae on the soft cuticle are synapomorphic for *T. heliconiae, T. fidelis, T. ochoai,* and *T. bisacculatus* as well as in the more distantly related *T. bakeri* (char. 2[1]). A similar condition is also present in *T. berryi* of the *chiriquensis* group.

Setae of R Series in Male (Character 3). Location of setae of the *R* series on the dorsal shield probably represents the ancestral condition. The derived condition, with the opisthonotal part of the shield reduced so that these setae are on soft cuticle adjacent to the shield, is present in the closely related *T. kressi* and *T. trinitatis* as well as in the more distantly related *T. naeemi.*

Anal Shield in Female (Characters 4–5). Within Melicharini, a broadly oval or subcircular anal shield with a moderately large anus in the female is probably a primitive character state. Most species of *Tropicoseius* have the anal shield clearly longer than wide, with a small anus. Females of some species of the *braziliensis* and *wetmorei* groups have roughly circular shields, which most likely represent 2 independent cases of reversals. Within the latter group such a condition (char. 5[1]) is present in *T. colombiensis* and *T. fairchildi,* 2 species that share several other derived character states. Within *Tropicoseius,* the distance between the posterior margin of the genital shield and the anterior margin of the anal shield is typically at least as long as half of the width of the anal shield, and within this space are placed setae *Jv1* and *Jv2* (e.g., Fig. 12b). In *T. kressi* and *T. trinitatis,* the distance is smaller (char. 4[1]) and setae *Jv2* are moved laterally (Fig. 28g).

Leg IV in Female (Character 6). In most species of *Tropicoseius* the legs of females are typical of Melicharini, relatively slender, with genu IV at least twice as long as wide. Females of 2 closely related species of the *wetmorei* group, *T. colombiensis* and *T. fairchildi,* however, share characteristically thick and stout legs, in which the width of genu IV is equal to its length.

Chelicerae (Characters 7–9). Males of the *wetmorei* group are characterized by having a relatively simple, unmodified spermatodactyl that lacks a subapical dorsal stylus (char. 7[1]). Several species—*T. bakeri, T. naeemi, T. analis, T. trinitatis, T. kressi, T. venezuelensis,* and *T. klepticos*—have spermatodactyls with apices modified to various degrees. The type that is probably more primitive has the apex narrowed and somewhat bent. In a more derived condition, present in *T. analis, T. trinitatis, T. kressi, T. venezuelensis,* and *T. klepticos,* the very tip of the spermatodactyl is spirally twisted (char. 9[1]). Females of most species of the *wetmorei* group are characterized by the presence, on the proximoventral surface of the movable digit of the chelicera, of a long mucro that always reaches, and often exceeds, the apex of the chela (char. 8[1]). This condition probably represents a derived condition, opposed to the short mucro present in *T. erro* and all other species of the genus *Tropicoseius.*

Maturation Pouch (Characters 10–14). Except for *T. erro,* all species of the *wetmorei* group share the presence of a maturation pouch in the female inseminating apparatus. The pouch may represent a greatly enlarged atrium characteristic of the phytoseiid type of apparatus. A long, tubelike pouch (char. 13[1] and 14[1]) in the female is correlated with the presence of a modified apex of the spermatodactyl in the male. Species with unmodified, straight spermatodactyls have maturation pouches of various shapes, but these pouches always are short and distally bent at a right angle (char. 12[1]). In most species the walls of the pouch are smooth, but the maturation pouches of *T. naeemi* and *T. bakeri* have characteristically striated walls (char. 11[1]). *T. ochoai* and *T. bisacculatus* share the presence of 2 pouches (char. 10[1]), the proximal one of which is probably a simple dilation of the major sperm duct, whereas the distal pouch is probably homologous to the atrium, with slightly thicker walls.

Taxonomic Treatment

In the *Material Examined* section for each mite species, the family for each host genus (plants and birds) appears in parentheses after the 1st occurrence of the host genus in that section. Numbers after collectors' names indicate the collector's field number for plant vouchers. Plant vouchers for specimens are deposited as follows: collections by W. J. Kress in NMNH; collections by J. Luteyn in New York Botanical Garden; collections by P. E. Berry and B. Stein in Missouri Botanic Garden. Plant vouchers and photographs of living plants for many collections by R. K. Colwell, D. S. Dobkin, S. Naeem, and A. J. Heyneman are available upon request from R.K.C.

Genus *Tropicoseius* Baker & Yunker, 1964

Tropicoseius Baker and Yunker 1964: 104 type species: *Tropicoseius wetmorei* Baker & Yunker, 1964.–Lindquist and Evans 1965: 52.–Hunter 1972: 26, 34.–Fain, Hyland, and Aitken 1977b: 101, 109, 137.–Fletchmann and Johnston 1978: 165.–Fain and Hyland 1980: 15.–Micherdzinski and Lukoschus 1980: 65, 77.–Naeem, Dobkin, and OConnor 1985: 338.–Zamudio 1985: 83.–Ohmer, Fain, and Schuchmann 1991: 484.–Farrier and Hennessey 1993: 47.–OConnor, Colwell, and Naeem 1997.

Diagnosis. Dorsal shield of male with distinct lateral incisions, rarely shield entire or completely divided into separate podonotal and opisthonotal shields; that of female with distinct lateral incisions, rarely completely divided; dorsal setae of male usually not modified, sometimes flagelliform; those of female usually very short, smooth, rarely some dorsal setae finely

serrated; setae *z3* absent; setae *s6* present; marginal *(r–R)* setae in female on soft cuticle; in male at least some marginal setae of *r* and all of *R* series on shield, rarely these setae on soft cuticle; *j1* usually as long as *J5* or shorter, rarely longer. Genital shield of female with anterior hyaline part broadly rounded; genital setae always on shield; peritrematic plates connected posteriorly with exopodal plates or free. Ventrianal shield in male usually large, trapezoidal; sometimes anterior part of shield reduced. Anterior margin of tectum in both sexes rounded or sharply tapering toward apex, rarely crenulate; corniculi in both sexes with inner margins parallel or slightly divergent; fixed digit of chelicera bi- or tridentate, movable chela edentate; pilus dentilis modified into hyaline lobe; male spermatodactyl always directed anteriad, usually simple, rarely with subapical lobiform projection. Leg II of male usually greatly enlarged and curved between femur and tibia; seta *av* on femur II enlarged, spine- or knoblike; setae *av1–av3* and *pv1* on tarsus II modified, spine- or knoblike; setae *av2* on tarsus III always and *pv1* and *av3* often knoblike. Setal formula of genua I-IV: 13–11–9–9; that of tibia: 13–10–9–10; seta *pl2* present on tibia III and IV. Female inseminating apparatus often with distal maturation pouch.

Male. *Dorsum.* Dorsal shield usually with distinct lateral incisions between setae *s6* and *S1,* often connected by a transverse suture (Fig. 24a), rarely entire (Fig. 4a) or completely divided into podonotal and opisthonotal shields (Fig. 19a); ornamentation developed over entire shield or restricted to its anterolateral regions; setae *z3* absent, rarely *S1* absent; of marginal setae, at least *r2–r3* on shield, opisthonotal *R*'s usually on shield; sometimes all marginals of *r* and *R* series on soft cuticle; *j1* usually as long as *J5* or shorter, rarely longer (in 1 species *J5* absent); dorsal setae generally unmodified, sometimes some or all dorsal setae flagelliform (Fig. 19a) or strongly shortened (Fig. 4a) but never large, spinelike; *Z5* sometimes modified, clublike (Fig. 17a). Peritremes usually reaching level of *z1* but sometimes only level of *s1.*

Venter. Sternogenital shield with 5 pairs of sternal setae and 3 pairs of pores, rarely posterior part of shield reduced such that setae *st5* on soft cuticle; paragenital setae present or absent; peritrematic plates united posteriorly with exopodal plates or free. Ventrianal shield usually large; setae *Jv1–Jv3, Zv1, Zv2,* para-anal, and postanal setae on shield; except for anal setae all or some of these setae sometimes on soft cuticle; opisthoventral setae frequently modified (i.e., very short [Fig. 25b] or very long flagelliform [Fig. 21b]). Ornamentation of ventral shields developed to various degrees, sometimes absent. Metapodal plates present, large; in one species fused with ventrianal shield (Fig. 27b).

Gnathosoma. Tectum either rounded apically or acuminate; smooth, rarely crenulate. Deutosternum with 7 rows of equally, moderately wide denticles; all rows connected, rows not widened, reduced or isolated; or some rows slightly widened. Capitular setae usually short, about half as

long as anterior rostral pairs, but sometimes as long as or somewhat longer than anterior rostral setae; *al1* on palpfemur and *al1* and *al2* on palpgenu spatulate; apotele on palptarsus 2-tined. Fixed digit of chelicera bi- or tridentate, movable chela edentate; pilus dentilis modified into hyaline lobe; spermatodactyl variable in shape and length but always directed anteriad; stylus sometimes well-developed, reaching end of spermatodactyl.

Legs. Coxae I with or without rows of small denticles; coxae II–IV each usually with pronounced, posteriorly convex boss. Leg II distinctly enlarged and curved between femur and tibia; seta *av* on femur, genu, and usually also tibia enlarged, spine- or knoblike; setae *av1–av3* and *pv1* on tarsus modified, knob- or spinelike; dorsal setae of femur, genu and tibia sometimes distinctly longer than width of their respective articles; setae *ad1* and *pd1* sometimes barbed. Tarsus of leg III with setae *av2* always, and *pv1* and *av3* usually, modified, knoblike. Setation of genua of legs I-IV, respectively, 13–11–9–9; that of tibia 13–11–9–10; seta *pl2* present on tibia III and IV. Coxa IV without posterior spur, but its rudiments sometimes discernible (Fig. 21b).

Female. *Dorsum.* Dorsal shield with distinct lateral incisions reaching or exceeding level of setae *z6,* usually connected by transverse suture; rarely dorsal shield completely divided (Fig. 22a); *z3* absent, rarely *S1* absent; all *r*'s and *R*'s on soft cuticle laterally, rarely *r1* on shield; most dorsal setae short, subequal; setae *j1* as long as or shorter than *J5,* rarely slightly longer; *J5* sometimes weakly serrated but without microspinules (Fig. 22a). Opisthonotal region of shield often with more or less developed lateral incisions near setae *S4* (Fig. 10a). Peritremes usually reaching level of setae *z1,* but sometimes shorter.

Venter. Anterior part of sternal shield with margin either forming 2 distinct, divergent lobes or distinctly incised; shield with 3 pairs of sternal setae (occasionally 1 or both setae *st3* on soft cuticle) and 2 pairs of pores, 4th pair of setae and 3rd pair of pores on soft cuticle behind shield. Genital shield with anterior hyaline part tapered (Fig. 27g) or broadly rounded (Fig. 12b), never incised; posterior part of shield widened and rounded. Peritrematic plates united posteriorly with exopodal plates or free; genital setae always on shield. Anal shield usually longer than wide, oval, narrower than posterior margin of genital shield; in some species roughly circular and broader than posterior margin of genital shield; metapodal plates small, elongate or triangular in outline. Inseminating apparatus with long major duct, and with or without maturation pouch (Fig. 2 k–o); small infundibulum rarely present.

Gnathosoma. Tectum shorter than that of male, convex or strongly attenuated. Corniculi more slender than in male, their inner margins parallel; fixed digit of chelicera uni- or bidentate, movable chela edentate (Fig. 2 g–j); ventroproximal mucro on movable chela elongated or not.

Legs. Coxae I with or (more often) without rows of small denticles. Leg II not modified, all setae normal; tarsus III with no modified setae. Setation of legs as noted for male.

Species Included:

Group *chiriquensis*

Tropicoseius berryi n. sp.
Tropicoseius colwelli (Hunter, 1972) n. comb.
Tropicoseius chazdonae n. sp.
Tropicoseius steini n. sp.
Tropicoseius cervus n. sp.
Tropicoseius kaliszewskii n. sp.
Tropicoseius chiriquensis Baker & Yunker, 1964
Tropicoseius peregrinator Baker & Yunker, 1964
Tropicoseius rowelli n. sp.
Tropicoseius ornatus (Fain & Hyland, 1980)
**Tropicoseius changensis* Baker & Yunker, 1964
**Tropicoseius bellavistensis* (Wiese & Fain, 1993) n. comb.
**Tropicoseius carlosalberti* (Wiese & Fain, 1993) n. comb.

Group *braziliensis*

Tropicoseius uniformis (Fain, Hyland & Aitken, 1977) n. comb.
Tropicoseius braziliensis Baker & Yunker, 1964
Tropicoseius phoreticus (Fain, Hyland & Aitken, 1977) n. comb.
Tropicoseius fuentesi n. sp.
Tropicoseius erioxynon n. sp.

Group *wetmorei*

Tropicoseius erro Baker & Yunker, 1964
Tropicoseius wetmorei Baker & Yunker, 1964
Tropicoseius heliconiae Baker & Yunker, 1964
Tropicoseius fidelis (OConnor, Colwell & Naeem, 1996) n. comb.
Tropicoseius ochoai n. sp.
Tropicoseius bisacculatus (Fain, Hyland & Aitken, 1977) n. comb.
Tropicoseius colombiensis (Fain & Hyland, 1980) n. comb.
Tropicoseius fairchildi Baker & Yunker, 1964
Tropicoseius bakeri Dusbabek & Cerny, 1970
Tropicoseius naeemi n. sp.
Tropicoseius analis (Fain & Hyland,1980) n. comb.
Tropicoseius trinitatis (Fain, Hyland & Aitken, 1977) n. comb.
Tropicoseius kressi n. sp.
Tropicoseius venezuelensis Baker & Yunker, 1964
Tropicoseius klepticos (OConnor, Colwell & Naeem, 1996) n. comb.

**Tropicoseius adsimilis* (Fain & Hyland, 1980) n. comb.
**Tropicoseius chlorestes* (Fain, Hyland & Aitken, 1977) n. comb.
**Tropicoseius eisenmanni* Baker & Yunker, 1964
**Tropicoseius perezgloriae* (Wiese & Fain, 1993) n. comb.

An asterisk indicates a species not included in the cladistic analysis.

Remarks. The genus *Tropicoseius* was proposed by Baker and Yunker (1964) to incorporate 10 species collected from the nasal cavities of hummingbirds and from flowers of hummingbird-pollinated plants. A year later, Lindquist and Evans (1965) synonymized *Tropicoseius* with the 2nd genus described by Baker and Yunker (1964), *Rhinoseius.* Lindquist and Evans did not publish their rationale, but a reluctance to recognize a monotypic genus was paramount and the combined taxon appeared to be a natural group or lineage (E. E. Lindquist, personal communication). Subsequently, most acarologists automatically placed any newly described species of a hummingbird flower mite that did not fit into a diagnosis of the genus *Proctolaelaps* Berlese into *Rhinoseius.* The only authors who still recognized *Tropicoseius* were Dusbabek and Cerny (1970). Our cladistic analysis indicates that *Tropicoseius* and *Rhinoseius* together do form a monophyletic group, as viewed by Lindquist and Evans (1965). Although the 2 lineages could be treated as subgenera within a single genus, *Rhinoseius,* we propose the reinstatement of *Tropicoseius* as a separate genus, for the following reasons: (1) both lineages, *Tropicoseius* and *Rhinoseius,* are supported by unique, synapomorphic features; (2) each group includes several to many species; (3) each group is ecologically and behaviorally distinct; and (4) subgeneric trinomials are awkward.

Among Melicharini, the following synapomorphies allow an easy recognition of species of the genus *Tropicoseius*: (1) modified, knoblike seta *pv1* on tarsus II in males; (2) modified, knoblike setae *pv1, av2,* and *av3* on tarsus III in males (sometimes *av3,* and rarely also *pv1,* not modified); (3) seta *pl2* present on tibia III in both sexes. It must be noted that the last character state, although invariably consistent within *Tropicoseius,* shows a variability among other genera of Melicharini (e.g., all species of *Mucroseius* Lindquist and most species of *Proctolaelaps* Berlese lack this seta). It is not clear therefore, whether the presence of *pl2* on tibia III in *Tropicoseius* represents a retention of an ancestral character state or a reversal, thus being a true autapomorphy of the genus. A cladistic analysis of the entire tribe Melicharini is necessary to address this and other questions about character evolution in this group of Ascidae.

Within the genus, 3 informal groups of species can be distinguished. We decided not to create any formal taxa (subgenera) for these groups principally because, from the cladistic point of view, they do not rank equally (i.e., group *chiriquensis* is a sister clade to groups *braziliensis* and *wetmorei* combined). However, each of the groups represents a well-defined assem-

blage of species that share many morphological and ecological traits. The groups of species discussed below are partly congruent with the division of the genus *Rhinoseius* (sensu Lindquist and Evans 1965) proposed by Fain (1992). However, Fain's group *tiptoni* is the equivalent of the genus *Rhinoseius* sensu Baker and Yunker (1964), group *ornatus* is the equivalent of our group *chiriquensis,* and his group *wetmorei* equals groups *braziliensis* and *wetmorei,* combined, as we define them.

Group *chiriquensis*

All species of the group are be characterized by pronounced sexual dimorphism, both in respect to the general body size and the development of the 2nd leg. In general, males in this group of species are distinctly larger than females, and their 2nd pair of legs is greatly enlarged, at least 3 times as wide as the 1st pair. The spermatodactyl in males is accompanied by a well-developed stylus, with *Tropicoseius berryi* n. sp., the only exception lacking the stylus, bearing instead a small membranous lobe on the ventral margin of the spermatodactyl. The female inseminating apparatus in this group lacks the maturation pouch; the major duct is long and threadlike, and the calyx and minor duct usually are easily discerned. Females in this group have probably the most primitive type of the chelicera among species of *Tropicoseius,* with the least reduced dentition of the fixed digit. The fixed digit of the chelicera is always longer than the movable chela, it is usually tri-, rarely bidentate; the mucro is short, reaching or only slightly surpassing half of the movable chela.

In many species of the group, males exhibit a tendency toward reduction in the size of the ventrianal and sternogenital shields. In the most extreme case, *T. chazdonae* n. sp. males do not have a typical ventrianal shield for Melicharini but only a small, circular anal shield, similar to that of females. Heteromorphism in respect to length of dorsal setae and presence of lateral incisions on the dorsal shield also is characteristic of males of most species in the group. Females of species of the *chiriquensis* group are rather uniform in their morphology, and females of some sets of species are difficult to tell apart. Characters useful in distinguishing females of different species include proportions of the length of podonotal and opisthonotal regions of the dorsal shield, shape of the anal shield, length of peritremes, and extent of lateral incisions on the opisthonotal region of the dorsal shield. Although the inseminating apparatus in most species is rather uniform, females in closely related species (e.g., *T. steini* n. sp. and *T. cervus* n. sp.) can be discriminated by the relative thickness of the major and minor ducts.

Tropicoseius colwelli (Hunter, 1972) **new combination**
(Figs. 1b, 6e)

Rhinoseius colwelli Hunter 1972: 26, 27, 30–35, fig. 3, male and female; type locality: Costa Rica, Cerro de la Muerte–Colwell 1973: 738, 743–746,748–750, fig. 1.–Colwell et al. 1974: 447, 451.–Fain, Hyland, and Aitken 1977b: 101, 109, 118, 123, 136, figs. 24, 36, 61.–Colwell and Naeem 1979: 489, 490.–Colwell 1979b: 463, 466.–Micherdzinski and Lukoschus 1980: 78.–Colwell 1983: 767–768, fig. on p. 619.–Colwell 1985: 58, fig.–Zamudio 1985: 82.–Colwell 1986b: 408, 409, 412, 413.–Fain 1992: 117–120, 123, 126, 133, figs. 5, 36.–Farrier and Hennessey 1993: 48.–Colwell and Naeem 1994: 25, 27.

Material Examined. Costa Rica: Alajuela Province, Monteverde, Woods near site J, ex *Tropaeolum* sp. (Tropaeoleaceae), 9-VIII-72, J. Hunt—1 male, 1 female; Monteverde, Ridge, ex *Centropogon* sp. (Campanulaceae), 11-VIII-72, J. Hunt—5 deutonymphs; Monteverde, site I/J, ex *Tropaeolum* sp., 13-VIII-72, J. Hunt—1 male, 1 female; Monteverde, ex *Campylopterus hemileucurus mellitus* Bangs (Trochilidae), 15-X-72, P. Feinsinger—2 males, 5 females; Divide above Monteverde, ex *Centropogon* sp., 22-VIII-72, P. Feinsinger—2 males, 2 females; Monteverde, ex *Columnea* (Gesneriaceae), 23-IV-72, G. Powell—4 males, 9 females; Monteverde, ex *Centropogon* sp., 16-IV-72, G. Powell—5 males, 21 females; Monteverde, Pantanoso Trail, elev. 1620 m, ex unidentified bromeliad, 10-II-77, P. Feinsinger—3 males, 2 females; Monteverde, Sendero Chumogo, ex *Symbolanthus pulcherrimus* Gilg (Gentianaceae), 3-VII-80, P. Feinsinger—3 males, 4 females; Monteverde, Cloud Forest, ex *Pitcairnia brittoniana* Mez (Bromeliaceae), 1-III-91, S. Cunningham—5 males, 16 females; same locality, ex *Centropogon solanifolius* Benth.- 9 males, 1 female; Heredia Province, Braulio Carrillo National Park, water supply line, elev. 2050 m, ex *Centropogon* sp., 7-I-89, R. K. Colwell—1 male, 2 females; Zona Protectora La Selva (Braulio Carrillo National Park), elev. 2050 m, ex *Centropogon* sp., 13-IV-86, R. Colwell—4 males, 12 females; Braulio Carrillo National Park, Barva, ex ?*Centropogon* sp., 6-VI-90, A. Fernandez—20 males, 35 females; Angel Falls, ex *Centropogon* sp., 23-III-71, R. K. Colwell—1 male, 6 females; La Selva Biological Station, SA 300, ex *Hamelia patens* (Rubiaceae), 8-I-89, R. K. Colwell), 1 female; same locality and host, laboratory clearing, 11-I-89, R. K. Colwell—1 male, 1 female; San Jose Province, Salsipuedes (Cerro de la Muerte), ex *Bomarea* sp. (Amaryllidaceae), 27-III-71, R. K. Colwell—2 males, 2 females; Cerro de la Muerte, ex *Eugenes fulgens spectabilis* (Lawrence) (Trochilidae), 7-VIII-76—1 female; Cerro de la Muerte, ex *Centropogon talamancensis* Wilbur, 8-VIII-76—4 males; same locality and date, ex *Centropogon valerii* Standley—1 male, 1 female.

Remarks. This species appears to be endemic to Costa Rica. It is most closely related to *Tropicoseius chazdonae, T. steini,* and *T. cervus* n. spp.,

and its adults can be distinguished from these species by the hooklike, curved apex of the spermatodactyl; presence of modified, knoblike seta *pv1* on male tarsus III; setae of series *s, r, S,* and *R* in the male distinctly longer than setae of series *j, z, J,* and *Z*; opisthonotal setae *Z5* in the male at least twice as long as any other opisthonotal setae; and opisthonotal part of the female dorsal shield with weakly developed incisions at the level of setae *Z3*.

Tropicoseius chazdonae, new species
(Figs. 2b, 3–5)

Diagnosis. Dorsal shield of male either entire or with lateral incisions; that of female always with narrow, deep lateral incisions; reticulate ornamentation of shield usually more distinct in male than in female. Dorsal setae of adults of both sexes generally subequal and quite short as for the genus (≈⅓ as long as distance between adjacent setal insertions). Sternogenital shield of male with only 3–4 pairs of setae, its posterior region reduced such that setae *st5,* and sometimes *st4,* on soft cuticle; male without large ventrianal shield, instead with small, elongate anal shield resembling that of female. Male with 2nd pair of legs strongly enlarged and with seta *av* on femur, genu, and tibia strongly spinelike; tarsus III with only seta *av2* knoblike. Female inseminating apparatus lacking maturation pouch; minor duct easily discerned.

Male. Dorsal shield 642–804 μm long, 342–480 μm wide (measured at level of setae *s4*; 11 specimens), either entire (Fig. 4a) or with shallow incisions between setae *s6* and *S1*; reticulation over entire dorsal shield, becoming more distinct laterally, in some specimens a weak trace of transverse suture discernible. Dorsal shield with 39 pairs of smooth, simple setae, including 20 pairs on podonotal and 19 pairs on opisthonotal regions; marginal setae *r5, r6, R5, R6,* and *UR*'s on soft cuticle. Dorsal setae of similar length (19–22 μm) but *s4* somewhat longer (24 μm) and distinctly moved anteriad; *j1, z1,* and *J5* noticeably shorter (13–14 μm).

Tritosternum typical for genus, with trapezoidal base and very slender, tapering pilose laciniae. Sternogenital shield usually with 3 pairs of pores and 3 or 4 pairs of setae; setae *st5* always and *st4* often on soft cuticle; posterior part of shield strongly narrowed, its outline highly irregular and variable; posterior part of shield with weak reticula. Paragenital setae absent. Metapodal plates comparatively large, variable in shape. Ventral shield absent; anal shield elongate, resembling that of female; with 3 anal setae; postanal seta about twice as long as para-anal setae. All setae of *Jv* and *Zv* series on soft cuticle, *Jv5* short (22 μm) (Fig. 4b). Peritrema extending anteriad to level of setae *z1*.

Gnathosoma with tectum rounded apically and steeply sided laterally, with smooth margins (Fig. 3f). Fixed digit of chelicera bidentate; movable chela edentate; spermatodactyl straight as seen laterally but noticeably ex-

curved at apex when seen from below, with long stylus extending almost to the apex of spermatodactyl (Fig. 3d). Deutosternum with 7 transverse rows of denticles; all rows connected; no rows widened. Rostral setae simple, slender, with anterior pair distinctly longer than posterior pairs, of which interior pair longer than exterior pair; capitular setae slender, simple. Corniculi slender, parallel or convergent; internal malae extending to tip of corniculi. Setae *al1* and *al2* on palpgenu and *pl* on palpfemur spatulate (Fig. 3b).

Leg I decidedly more slender than legs III and IV. Leg II strongly enlarged, distinctly curved ventrally between femur and tarsus; femur with seta *av* very stout, spinelike, moderately long; genu and tibia each with seta *av* stout and short, spinelike; tarsus with setae *pv1* and *av1* short, stout and spinelike, seta *av2* stout and about twice as long as *av1,* and with seta *av3* very large, almost twice as large as *av2* (Fig. 3A). Tarsus of leg III with seta *av2* stout, knoblike; *pv1* and *av3* unmodified (Fig. 2b). Coxa I with 2 rows of small denticles, coxae II–III with pronounced bosses, bosses not discernible on coxae IV. Setation of legs as noted for genus.

Female. Dorsal shield 582–690 μm long, 294–360 μm wide (measured at level of setae *s4*; 11 specimens), with distinct, narrow lateral incisions between setae *s6* and *S1* extending nearly to level of setae *Z1* (Fig. 5a); transverse suture very weakly indicated. Reticulation less conspicuous than in males, restricted to anterolateral region. Dorsal shield with 32 pairs of smooth, simple setae, including 17 pairs on podonotal and 15 pairs on opisthonotal regions; marginal setae *r2–r6* and *R1–R6* (in 1 specimen also 1 of setae *s2*) on soft cuticle laterally; 4 pairs of submarginal setae (*UR*) also on soft cuticle posteriad coxae IV; dorsal setae collectively very short, subequal.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; sternal shield without reticulation, its anterior margin distinctly incised medially; except for anterior lobes sternal shield almost square in shape. Fourth pair of sternal setae and 3rd pair of sternal pores on soft cuticle behind posterior margin of sternal shield. Anterior hyaline part of genital shield narrowly rounded; ornamentation of shield weakly indicated; shield only slightly widened behind genital setae. Metapodal plates small, elongate. Anal shield elongate, about twice as long as wide, weakly reticulate; postanal seta twice as long as para-anal setae. Eight to 9 pairs of opisthogastric setae on soft cuticle around anal shield, these setae, including *JV5,* similarly short but *JV2* somewhat longer (Fig. 5b). Inseminating apparatus with long (150–190 μm), threadlike major duct, without a maturation pouch; minor duct easily discerned (Fig. 3e).

Tectum rounded, somewhat wider than that of male. Corniculi more slender than in male, their inner margins straight and parallel; fixed digit of chelicera tridentate, movable chela edentate; mucro surpassing half of chela but not reaching its apex (Fig. 3c).

Leg chaetotaxy as in male, except leg II not modified, also no modified seta on tarsus of leg III.

Type Material. Costa Rica: Heredia Province, Angel Falls, by waterfall, ex *Centropogon nutans* Planch. & Oerst.(Campanulaceae), 7-I-89, R. K. Colwell—male (holotype), female (allotype), 3 males (paratypes); Zona Protectora La Selva (Braulio Carrillo National Park), elev. 300 m, ex *Centropogon* sp., 5-IV-86, R. Chazdon—8 males, 5 females (paratypes), 16 deutonymphs; Puntarenas Province, San Vito de Java, 1 km NW Finca Las Cruces (Wilson Botanic Garden), ex *Centropogon nutans* Planch. & Oerst, 17-III-71, R. K. Colwell—1 male, 1 female (paratypes); **Ecuador:** Morona-Santiago, elev. 1900–2000 m, ex *Centropogon granulosus* Presl, 18-V-85, B. Stein—4 males, 4 females (paratypes); same locality and host, elev. 1650 m, 17-V-85—2 males, 4 females (paratypes); Napo, elev. 2100–2150 m, ex *Centropogon curvatus* Wimmer, 28-V-85, B. Stein, 2872—4 males, 7 females (paratypes); Napo, Reventador, elev. 1400 m, ex *Centropogon* sp., 26-IV-85, B. Stein, 2627—1 male, 2 females (paratypes); Pastaza, elev. 1000–1050 m, ex *Centropogon gamosepalus* Zahlbr., 9-VI-85, B. Stein, 3020—4 males, 2 females (paratypes); Zamora-Cinchipe, elev. 1050–1250 m, ex *Centropogon granulosus* Presl, 12-V-85, B. Stein, 2757—5 males, 1 female (paratypes); Pichincha, elev. 2300 m, ex *Palicourea* sp. (Rubiaceae), 26-V-85, B. Stein, 2857—1 male (paratypes); **Peru:** Cuzco, Urubamba, elev. 2020 m, ex *Centropogon urubambae* Wimmer, 12-V-85, B. Stein, 2387—5 females (paratypes); Cuzco, Paucartambo, elev. 3000 m, ex *Centropogon urubambae* Wimmer, 26-V-85, B. Stein, 2438—4 males, 4 females (paratypes); Cuzco, Paucartambo, elev. 2000 m, ex *Centropogon umbrosus* Wimmer, 5-IV-85, B. Stein, 2510—3 males, 2 females (paratypes); San Martín, Rioja, elev. 1500 m, ex *Centropogon* sp., 9-II-85, B. Stein, 2124—5 females (paratypes); San Martin, Moyobamba, elev. 1100 m, ex *Centropogon granulosus* Presl, 9-II-85, B. Stein, 2125—1 male, 7 females (paratypes); Junín, Satipo, elev. 900–1000 m, ex *Centropogon granulosus* Presl, 7-III-85, B. Stein, 2342—3 males, 5 females (paratypes).

Etymology. Named for Dr. Robin Chazdon, botanist, who collected a paratype series during the 1986 National Geographic Elevational Transect Expedition to the Zona Protectora La Selva (now Braulio Carrillo National Park), Costa Rica.

Remarks. *Tropicoseius chazdonae* n. sp. is most closely related to *T. steini* and *T. cervus* spp. n., sharing the entire dorsal shield and extremely enlarged leg II in the male. The 3 species also are the only species of the genus with unmodified seta *pv1* on male tarsus III. Males of *T. chazdonae* can be distinguished easily from these 2 species by the relatively simple structure of the spermatodactyl, which lacks the apical hook. Moreover, of the 3 species, *T. chazdonae* shows the most drastic reduction of ventral shields in males. The female inseminating apparatus shows many primitive features, lacking the maturation pouch and having a well-developed minor

duct. Along with *T. colwelli* (Hunter), all the above mentioned species have the largest body sizes among all known species of the hummingbird flower mites, with the length of male dorsal shield often exceeding 800 μm.

Tropicoseius cervus, new species
(Figs. 6–8)

Diagnosis. Dorsal shield of male entire, without lateral incisions; dorsal shield of female with narrow lateral incisions; reticulate ornamentation of shield of both sexes dense and distinct. Dorsal setae of both sexes generally subequal and relatively short, ≈⅓–½ as long as distance between adjacent setal insertions; opisthonotal part of female dorsal shield with distinct, irregular incisions at level of setae *Z3*. Femur of leg II of male with setae *pv1* and *pv2* unmodified; male with tarsus of leg III with seta *av2* modified, knoblike, other tarsal setae unmodified. Spermatodactyl highly modified, hooklike. Posterior part of sternogenital shield and ventrianal shield of male noticeably reduced. Inseminating apparatus of female lacking maturation pouch; minor duct relatively long, easily discernible.

Male. Dorsal shield 726–738 μm long, 457–472 μm wide (measured at level of setae *s4*, 3 specimens), without lateral incisions; dense and distinct reticulation clearly visible over entire shield (Fig. 7a). Dorsal shield with 40 pairs of smooth, simple setae, including 21 pairs on podonotal and 19 pairs on opisthonotal regions; marginal setae *r2–r6* and *R1–R4* on dorsal shield. Setae of dorsum in most specimens relatively short: *j3* 17–18, *z1* 25–27, *z4* 52, *s2* 28, *s3* 51, *r2* 36, *r3* 54–56 μm; podonotal setae *j1* noticeably longer than opisthonotal setae *J5* (25–27 and 11–14 μm, respectively), *Z5* short (28–34 μm).

Tritosternum with very long, slender pilose laciniae and trapezoidal base. Sternogenital shield with 5 pairs of setae and 3 pairs of pores, but its posterior part distinctly reduced; reticulation of shield well-developed. Paragenital setae generally absent, but 1 paragenital seta present in 1 specimen. Metapodal plates large, roughly circular in shape. Ventrianal shield partly reduced, its anterior part separated, forming small, transverse platelet; middle part of shield irregularly incised laterally; only setae *Jv1* and *Jv2*, and para-anal and postanal setae on shield; reticulate pattern distinct over entire shield (Fig. 7b). Peritrema extending anteriad almost to level of seta *z1*.

Gnathosoma with tectum rounded or very weakly incised apically and steeply sided laterally, with smooth margins (Fig. 6d). Fixed digit of chelicera bidentate, its apex not modified; spermatodactyl on the movable chela highly modified, its apex forming a biramous hook, but tip of its apical branch not twisted; stylus slightly exceeding apex of spermatodactyl (Fig. 6c). Deutosternum with 7 rows of denticles; all rows connected; none widened. Rostral setae simple, slender; anterior pair noticeably shorter than posterior interior pair (34 and 47 μm, respectively), posterior exterior setae

somewhat shorter (18 μm); capitular setae slender, simple (25 μm). Corniculi slender, slightly convergent; internal malae very narrow, reaching tip of corniculi. Setae *al1* and *al2* on palpgenu and *pl* on palpfemur spatulate (Fig. 6b).

Leg II stout, strongly curved ventrally between femur and tarsus; femur with seta *av* very stout, spinelike, setae *pv1* and *pv2* not modified; genu and tibia with setae *av* short and stout, knoblike; *av1* and *pv1* of tarsus spurlike, about half as long as *av* of femur; *av2* of tarsus spurlike, slightly longer than *av* of femur; *av2* and *av3* of tarsus stout, spinelike (Fig. 6a). Tarsus of leg III with seta *av2* modified, knoblike; setae *pv1* and *av3* unmodified. Coxa I with 1 internal and 3 external rows of denticles, coxae II–IV with pronounced bosses convex posteriorly. Leg setation as noted for genus.

Female. Dorsal shield 649–693 μm long, 295–339 μm wide (measured at level of setae *s3*; 4 specimens), with distinct, narrow lateral incisions between setae *s6* and *S1* extending almost to level of seta *J1*; transverse suture not indicated; opisthonotal part of shield with distinct, irregular incisions at level of setae *Z3*. Reticulation as conspicuous as in males. Dorsal shield with 31–32 pairs of smooth, simple setae, including 17 pairs on podonotal and 14–15 pairs on opisthonotal regions (*S3* sometimes on soft cuticle); marginal setae *r2–r6, R1–R6* and *UR*'s on soft cuticle; all dorsal setae very short, subequal (less than a half as long as distance between adjacent setal insertions). Opisthonotal part of dorsal shield with deep, irregular incisions at level of setae *S4* (Fig. 8a).

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; faint reticulation on anterior ⅓ of shield. Sternal shield trapezoidal in shape, wider posteriorly; 4th pair of sternal setae and 3rd pair of sternal pores on soft cuticle; no endopodal plates. Anterior margin of genital shield convex but not strongly rounded; ornamentation of shield weak; shield somewhat widened behind genital setae. Metapodal plates small, narrowly ellipsoidal. Anal shield oval, only slightly longer than wide, distinctly reticulate; postanal seta about twice as long as para-anal setae. Eleven to 15 pairs of opisthogastric setae on soft cuticle around anal shield; setae *Sv2* absent (Fig. 8b). Inseminating apparatus long, major duct lacking maturation pouch; minor duct easily discerned, relatively long (Fig. 8c).

Tectum weakly rounded, distinctly shorter and wider than that of male; fixed digit of chelicera bi- or tridentate, movable chela edentate; mucro surpassing half of chela but not reaching its apex. Corniculi more slender than in male, their inner margins straight, parallel.

Second leg not modified, without spine- or knoblike setae; tarsus of leg III with all setae normal; legs I and IV as in male.

Type Material. Ecuador: Tungurahua, elev. 2100 m, ex *Centropogon affinus* McVaugh (Campanulaceae), 2-VI-85, B. Stein, 2930—male (holotype), female (allotype), 2 males (paratypes); Zamora Chinchipe, elev. 2280–2560 m, ex *Centropogon densiflorus* Benth., 15-V-85, B. Stein, 2781—1 male, 7 females (paratypes).

Etymology. The specific epithet *cervus* refers to the unusual structure of the male spermatodactyl, which resembles deer antlers.

Remarks. A highly sexually dimorphic species, characterized by an entire dorsal shield, *T. cervus* has a tendency toward a reduced ventrianal shield, and a hooklike spermatodactyl in the male. Females have a relatively primitive type of inseminating apparatus, with no maturation pouch, but with a well-developed minor duct. *T. cervus* can be distinguished from the closely related *Tropicoseius steini* n. sp. by the structure of the fixed digit of the male chelicera, which lacks the apical elongation, and by a different structure of the spermatodactyl. Females of *T. cervus* have a noticeably less reduced opisthonotal part of the dorsal shield in the region of setae *Z3* than females of *T. steini*.

Tropicoseius steini, new species
(Figs. 9–10)

Diagnosis. Dorsal shield of male usually undivided, without lateral incisions; dorsal shield of female with narrow lateral incisions; reticulate ornamentation of shield of both sexes dense and distinct. Dorsal setae of male relatively short and uniform in length, only Z5 distinctly longer than remaining dorsal setae; in female all setae short and subequal in length; opisthonotal part of female dorsal shield with distinct, irregular incisions at level of setae *Z3* and *Z4*. Leg II of male with seta *av* of femur, genu and tibia spinelike; tarsus of leg III with seta *av2* modified, knoblike, seta *pv1* not modified. Spermatodactyl with hooklike apex; apex of fixed digit of chelicera characteristically elongated. Inseminating apparatus of female lacking maturation pouch but with distinct minor duct.

Male. Dorsal shield 590–667 μm long, 339–413 μm wide (measured at level of setae *s4*; 4 specimens), without lateral incisions in most specimens, in 1 specimen lateral incisions present between setae *s6* and *R1*, connected by a weak transverse suture (Fig. 9a); dense and distinct reticulation clearly discernible over entire dorsal shield. Dorsal shield with 41 pairs of smooth, simple setae, including 21 pairs on podonotal and 20 pairs on opisthonotal regions; marginal setae *r2–r5*, and *R1–R5* on dorsal shield; *r6* absent. Setae of dorsum in most specimens relatively short, but some setae may vary considerably in their length among specimens: *z2* 28–52, *z4* 45–84, *s2* 17–50, *s3* 22–56, *r2* 20–50, *r3* 39–56 μm (4 specimens); podonotal setae *j1*, and opisthonotal setae *J5* very short (17- and 11–12 μm, respectively), *Z5* long (74–180 μm).

Tritosternum with very long, slender pilose laciniae and trapezoidal, elongated base. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; reticulation of shield well-developed in its posterior region. Paragen-

ital setae absent. Metapodal plates large, irregular in shape. Ventrianal shield relatively narrow, irregular in outline, with setae *Jv1, Jv2, Zv1, Zv2,* and para-anal and postanal setae; setae *Jv3* either on shield or on soft cuticle; reticulate pattern distinct over entire ventrianal shield (Fig. 9b). Peritrema extending anteriad almost to level of seta *z1*.

Gnathosoma with tectum rounded apically and steeply sided laterally, its margins smooth. Fixed digit of chelicera bidentate, its apex characteristically elongated; spermatodactyl on movable chela highly modified, its apex forming a biramous hook, tip of its terminal branch twisted outward; stylus slightly exceeding apex of spermatodactyl (Fig. 9c). Deutosternum with 7 rows of denticles, all rows connected, none widened. Rostral setae simple, slender; anterior pair slightly shorter than posterior interior pair (25–34 and 29–38 μm, respectively), posterior exterior setae somewhat shorter (17–20 μm); capitular setae slender, simple (19–23 μm). Corniculi slender, slightly convergent; internal malae very narrow, reaching tip of corniculi. Setae *al1* and *al2* on palpgenu and *pl* on palpfemur spatulate (Fig. 9d).

Legs I, III, and IV not modified; leg I not more slender than legs III and IV. Leg II stout, strongly curved ventrally between femur and tarsus; femur with seta *av* very stout, spinelike, setae *pv1* and *pv2* not modified; genu and tibia with seta *av* short and stout, knoblike; *av1* and *pv1* of tarsus spurlike, about half as long as *av* of femur; *av2* of tarsus spurlike, slightly shorter or as long as *av* of femur; *av3* of tarsus stout, spinelike (Fig. 10e). Tarsus of leg III with seta *av2* modified, knoblike; seta *pv1* not modified. Coxa I with 1 internal and 3 external rows of denticles, coxae II–IV with pronounced bosses convex posteriorly. Setation formulas of legs typical for genus.

Female. Dorsal shield 614–631 μm long, 289–318 μm wide (measured at level of setae *s4*; 5 specimens), with distinct, narrow lateral incisions between setae *s6* and *S1* extending somewhat past setae *Z1*; transverse suture not indicated; opisthonotal part of shield with distinct, irregular incisions at level of setae *Z3* and *Z4* (Fig. 10a). Reticulation as conspicuous as in males. Dorsal shield with 32 pairs of smooth, simple setae, including 17 pairs on podonotal and 15 pairs on opisthonotal regions; marginal setae *r2–r5, R1–R6,* and *UR'* s on soft cuticle; seta *r6* absent; all dorsal setae very short (shorter than distances between adjacent setal insertions), subequal.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; faint reticulation on anterior ⅓ of shield. Sternal shield trapezoidal in shape, wider posteriorly; 4th pair of sternal setae and 3rd pair of sternal pores on soft cuticle. Anterior hyaline part of genital shield convex but not strongly rounded; ornamentation of shield poorly discernible; shield somewhat widened behind genital setae. Metapodal plates small, narrow. Anal shield oval, slightly longer than wide, distinctly reticulate; postanal seta about twice as long as para-anal setae. Ten to 13 pairs of opisthogastric

setae on soft cuticle around anal shield; setae *Sv2* absent (Fig. 10b). Inseminating apparatus with long, threadlike major duct; without maturation pouch; minor duct easily discernible, well-developed (Fig. 10c).

Tectum weakly tridentate, distinctly shorter and wider than that of male; fixed digit of chelicera tridentate, movable chela edentate; mucro not reaching apex of chela (Fig. 10d).

Second leg not modified, without spine- or knoblike setae; tarsus of leg III with all setae normal; legs I and IV as in male.

Type Material. Ecuador: Cañar Province, elev. 1650–1800 m, ex *Centropogon gesneraeformi* Drake (Campanulaceae), 21-V-85, B. Stein, 2845—male (holotype), female (allotype), 4 males, 8 females (paratypes); tributary of Rio Papallacta, 5 km E of Papallacta, elev. 2865 m., ex *Centropogon* sp., 9 Feb. 1976, P. Feinsinger—2 males, 1 female (paratypes); Napo, Rd. to Puyo, 0°27′S, 77°51′W, elev. 1830 m, 9.5 km S Beza, ex *Ceratostema peruvianum* Gmelin (Ericaceae), 16-X-92, J. L. Luteyn, 14697—1 male (paratype); **Peru:** Cajamarca, Cajamarca-Celendin rd., 7°5′S, 78°25′W, elev. 3080 m, 89 km E Cajamarca, ex *Siphocampylus sanguineus* A. Zahlbr.(Campanulaceae), 12-II-85, J. L. Luteyn, 11314—1 male, 15 females (paratypes).

Etymology. Named for Bruce Stein, botanist (The Nature Conservancy, Arlington, VA), who collected many specimens for this study, including some of the type specimens of this species.

Remarks. This species is quite closely related to *T. cervus* n. sp. but is easily distinguished by the characteristic, elongated apex of the fixed digit on the male chelicera and outwardly twisted tip of the main arm of the spermatodactyl. Ventral shields in the male are relatively little reduced and opisthoventral setae *Zv1* are always on the shield. The dorsal shield in the male is usually entire but in 1 specimen, lateral incisions are present, which correlates with the less enlarged leg II. Females of *T. steini* n. sp. differ from those of *T. cervus* in having better developed incisions in the region of the opisthonotal setae *S3–S5*.

Tropicoseius kaliszewskii, new species
(Figs. 11–12)

Diagnosis. Dorsal shield of male usually undivided, without lateral incisions, but in some specimens shallow incisions present and connected by a faint transverse suture; dorsal shield of female always with narrow lateral incisions; reticulate ornamentation of shield of both sexes dense and distinct. Median dorsal setae of male decidedly shorter than marginal setae of series *r* and *R*; in female all setae short and subequal in length. Femur of leg II of male with seta *av* enlarged, spinelike, and small chitinous protuberance not of setal origin; seta *av* on genu spinelike; seta *av* on tibia of leg II not modified. Tarsus III with setae *av2* and *pv1* modified, knoblike.

Inseminating apparatus of female without maturation pouch; minor duct discernible. Peritrema in both sexes almost reaching level of setae *z1*.

Male. Dorsal shield 540–660 μm long, 360–420 μm wide (measured at level of setae *s4*; 6 specimens), entire, without lateral incisions in most specimens; in some specimens shallow lateral incisions between setae *s6* and *S1* present and connected by weak transverse suture; reticulate ornamentation over entire dorsal shield (Fig. 11a).

Dorsal shield with 39–42 pairs of smooth, simple setae, including 19–21 pairs on podonotal and 19–21 pairs on opisthonotal regions; marginal setae *r3–r5*, and sometimes *R1*, on soft cuticle; *r6* absent. Dorsal setae of series *z, s, r, Z, S,* and *R* noticeably longer than setae of series *j* and *J*. Length of some setae may vary considerably: *z2* 27–50 μm, *z4* 29–59 μm, *s2* 16–59 μm, *r2* 31–68 μm, *r3* 56–68, *r4* 59–78 (6 specimens). Setae *j1* and *J5* short: 16–22 μm and 12–16 μm respectively; setae *Z5* stout, very long (170–263 μm).

Tritosternum with long, slender pilose laciniae and trapezoidal base. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; reticulate ornamentation of shield poorly discernible. Paragenital setae absent. Metapodal plates large, roughly circular in shape. Ventrianal shield relatively narrow, irregular in outline but always constricted at the level of setae *Jv2* and bearing only setae *Jv1–Jv2, Zv1–Zv2* and para-anal and postanal setae; reticulate ornamentation well-developed over entire shield (Fig. 11b). Peritrema extending anteriad to level of seta *z1*; peritrematic plates not connected with exopodal plates.

Gnathosoma with tectum rounded apically and steeply sided laterally, its margins smooth (Fig. 11c). Fixed digit of chelicera bidentate, teeth very widely spaced along digit; movable chela edentate, with spermatodactyl dilated subapically (Fig. 12e), its apex slightly bent outward (as seen dorsally) (Fig. 12d). Deutosternum with 7 rows of denticles; all rows connected; some rows slightly widened. Rostral setae simple, slender; anterior pair of about the same length as posterior interior pair (30–32 μm), posterior exterior setae somewhat shorter (24 μm); capitular setae slender, simple. Corniculi slender, slightly convergent; internal malae very narrow, reaching or slightly surpassing tips of corniculi. Setae *al1* and *al2* on palpgenu spatulate, *pl* on palpfemur slightly widened apically but not distinctly spatulate (Fig. 12d).

Leg II stout, curved ventrally between femur and tarsus; femur and genu with seta *av* very stout, spinelike; femur with small chitinous protuberance, probably not of setal origin (no corresponding seta in female); tibia with no modified setae; *av1* and *pv1* of tarsus spurlike, about half as long as *av* of femur; *av2* of tarsus spinelike, as long as *av* of femur; *pv1* and *av3* of tarsus spinelike but shorter than *av2* (Fig. 11e). Tarsus of leg III with setae *av2* and *pv1* modified, knoblike. Coxa I with 1 internal and 2

external rows of denticles, coxae II–IV with pronounced bosses convex posteriorly. Setation of legs as noted for genus.

Female. Dorsal shield 588–630 μm long, 288–330 μm wide (measured at level of setae *s3*; 5 specimens), with distinct, narrow lateral incisions between setae *s6* and *S1* extending from level of seta *s5* in some specimens, up to more than half way to the midline of dorsal shield in others; transverse suture usually well indicated. Reticulate ornamentation well-developed over entire shield (Fig. 12a).

Dorsal shield with 32 pairs of smooth, simple setae, including 17 pairs on podonotal and 15 pairs on opisthonotal regions; marginal setae of series *r, R,* and *UR* on soft cuticle; setae *r6* absent; all dorsal setae about as long as ⅓ of distances between adjacent setal insertions.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; weak reticulate ornamentation discernible on anterior portion of shield; 4th pair of sternal setae and 3rd pair of sternal pores on soft cuticle. Anterior hyaline part of genital shield convex but not strongly rounded; ornamentation on posterior part of shield weakly developed; shield somewhat widened behind genital setae. Metapodal plates small, narrow. Anal shield oval, ≈1.5 times longer than wide, distinctly reticulate; postanal seta twice as long as para-anal setae. Ten to 11 pairs of opisthogastric setae on soft cuticle around anal shield; setae *Sv2* absent (Fig. 12b). Inseminating apparatus with long, threadlike major duct, without maturation pouch; minor duct present but poorly discernible (Fig. 12c).

Tectum rounded, distinctly shorter and more broadly rounded than that of male (Fig. 11d); fixed digit of chelicera bidentate, movable chela edentate; mucro not reaching apex of chela (Fig. 12f). Corniculi more slender than in male; their inner margins parallel.

Second leg not modified, without modified setae and chitinous protuberance; tarsus of leg III with all setae normal; legs I and IV as in male.

Type Material. Venezuela: Territorio Federal Amazonas, Departamento Atures, Sierra Maigualida, NW sector, small valley along an upper tributary of the Caño Iguana, elev. 2000 m, 5°30′N, 65°15′W, ex *Kunhardtia rhodantha* Maguire (Rapateaceae), 28 Feb.–3 Mar. 1991, Paul E. Berry Otto Huber and Judith Rosales; Berry 4808—male (holotype), female (allotype), 5 males, 5 females (paratypes).

Etymology. Named in honor of our colleague and friend the late Marek J. Kaliszewski (1954–92), formerly of Brigham Young University (Provo, UT), who participated in the early stages of this study.

Remarks. *Tropicoseius kaliszewskii* n. sp. seems to be most closely related to *T. chiriquensis* Baker & Yunker, *T. peregrinator* Baker & Yunker, *T. ornatus* (Fain & Hyland), and *T. rowelli* n. sp. It can be distinguished from all these species by the presence of a unique chitinous protuberance (knob) on the femur of the 2nd leg in males, very widely spaced teeth along the fixed digit of the chelicera, and an entire dorsal shield in males that, in

most specimens, lacks lateral incisions. Within this species there is a considerable variation of the length of dorsal setae in males, with some setae (e.g., *z4, s2, r2*) differing by 200–300% among different individuals. Possibly because of the small sample size, however, well-defined morphs cannot be distinguished.

This is the only species of hummingbird flower mites known to feed on flowers of plants of the family Rapateaceae.

Tropicoseius chiriquensis Baker & Yunker, 1964

Tropicoseius chiriquensis—Baker and Yunker 1964: 105, figs. 16–23, female; type locality: Panama, Chiriqui.

Rhinoseius chiriquensis—Fain, Hyland, and Aitken 1977b: 109, 118, 121, 136, 149–150, figs. 23, 38, 59.– Colwell and Naeem 1979: 489, 490.– Colwell 1983: 768.– Ohmer, Fain, and Schuchmann 1991: 481, 482.– Fain 1992: 119, 121–123, 126, 132, figs. 4, 34.– Farrier and Hennessey 1993: 48.– Colwell and Naeem 1994: 25.

Rhinoseius epoecus Colwell and Naeem 1979: 485–490, figs. 1–12, **n. syn.**– Colwell 1986a: 488–489.– Colwell 1986b: 408.– Heyneman, A. J. et al.1991: 455, 457, 458, 463–466, 470.– Christiansen, Colwell, and Kaliszewski 1992: 98, 102.– Fain 1992: 117–119,121, 123, 127, 132.– Wiese and Fain 1993: 70, 85, 89, 98.– Farrier and Hennessey 1993: 48.– Colwell and Naeem 1994: 25.

Type Material. Panama: Cerro Punta, Chiriqui, elev. 1615 m, ex *Amazilia edward* (DeLattre & Bourcier) (Trochilidae), 28 Apr. 1961, C. E. Yunker—female (holotype) (NMNH).

Material Examined. Panama: Cerro Punta, ex *Eugenes fulgens* (Swainson)] (Trochilidae), 14-III-68, P. Kirmse—1 female; **Colombia:** Mozambique (3°83′N, 73°3′W), ex *Amazilia versicolor* (Vieillot) 21-VII-73, W. W. Moss—1 male, 2 females; **Costa Rica:** Alajuela Province, Monteverde, ex *Lobelia laxiflora* (Campanulaceae), 19-X-72, P. Feinsinger—1 male, 6 females; same locality, ex *Amazilia saucerottei hoffmanni* (Cabanis & Heine), 22-I-73, P. Feinsinger—7 females; same locality and date, ex *Colibri thalassinus cabanidis* (Heine) (Trochilidae—22 females; same locality and host, 1-XII-73, P. Feinsinger—1 male, 9 females; same locality, ex *Chlorostilbon canivetii canivetii* (Lesson) (Trochilidae), 14-X-72, P. Feinsinger—3 females; **Mexico:** most of the specimens of *R. epoecus* from Mexico listed in Colwell and Naeem (1979) plus the following: Jalisco, Volcán Colima, Plant #2, 1-I-78, A. J. Heyneman & B. Hallet—3 males, 2 females; Volcán Colima road, ex *Hylocaris leucotis leucotis* (Vieillot) (Trochilidae), 31-XII-77, A. J. Heyneman & B. Hallet—1 male; same locality and date, ex *Eugenes fulgens fulgens* (Swainson—2 males, 3 females; same locality, ex *Lampornis amethestinus brevirostris* (Ridgway) (Trochilidae), 2-I-78, A. J. Heyneman & B. Hallet—2 males, 3 females; Tamalipas, Rancho Cielo, ex *Campylopterus curvipennis curvipennis* (Lichtenstein). (Trochilidae), 16-VII-73, R. K. Colwell—1 male; Oaxaca, Guelatao, Hwy. 175, ex *Lobelia laxiflora* Kunth, 10-X-78, R. K. Colwell—1 male, 1 female; **USA:** most of the specimens of *R. epoecus* from California listed in Colwell and Naeem (1979), including the holotype; Arizona, Mt. Lemmon, elev. 250 m, ex *Penstemon barbatus* (Cavanilles) Roth (Scrophulariaceae), 24-IX-94, R. Levin—2 females.

Remarks. *Tropicoseius chiriquensis* Baker & Yunker was originally described on the basis of a single female collected in Panama from a hummingbird, *Amazilia edward.* Colwell and Naeem (1979: 489) listed a number of characters that distinguished their new species, *Rhinoseius epoecus,* described from California and Mexico, from *T. chiriquensis.* However, a reexamination of the type material of the 2 species as well as examination of a number of new specimens from localities in Panama, Costa Rica, and Mexico revealed intermediate forms in respect to all those characters at most localities. The character "seta *d3* of the palpgenu spinelike, and bifid apically," supposedly characteristic of males of *R. epoecus,* could be found in only 1 specimen from the type series of the species and therefore must be treated as an aberration of no taxonomic significance. *R. epoecus,* was supposed to have the transverse suture that connects lateral incisions of the dorsal shield less distinct than that of *T. chiriquensis.* As we discussed earlier in the text, the degree of development of the suture is subject to great intraspecific variation and should not be considered a useful taxonomic character. The absence of a boss on coxa III in the holotype of *T. chiriquensis* also should not be considered a taxonomically meaningful character because it also is not discernible in many specimens from the type series of *R. epoecus,* whereas the boss is present in another specimen from the type locality of *T. chiriquensis.* Moreover, because there are no discrete differences between the 2 species either in the characteristics of inseminating structures of either males and females or in the arrangement and size of setae, we consider them conspecific. *R. epoecus* should be considered a junior synonym of *T. chiriquensis.*

The undetermined mite of the genus *Rhinoseius* described and illustrated in the paper by Zamudio (1985) probably is *T. chiriquensis,* although we were unable to study the specimens on which the description is based.

Tropicoseius chiriquensis is the most widely distributed species of hummingbird flower mite known, with records from central Colombia to California and Arizona in the United States. Its range extends farther north than any other species of hummingbird flower mite. It is known to feed on flowers of at least 14 species of plants that belong to 6 families.

Tropicoseius ornatus (Fain & Hyland, 1980), **new combination**
(Fig. 6 f and g)

Rhinoseius ornatus Fain and Hyland 1980: 15, 19, figs. 3, 6, 13, 16–18, male and female; type locality: Colombia, Antioquia.

Rhinoseius ornatus, Ohmer, Fain, and Schuchmann 1991: 481, 482.
Rhinoseius ornatus, Fain 1992: 119–120, 123, 126, 133, fig. 33.
Rhinoseius ornatus, Wiese and Fain 1993: 87.

Type material. Colombia: Antioquia, ex *Phaethornis superciliosus* (Linnaeus) (Trochilidae), 2–12-VIII-71, R. B. Waide—1 male (allotype); Antioquia, ex *Phaethornis guy* (Lesson), 1971, R. B. Waide—1 female (paratype) (IRSNB).

Material Examined. Dominica (West Indies): Laudat Rd, 5 km from Roseau Bridge, ex *Lobelia* #1 (Red fl.) (*Lobelia ?persicaefolia* Lam.) (Campanulaceae), 20-III-79, R. K. Colwell—15 males, 27 females; View Pt. above Fresh Water Lake, ex *Lobelia* #2 (White fl.) (*Lobelia ?flavescens* E. Wimm.), 21-III-79, R. K. Colwell—7 males, 17 females.

Remarks. *Tropicoseius ornatus* is easily distinguishable from other species of the *chiriquensis* group by the characteristic ornamentation of the dorsal shield in both sexes, in which the anterior part of the podonotal region of the shield bears dense, parallel striations. The species shows a remarkable degree of within-population variation in the length of opisthosomal setae in males. Most specimens studied had very short dorsal setae, as in the allotype, shorter than ⅓ of the distance to the nearest adjacent setal insertion. In some specimens, however, setae of the rows *z, s, r, Z, S,* and *R* are as long as or longer than these distances. The development of the dorsal setae in males of this species is correlated with the development of the knoblike setae on tarsi III. Heteromorphic males (those with longer setae) have setae *pv1, av2* and *av3* on the 3rd tarsus short but knoblike, whereas homeomorphic males (with short setae) have setae *pv1* and *av2* spinelike (apices not blunt), and setae *av3* resemble regular, unmodified setae except for enlarged, almost bulbous bases. Males with dorsal setae of intermediate length have intermediate forms of the tarsal setae. *T. ornatus* is most closely related to *T. peregrinator* Baker & Yunker from Mexico and *T. rowelli* n. sp. from Jamaica. These 3 species share similarities in the form of the spermatodactyls and the setation of tarsus III in males, as well as in the form of the inseminating apparatus in females.

We could not find any differences between the type specimens of *T. ornatus* and our specimens from Dominica, either in males or females, therefore we must consider them conspecific. The observed discontinuity in the distribution of the species may reflect either incomplete sampling, and the species in fact occurs through Colombia, Venezuela, and southern part of the Lesser Antilles; or its presence on Dominica is the effect of a recent colonization event, possibly an accidental introduction with plants. No species of hummingbirds occur both in Colombia and on Dominica. Given the degree of the similarity of specimens from Colombia and Dominica, it seems unlikely that the Dominican mites are descendants of mites from

Greater Antilles (e.g., Jamaica), convergent with *T. ornatus,* as might be suggested by the distribution of the closest relatives of this species.

Tropicoseius peregrinator Baker & Yunker, 1964
(Fig. 2d)

Tropicoseius peregrinator Baker and Yunker 1964: 107–108, figs. 96–108, male and female; type locality: Mexico, at Texas quarantine.
Rhinoseius peregrinator, Hunter 1972: 34.–Fain, Hyland, and Aitken 1977b: 118, 123, 136, figs. 20, 37, 60.–Fain 1992: 119, 123, 125, 133, fig. 32.–Farrier and Hennessey 1993: 48.

Type Material. Mexico: D. F., at Laredo (Texas quarantine), ex "bromeliad," 17-V-51, Cary and Fouts—1 female (holotype), 1 male (paratype) (NMNH). (The geographic origin of this specimen is unknown. "D. F." (Distrito Federal) was probably the shipping point for the plants examined at the Mexico/U.S. border quarantine.)

Remarks. *Tropicoseius peregrinator* is known only from the type series but is easily distinguishable from the closely related *T. rowelli* n. sp. by the features noted in the diagnosis of that new species. Although the paratype males have relatively very long dorsal and opisthoventral setae, it is possible that they represent a heteromorphic form of the species and that individuals with short setae also occur.

Tropicoseius rowelli, new species
(Figs. 13–15)

Diagnosis. Dorsal shield of both sexes with distinct lateral incisions connected by transverse suture, and conspicuous reticulation over entire shield. Dorsal setae in both sexes short, subequal (⅓–½ as long as distance between adjacent setal insertions). Posterior margin of sternogenital and anterior margin of ventrianal shields of male often reduced; opisthoventral setae *Zv1* and *Zv2* in male either on ventrianal shield or soft cuticle, setae *Jv3* always on soft cuticle; paragenital setae present in both sexes. Second pair of legs in male greatly enlarged, seta *av* of femur and genu spinelike, that of tibia unmodified; seta *av2* of tarsus II spinelike, larger than *av* of femur. Setae *pl1, av2,* and *av3* on tarsus of 3rd leg in males knoblike. Female inseminating apparatus threadlike, without maturation pouch but with easily discerned atrium and minor duct.

Male. Dorsal shield 631–690 μm long, 384–413 μm wide (measured at the level of setae *s3*; 6 specimens), with lateral incisions between setae *s1* and *S1* reaching level of setae *z6,* connected by transverse suture; reticulate ornamentation distinct over entire shield (Fig. 14a). Dorsal shield with 35 pairs of smooth, simple setae, including 20 pairs on podonotal and 15 on opisthonotal regions; marginal setae *r5, r6, R1–R5* and *UR*'s on soft

cuticle. Most dorsal setae relatively short (11–38 μm); *Z5* somewhat thicker and noticeably longer (68–113 μm) than remaining dorsal setae.

Tritosternum typical for genus, with trapezoidal base and slender, tapering pilose laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; posterior part of shield often reduced (irregularly incised), with distinct reticulate ornamentation. Paragenital setae present. Metapodal plates comparatively large, irregular in shape. Ventrianal shield narrow, distinctly reticulate, often its anterior portion separated as a small platelet (Fig. 14b); setae *Zv1* and *Zv2* either on shield or soft cuticle; setae *Jv3* always on soft cuticle; *Jv5* about as long as postanal seta (45–74 μm). All ventral setae relatively short (27–45 μm). Peritrema extending anteriad almost to level of setae *z1*; peritrematic plated fused with exopodal plates at level of 4th coxae.

Gnathosoma with tectum narrowly rounded apically, with smooth margin. Fixed digit of chelicera edentate; movable chela edentate, with short (50–68 μm), weakly curved spermatodactyl directed anteriad (Fig. 13c); stylus not reaching apex of spermatodactyl. Deutosternum with 7 transverse rows of denticles, all connected, none widened. Rostral setae simple, slender, all pairs of almost equal length; capitular setae slender, simple. Corniculi slender, their inner margins parallel; internal malae extending to tip of corniculi (Fig. 13b). Setae *al1* and *al2* on palpgenu spatulate, *pl* on palpfemur slightly widened apically but not distinctly spatulate.

Coxa of leg I with 2 internal and 3 external rows of minute denticles. Leg II distinctly enlarged, curved ventrally between femur and tarsus; femur and genu with seta *av* thick, spinelike; that of tibia not modified; tarsus with setae *av1–av3* and *pv1* enlarged, spinelike; *av2* of tarsus 1.5 larger than *av* of femur (Fig. 13a). Tarsus III with setae *pl1, av2* and *av3* enlarged, knoblike. Small bosses present on coxae of legs II–IV. Leg setation as noted for genus.

Female. Dorsal shield 608–649 μm long, 295–336 μm wide (measured at the level of setae *s3*; 6 specimens), with distinct, narrow lateral incisions between setae *s6* and *S1* extending to level of setae *z6*, connected by transverse suture. Reticulation distinct over entire shield (Fig. 15a). Posterior part of opisthonotal part of shield with irregular narrow incisions at level of setae *R4* and *S4*. Dorsal shield with 32 pairs of smooth, simple setae, including 17 pairs on podonotal and 15 pairs on opisthonotal regions; marginal setae *r*'s, *R*'s and *UR*'s on soft cuticle laterally; dorsal setae short, collectively subequal (11–23 μm).

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores, shield weakly ornamented only at its anterior region. Fourth pair of sternal setae and 3rd pair of sternal pores on soft cuticle behind posterior margin of sternal shield. Genital shield with anterior hyaline part broadly rounded, its posterior part distinctly reticulate, slightly widened behind genital setae; posterior part of shield often accompanied by 4 minute, transverse platelets. Paragenital setae present. Metapodal plates very small, elongate. Anal shield somewhat longer than wide, distinctly reticulate (Fig. 15b). Nine to 10 pairs of opisthogastric setae on soft cuticle around anal shield, all setae similarly short (27–34 μm). Peritrema extending anteriad almost to level of setae *z1*; peritrematic plated fused with exopodal plates at level of 4th coxae. Inseminating apparatus threadlike, 230–248 μm long, lacking maturation pouch; atrium and minor duct easily discerned (Fig. 13e).

Tectum with anterior margin smoothly rounded, sometimes shorter than that of male. Fixed digit of chelicera bidentate, movable chela edentate; mucro short, reaching half length of movable chela (Fig. 13d). Corniculi more slender than in male; their inner margins parallel.

Leg chaetotaxy as in male, except no setae modified on legs II and III.

Etymology. Named in honor of C.H.F. Rowell (Zoologisches Institut der Universität Basel, Basel), entomologist and neurophysiologist, discoverer of this species, and collector of many other specimens for this study.

Type Material. Jamaica: John Crow Mts., ex *Columnea hirsuta* Swartz (Gesneriaceae),-XII-79, C.H.F. Rowell—1 male (holotype), 1 females (allotype), 16 males, 21 females (paratypes); same locality, ex *Besleria lutea* Linnaeus (Gesneriaceae—6 males, 6 females (paratypes); Blue Mts., ex *Lobelia martagon* Hitchc. (Campanulaceae—6 males, 11 females (paratypes).

Remarks. *Tropicoseius rowelli* n. sp. is closely related and morphologically similar to *T. peregrinator* Baker & Yunker and *T. ornatus* (Fain & Hyland, 1980). From *T. peregrinator* it differs mainly in structure of the male spermatodactyl, which in *T. peregrinator* is distinctly wider, with the stylus reaching or surpassing its very blunt apex, whereas in *T. rowelli* the apex is narrow and almost pointed. From *T. ornatus* it can be distinguished by the absence of characteristic, parallel striations on anterolateral regions of the dorsal shield in both sexes, and the absence of a tooth on the fixed digit of chelicera in the male (the fixed digit is unidentate in *T. ornatus*), and the length of the mucro on the movable chela in the female (almost reaching apex of the chela in *T. ornatus,* hardly reaching half the length of the chela in *T. rowelli*). The spermatheca in *T. rowelli* is distinctly wider than that of *T. peregrinator,* and the peritremes are shorter, never reaching the level of podonotal setae *z1*. In *T. rowelli,* the opisthonotal part of the female dorsal shield is shorter than the podonotal region and widest at the level of setae *S2*. In *T. peregrinator,* the opisthonotal region of the female dorsal shield is distinctly longer than the podonotal region and widest at the level of setae *S1*. In all studied specimens of the new species, the dorsal setae of males are very short, never longer than half the distance between adjacent setal insertions, whereas in *T. peregrinator* the dorsal setae of males are long, always reaching and often surpassing the distance between

adjacent setal insertions. Because this last character is subject to strong intraspecific variation in many species of *Tropicoseius*, however, it should not be regarded as a definitive feature of the new species.

Tropicoseius berryi, new species
(Figs. 16–18)

Diagnosis. Dorsal shield of male with narrow lateral incisions, not connected by transverse suture; dorsal shield of female usually with narrow lateral incisions; reticulate ornamentation of shield of male dense and distinct over entire shield except for its antero-lateral regions; ornamentation of female weak. Most of median dorsal setae in both sexes short (less than half of distance between adjacent setal insertions); setae *r3* and *Z5* in male, and *Z5* in female long, stout, and with slightly dilated apices. Femur of leg II of male with seta *av1* large, spurlike; *pv1* and *pv2* not modified; seta *av1* on tibia of leg II knoblike; tarsus of leg III with setae *pv1* and *av2* knoblike. Inseminating apparatus of female lacks a maturation pouch; major duct short, threadlike.

Male. Dorsal shield 750 μm long, 450 μm wide (measured at level of setae *s3*, holotype), with narrow lateral incisions between setae *s6* and *S1* surpassing level of setae *z6*; dense and distinct reticulation over entire dorsal shield, except for its antero-lateral regions (Fig. 17a). Dorsal shield with 42 pairs of setae, including 21 pairs on podonotal and 21 pairs on opisthonotal regions; *r6* absent. All marginal *r*'s and *R*'s on shield, *UR*'s on soft cuticle; marginal setae *r3* and opisthonotal *Z5* stout and long (59 and 99 μm, respectively), with slightly dilated apices. Dorsal setae generally short, subequal: *j2* 22 μm, *j3* 22 μm, *z4* 24 μm, *z5* 26 μm, *s2* 18 μm, *J1* 26 μm, *J2* 22 μm, *Z1* 26 μm, *Z2* 24 μm; setae *j1* and *J5* very short (11 μm).

Tritosternum with long, slender pilose laciniae and trapezoidal base. Sternogenital shield with slightly reduced posterior part, with 4 pairs of setae and 3 pairs of pores, 5th pair of sternal setae on soft cuticle; longitudinal ornamentation of shield faint. Paragenital setae absent. Metapodal plates large, irregular in outline. Ventrianal shield relatively narrow, with lateral margins roughly parallel; shield with setae *Jv1–Jv3, Zv1, Zv2,* and para-anal and postanal setae (plus a single superfluous seta between setae *Jv1* and *Jv2*); ornamentation distinct over entire ventrianal shield. Setae *Jv5* long (77 μm), stout, and with slightly dilated apices (Fig. 17b). Peritrema extending anteriad almost to level of seta *z1*, but not reaching it.

Gnathosoma with tectum rounded apically and very steep-sided laterally, its margins smooth (Fig. 16d). Fixed digit of chelicera bidentate; movable chela with short (62 μm), stout and slightly incurved spermatodactyl (as seen from below); stylus lacking but spermatodactyl with small, hyaline lobiform projection subapically (Fig. 16c). Deutosternum with 7 rows of denticles; all rows connected; none widened. Rostral setae simple, slender; anterior pair shorter than posterior interior pair (24 and 33 μm, respectively), posterior exterior setae somewhat shorter (20 μm); capitular setae slender, simple, 22 μm long. Corniculi slender, slightly convergent; internal malae very narrow, slightly extending tip of corniculi (Fig. 16b).

Legs I, III and IV not modified; leg I not more slender than legs III and IV. Coxa I with 1 internal row of denticles, coxae II–IV with pronounced bosses convex posteriorly. Leg II stout, strongly curved ventrally between femur and tarsus; femur with seta *av* very stout, spurlike; *pv1* and *pv2* of femur not modified; genu and tibia with seta *av* short, knoblike; *av2* of tarsus large, spurlike; *av1, av3,* and *pv1* of tarsus knoblike (Fig. 16a). Tarsus of leg III with setae *pv1* and *av2* of tarsus modified, knoblike. Leg setation as noted for genus.

Female. Dorsal shield 690–750 μm long, 330–390 μm wide (measured at level of setae *s3*; 3 specimens), with distinct, narrow lateral incisions between setae *s6* and *S1* extending to somewhat past base of seta *z6*; transverse suture usually well indicated. Reticulation very weak, restricted mainly to antero-lateral regions of shield (Fig. 18a). Dorsal shield with 32 pairs of smooth, simple setae, including 17 pairs on podonotal and 15 pairs on opisthonotal regions; marginal setae *r*'s, *R*'s and *UR'* s on soft cuticle; seta *r6* absent; all dorsal setae very short, subequal, except *Z5* long (88–100 μm), stout, with slightly dilated apices.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; faint reticulation on anterior ⅓ of shield. Sternal shield trapezoidal in shape, wider posteriorly; 4th pair of sternal setae and 3rd pair of sternal pores on soft cuticle. Anterior hyaline part of genital shield convex but not strongly rounded; ornamentation of shield weak; shield somewhat widened behind genital setae. Metapodal plates small, narrow. Paragenital setae absent, but in 1 specimen 1 rudimentary seta present. Anal shield obovate, ≈1.5 times longer than wide, weakly reticulate; postanal seta ≈2.5 times as long as para-anal setae. Nine to 10 pairs of opisthogastric setae on soft cuticle around anal shield, plus 1 or 2 superfluous setae between *Jv1* and *Jv2*; *Jv5* long (73–79 μm), stout, and with slightly dilated apices (Fig. 18b). Inseminating apparatus hardly discernible, with short, threadlike major duct; without a maturation pouch.

Tectum rounded, shorter and wider than that of male; corniculi more slender than in male, their inner margins parallel. Fixed digit of chelicera bidentate, movable chela edentate.

Second leg not modified, without spine- or knoblike setae; tarsus of leg III with all setae normal; legs I and IV as in male.

Type Material. Brazil: Estado Rio de Janeiro, Municipio Macaé de Cima, Rio das Flores, Serra da Siberia, cloud forest, elev. 1000 m, ex *Fuchsia regia* (Vellozo) Munz (Onagraceae), 12-I-93, Paul E. Berry 5411—male (holotype), female (allotype), 2 females (paratypes).

Etymology. Named in honor of Paul E. Berry (Missouri Botanic Garden, St. Louis, MO), botanist, discoverer of this species and collector of many other specimens in this study.

Remarks. *Tropicoseius berryi* n. sp. is characterized by the least enlarged 2nd leg in males among all species of the *chiriquensis* group. It has relatively poorly developed spurlike setae *av* on femur II, no reduction in the ventrianal shield in the male and the spermatodactyl without a well-developed stylus but with a small, hyaline, lobiform projection instead. The sexes share the presence of clublike setae *Jv5* and *Z5*, unique within the genus.

Tropicoseius berryi is the only species of the genus known to feed on flowers of the family Onagraceae, in spite of long-standing efforts to examine species of this family, which is rich in hummingbird-pollinated species.

Tropicoseius changensis Baker & Yunker, 1964

Tropicoseius changensis Baker and Yunker 1964: 105, figs. 24–31, female; type locality: Panama, Bocas del Toro.

Rhinoseius changensis, Fain, Hyland, and Aitken 1977b: 117, 121, 136, figs. 26, 35, 58.–Fain 1992: 119, 122–123, 125, 132, fig. 35.–Farrier and Hennessey 1993: 48.

Remarks. This species is known only from the holotype female (not seen by the authors) collected from the hummingbird *Phaethornis guy* and is not included in the cladistic analysis. The detailed original description was accompanied by good drawings, however, and the supplementary description provided by Fain (1992) allows us to draw some conclusions as to the relationships of the species. The absence of a maturation pouch in the inseminating apparatus, the shape of dorsal and genital shields, as well as the structure of chelicera (fixed digit distinctly longer than the movable chela) indicate a close relationship with species of the *chiriquensis* group. It is very likely that if a male of this species is found, it will be characterized by a spermatodactyl directed anteriad, with a long stylus, and the 2nd leg with seta *av2* of the tarsus greatly enlarged. Most species of *Tropicoseius* that share similar character states are associated primarily with plants of the family Campanulaceae.

Tropicoseius bellavistensis (Wiese and Fain, 1993), **new combination**

Rhinoseius bellavistensis Wiese and Fain 1993: 84–92, figs. 13–18, male and female; type locality: Colombia, Cordilliera Central.

Remarks. We did not have an opportunity to examine specimens of this recently described species, but its detailed description leaves no doubts about its relationships. As pointed out by Wiese and Fain (1993), *T. bellavistensis* is closely related to *T. colwelli* Hunter (as well as to *T. chazdonae, T. steini,* and *T. cervus* spp. n.), having spinelike seta *av1* on tibia II and seta *av2* on tarsus II in males, as well as all characters typical for the species of the group *chiriquensis.*

Specimens of *T. bellavistensis* were collected from flowers of an unidentified species of Gesneriaceae, a family of plants with which *T. colwelli* also is (secondarily) affiliated.

Tropicoseius carlosalberti (Wiese & Fain, 1993), **new combination**

Rhinoseius carlosalberti Wiese and Fain 1993: 92–96, figs. 19–21 (male; type locality: Colombia, Cordilliera Central).

Remarks. We did not see the type specimens of this species. It seems that *T. carlosalberti,* like *T. bellavistensis,* also is closely related to *T. colwelli,* sharing the same character states as the species mentioned above. In fact, it is not unlikely that *T. carlosalberti* is conspecific with *T. bellavistensis.* The 2 species were described on the basis of few specimens (4 males; and 3 males and 1 female, respectively) collected from the same locality and host. Species in the group *chiriquensis* often exhibit a remarkable intraspecific variation in respect to the length of dorsal setae and development of the lateral incisions of the dorsal shield in males (see descriptions of *T. chazdonae, T. kaliszewskii, T. steini*) as well as the degree of reduction of the ventrianal shield and shape of metapodal plates in males. Any definitive decision as to the taxonomic status of *T. carlosalberti,* however, cannot be made until more material becomes available.

Group *braziliensis*

Species included in this group share the presence of serrated seta *ad* on trochanter I in both sexes and usually other serrated setae on legs I and II in both sexes as well as on the opisthonotum in females. Males of all included species are characterized by flagelliform setae of the opisthosomal venter, although in some species homeomorphic males with short, simple setae also occur. Spermatodactyls of males usually are very long (longer than 2nd segment of the chelicera), often bent or coiled, without styli. Chelicerae of females are characterized by a unidentate fixed digit (most likely a derived condition) and a short mucro, only half as long as the movable chela. The female inseminating apparatus lacks a maturation pouch, but unlike species of the group *chiriquensis,* the calyx and minor duct usually are poorly visible. The inseminating apparatus in females of *T. erioxynon* n. sp. has in addition a small but easily discernible infundibulum. The dorsal shield in both sexes of species in this group either has deep lateral incisions or is completely divided into separate podonotal and opisthonotal shields.

Tropicoseius uniformis (Fain, Hyland & Aitken, 1977), new combination
(Fig. 2 c and h)

Rhinoseius uniformis Fain, Hyland, and Aitken 1977a: 185, female; type locality: Brazil, Pará.–Fain, Hyland, and Aitken 1977b: 113, 119, 121, 137, 143, figs. 18, 44, 65, 108–109.–Fain 1992: 119, 123, 128, 132, fig. 13, 53.–OConnor, Colwell, and Naeem 1997: 20–23, figs. 48–53 (male).–Colwell and Naeem 1994: 26, fig. 2.1.

Rhinoseius hirsutus (nomen nudum), Colwell 1986b: 408, 409, 414.–Colwell et al. 1991: 456, 467, fig. 20–1, male.

Type Material. Brazil: Pará, Maritulea, Mosqueiro Ferry, ex *Phaethornis superciliosus* (Linné) (Trochilidae), 7-II-69, T.H.G. Aitken & T. E. Lovejoy—1 female (paratype) (USDA).

Material Examined. Trinidad: Arima Valley, La Laja Trace, ex *Psychotria poeppigiana* Mueller Argoviensis (Rubiaceae), 10-VIII-75, R. K. Colwell—1 male; same locality and host, 15-III-79—12 females, R. K. Colwell); Arima Valley, 2/3 way up La Laja Trace., ex *Psychotria poeppigiana* Mueller Argoviensis, 17-III-80, R. K. Colwell—14 males, 9 female; Arima Valley, Lower La Laja Trace, ex *Psychotria poeppigiana* Mueller Argoviensis, 23-II-76, R. K. Colwell—2 males, 3 females; Arima Valley, Cooker Trace, La Laja, ex *Psychotria poeppigiana* Mueller Argoviensis, 7-III-87—3 males, 4 females; Arima Valley, Temple Village Cricket Pitch, ex *Psychotria poeppigiana* Mueller Argoviensis, 16-II-79, R. K. Colwell—3 males, 6 females; Arima Valley, mi 19 marker, Blanchisseusse Rd., ex *Psychotria poeppigiana* Mueller Argoviensis, 13-III-79, R. K. Colwell—2 females; Arima Valley, Andrews Trace, ex *Psychotria* sp., 2-VIII-75, R. K. Colwell—1 female; Arima Valley, La Laja Trace, ex *Psyguria triphylla* Miq. (Cucurbitaceae), 15-III-79—1 female; Arima Valley, La Laja Plantation, ex *Costus spicatus* (Jacquin) Swartz (Costaceae), 11-III-79, R. K. Colwell—5 females; Arima Valley, La Laja Plantation Corner, ex *Aechmea fendleri* Andre (Bromeliaceae), 15-III-79—2 larvae, 2 females.

Remarks. *Tropicoseius uniformis* was redescribed by OConnor et al. (1997), who also described the male for the first time. The species is closely related to *T. phoreticus* (Fain, Hyland & Aitken), with which it shares the presence of barbed setae on femur II and long, flagelliform dorsal setae in males. Females of *T. uniformis* can be identified easily by the presence of dense, parallel striations in the anterolateral region of the dorsal shield. Like *T. phoreticus,* this species retains a plesiomorphic female inseminating apparatus, which lacks a maturation pouch but has a well-developed minor sperm duct.

Tropicoseius erioxynon, new species
(Figs. 19–20)

Diagnosis. Dorsal shield of both sexes completely divided into podonotal and opisthonotal dorsal shields; reticulate ornamentation of dorsal shield of male obliterated in its medial part; reticulation in female more distinct. Length of dorsal setae of male variable, ranging from very short, similar to that of female, to long and flagelliform; setae *Z5* of female longer than remaining dorsal setae, and finely serrated; opisthonotal seta *S1* missing in both sexes. Spermatodactyl of unique shape, its apex forming a superficial loop, with small subapical lobe; inseminating apparatus of female threadlike, with small infundibulum. Peritrema extending anteriad almost to level of seta *z1*.

Male. Dorsal shield 519–602 μm long, 313–354 μm wide (measured at level of setae *s3*; 10 specimens), completely divided into 2, podonotal and opisthonotal, shields; reticulation more distinct in anterior and lateral regions of shields (Fig. 19a). Dorsal shields with 34–35 pairs of smooth, setae, including 20 pairs on podonotal and 14–15 pairs on opisthonotal shields; opisthonotal seta *S1* usually missing, but rarely 1 or both setae present; marginal setae *r3–r6, R1–R6* and *UR*'s on soft cuticle, but sometimes *r3, r4, R3,* and *R4* on shield. Length of dorsal setae variable among specimens, ranging from very short (setae shorter than distances between adjacent setal insertions) to very long, flagelliform (intermediate forms are frequent); range of lengths of some setae as follows: *j1* 18–23 μm, *j2* 25–50 μm, *j3* 17–23 μm, *z2* 34–51 μm, *z4* 29–61 μm, *z5* 27–45 μm, *s3* 34–72 μm, *J1* 45–79 μm, *J2* 39–59 μm, *Z5* 38–216 μm; setae *J5* the shortest of all dorsal setae (11–12 μm.) both in homo- and heteromorphic forms (Fig. 19a).

Tritosternum with broadly trapezoidal base and long, slender, pilose laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; reticulate ornamentation distinct in posterior part of shield. Paragenital setae absent. Metapodal plates large, irregular in shape. Ventrianal shield elongate, weakly constricted at level of setae *Jv3*; shield, with setae *Jv1–Jv3, Zv1, Zv2,* para-anal, and postanal setae; reticulation of ventrianal shield distinct. Ventral setae of variable length, ranging from short to very long and flagelliform (Fig. 19b). Peritrema extending anteriad almost to level of seta *z1*.

Gnathosoma with tectum rounded apically and steeply sided laterally, with smooth margins, and sometimes with a small notch at apex. Fixed digit of chelicera unidentate; movable chela edentate, with long spermatodactyl forming superficial loop and with subapical lateral lobe (Fig. 19 c and d). Deutosternum with 7 transverse rows of denticles; all rows connected, no rows widened. Rostral setae simple, slender; anterior rostral setae long (39–45 μm), posterior interior pairs 38–41 μm, posterior exterior pairs

somewhat shorter (18–28 μm); capitular setae slender, simple (23–25 μm). Corniculi with internal margins straight; internal malae strongly narrowed toward apex, exceeding tips of corniculi. Setae *al1* and *al2* on palpgenu and *pl* on palpfemur dilated apically but not distinctly spatulate; dorsal setae on palpfemur finely serrate (Fig. 19c).

Legs I, III, IV not modified; leg I almost the same size as legs III and IV. Leg II stouter and weakly curved ventrally between femur and tarsus; femur with seta *av1* very stout, spinelike; genu and tibia with seta *av2* short, knoblike; tarsus with setae *av1–av3* and *pv1* spinelike, all equal in length (Fig. 20d). Tarsus of leg III with setae *av2* and *pv1* modified, knoblike. Coxa I with 1 internal and 2 external rows of denticles; coxae II–IV each with pronounced boss; coxa IV not modified. Leg setation as noted for genus.

Female. Dorsal shield 545–590 μm long, 280–306 μm wide (measured at level of setae *s3*; 10 specimens), completely divided into podonotal and opisthonotal shields (Fig. 20a). Reticulate ornamentation of dorsal shield more distinct than in males.

Dorsal shields with 31 pairs of setae, including 17 pairs on podonotal, and 14 pairs on opisthonotal shield; opisthonotal setae *S1* always missing; all setae smooth, except setae *Z5* (65–73 μm), which are usually finely serrated; setae of median part of dorsum (*j*'s, *z*'s, *J*'s, *Z*'s) shorter than lateral ones, but *j2* noticeably longer (50–54 μm), than *j3* (17–20 μm) and other *j*'s; setae *J5* very short (13–14 μm); all setae *r*'s and *R*'s on soft cuticle.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; anterior margin of shield forms 2 small lobes with distinct ornamentation. Fourth pair of sternal setae and 3rd pair of sternal pores on soft cuticle. Anterior hyaline part of genital shield strongly widened, its anterior margin broadly rounded, central region of shield constricted, then widened again behind genital setae; ornamentation of shield distinct. Metapodal plates small, usually elongate. Anal shield subquadrate, about as long as wide, or slightly wider than long, with distinct ornamentation; post-anal setae twice as long as para-anal setae. Ten or 11 posteroventral setae on soft cuticle around anal shield (Fig. 20b). Inseminating apparatus with long (180–220 μm), threadlike major duct and with small, rudimentary infundibulum (Fig. 20c); minor duct not discernible.

Tectum rounded, distinctly shorter and wider than that of male; fixed digit of chelicera unidentate, movable chela edentate; mucro not reaching apex of chela (Fig. 20e); corniculi more slender than in male, their inner margins straight.

Second leg not modified, without spine- or knoblike setae; some dorsal setae of trochanters, femora and genua of legs I–IV finely serrated.

Type Material. Ecuador: Cotopaxi National Park, 16 km SE Pan American Highway, elev. 3850 m, ex *Puya clava-hercules* Mez & Sodiro (Bromeliaceae), 11 Aug. 1976, R. K. Colwell—male (holotype), female (allotype), 19 males, 30 females (paratypes); Limpiopungo, SW slope, Cotopaxi Mt., ex *Puya* sp., 1976, R. K. Colwell), 7 Aug. 1974—34 males, 30 females (paratypes); Highlands, ex *Bomarea* sp. (Amaryllidaceae), 20-VI-79, F. Ortiz—7 males, 10 females (paratypes); 5 km W Baeza, ex cf. *Lobelia* sp. (Campanulaceae), 5 Feb. 1976, P. Feinsinger—1 male, 1 female (paratypes).

Etymology. The name, derived from the Greek *erion* (wool) and *xynon* (companion), refers to the characteristically long dorsal setae of the male. The name honors Peter Feinsinger, avian ecologist and indefatigable collector of hummingbird flower mites.

Remarks. *Tropicoseius erioxynon* n. sp. is most closely related to *T. fuentesi* n. sp. but is easily distinguishable by the absence of opisthonotal setae *S1* in both sexes, the unique shape of the spermatodactyl which bears a small, lobiform projection, and the presence of a small infundibulum in the female inseminating apparatus. The presence of the infundibulum represents either an independently derived feature of this species or is a retained, plesiomorphic condition shared with all species of the sister genus, *Rhinoseius*. However, the presence of an almost identical structure of the inseminating apparatus, with a small infundibulum and a long major duct in *R. tiptoni*, one of the most basal species of the sister genus, seems to support the latter alternative. The remaining species of *Rhinoseius* show a tendency toward a larger infundibulum and a shorter major duct.

Tropicoseius fuentesi, new species
(Figs. 21–22)

Diagnosis. Dorsal shield of both sexes completely divided into podonotal and opisthonotal dorsal shields; reticulate ornamentation of dorsal shield of male obliterated in its medial part; reticulation in female more distinct. Dorsal setae of male very long, flagelliform, that of female very short (about half as long as distance between adjacent setal insertions), except for distinctly longer and finely serrated setae *Z5*. Leg II in male with finely serrated setae *pd1* and *ad1* on femur, *pd1* and *al2* on genu and *pd2* on tibia. Fourth coxa in both sexes with rudimentary posterior spur. Spermatodactyl long and slender, usually bent in half; inseminating apparatus of female without maturation pouch. Peritrema in both sexes reaching level of setae *s1* or somewhat past it.

Male. Dorsal shield 534–600 μm long, 288–330 μm wide (measured at level of setae *s3*; 5 specimens), completely divided into 2, podonotal and opisthonotal, shields (depending on the condition of the mounted specimen shields may be separated by a distinct gap, touching or overlapping); reticulation more distinct in anterior and lateral regions of podonotal shield, absent on opisthonotal shield (Fig. 21a).

Dorsal shields with 33–34 pairs of smooth, long, flagelliform setae, including 18 pairs on podonotal and 15–16 pairs on opisthonotal shields; marginal setae *r3–r6, R1–R6* and *UR*'s on soft cuticle, 1 or both setae *R3* sometimes on opisthonotal dorsal shield. Dorsal setae very long: *j2* 75–84 μm, *j3* 93 μm, *j4* 48–76, *j5* 68–71 μm, *z2* 105–109 μm, *z4* 102–105 μm, *s1* 65–68 μm, *s2* 62–71 μm, *J1* 105–121 μm, *J2* 81–96 μm, *Z5* 180–186 μm; setae *j1* and *z1* short, respectively 22–31 μm and 31 μm; setae *J5* the shortest of all dorsal setae: 8–9 μm.

Tritosternum with broadly trapezoidal base and long, slender, pilose laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; reticulate ornamentation distinct over entire shield. Paragenital setae absent. Metapodal plates large, irregular in shape. Ventrianal shield elongate, weakly narrowing toward hind margin, or lateral margins of shield almost parallel; shield with setae *Jv1–Jv3, Zv1, Zv2,* para-anal, and postanal setae; setae *Jv3* sometimes on soft cuticle; reticulation of ventrianal shield distinct. All ventral setae, except sternal and para-anal setae, very long and flagelliform (Fig. 21b). Peritrema extending anteriad to level of seta *s1* or somewhat past it, but not reaching seta *z1*.

Gnathosoma with tectum rounded apically and steeply sided laterally, with smooth margins (Fig. 21c). Fixed digit of chelicera unidentate; movable chela edentate, with long, slender spermatodactyl, usually bent at about the midpoint of its length (Fig. 22e). Deutosternum with 7 transverse rows of denticles; all rows connected, some rows somewhat widened. Rostral setae simple, slender; anterior rostral setae of about same length as posterior interior pairs (37–40 μm), posterior exterior pairs somewhat shorter; capitular setae slender, simple. Corniculi with internal margins straight or weakly converging; internal malae strongly narrowed toward apex, exceeding tips of corniculi. Setae *al1* and *al2* on palpgenu and *pl* on palpfemur dilated apically but not distinctly spatulate (Fig. 22d).

Leg II stout and weakly curved ventrally between femur and tarsus; femur with seta *av1* very stout, spinelike; genu and tibia with seta *av* short, knoblike; tarsus with setae *av1–av3* and *pv1* spinelike, almost equal in length (Fig. 21d). Tarsus of leg III with setae *av2* and *pv1* modified, knoblike. Setae *ad1, pd1* of femur II, *al2* and *pd2* of genu II, and *pd2* of tibia II finely serrated. Coxa I with 1 internal and 2 external rows of denticles; coxae II–IV with pronounced boss; coxa IV with rudimentary posterior spur, sometimes hardly discernible. Leg setation as noted for genus.

Female. Dorsal shield 482–546 μm long, 270–300 μm wide (measured at level of setae*s3*; 10 specimens), completely divided into podonotal and opisthonotal shields (Fig. 22a). Reticulate ornamentation of dorsal shield more distinct than in males. Dorsal shield with 32 pairs of setae, including 17 pairs on podonotal and 15 pairs on opisthonotal shields; setae smooth and simple, except finely serrate setae *Z5*; all setae short, subequal in length, except setae *J5* distinctly shorter, and setae *Z5* at least twice as long as most of dorsal setae; *r2–r6* and *R*'s on soft cuticle.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; anterior margin of shield forms 2 small lobes with distinct ornamentation. Fourth pair of sternal setae and 3rd pair of sternal pores on soft cuticle. Anterior part of genital shield strongly widened, its anterior margin narrowly rounded, central region of shield constricted, then widened again behind genital setae; ornamentation of shield weak. Metapodal plates small, usually elongate but often roughly circular in outline. Anal shield subquadrate, about as long as wide, with distinct ornamentation; postanal setae twice as long as para-anal setae. Nine or 10 posteroventral setae on soft cuticle around anal shield (Fig. 22b). Inseminating apparatus long (110–150 μm), threadlike, without a maturation pouch; minor duct not discernible (Fig. 22c).

Tectum rounded, shorter and wider than that of male; fixed digit of chelicera unidentate, movable chela edentate; mucro not reaching apex of chela (Fig. 22f). Corniculi more slender than in male; their inner margins parallel.

Second leg and tarsus III not modified, without spine- or knoblike setae; as in male some setae of trochanters, femora and genua of legs I–IV finely serrated.

Type Material. Chile: Region V, 6 km S of Papudo, ex *Lobelia salicifolia* Sweet (Campanulaceae), 17-IX-72, R. K. Colwell—1 male (holotype), 1 female (allotype), 3 males, 6 females (paratypes); Region IV, 10 km SSE of El Tofo, ex *Lobelia salicifolia,* 17-IX-72, R. K. Colwell—5 males and 16 females (paratypes); Los Molles, ex *Puya violacea* Mez (Bromeliaceae), 29-XI-72, E. Fuentes—2 females (paratypes); La Portada, Juan Soldado, ex *Patagona gigas gigas* (Vieillot) (Trochilidae), 8-X-73, R. K. Colwell—10 females (paratypes).

Etymology. Named in honor of Eduardo Fuentes (Universidad Católico de Chile), Chilean ecologist and an early collector of this species.

Remarks. *Tropicoseius fuentesi* n. sp. is most closely related to *T. erioxynon* n. sp., sharing completely divided dorsal shields in both sexes, an elongated spermatodactyl and serrated setae *Z5* in females. It differs in the structure of the spermatodactyl, which lacks the lobiform projection present in *T. erioxynon*; the presence of serrated setae on leg II in the male; and in the presence of opisthonotal setae *S1,* which are absent in *T. erioxynon.* Only heteromorphic males of this species are known, with most opisthosomal setae in the male long and flagelliform.

Tropicoseius braziliensis Baker & Yunker, 1964
(Fig. 2f)

Tropicoseius braziliensis: Baker and Yunker 1964: 107, figs. 88–95 (female; type locality: Brazil, at Miami quarantine, Florida).

Rhinoseius braziliensis: Fain, Hyland, and Aitken 1977b: 113, 119, 121, 137, figs. 21, 39.–Fletchmann and Johnston 1978: 165, figs. 1–6, male.–Fain 1992: 117, 119–121, 123, 128, 134, figs. 2, 39.–Wiese and Fain 1993: 89.

Type Material. Brazil: (at Miami quarantine, Florida, USA), ex "bromeliad plant," 1-VII-59, A. S. Mills—1 female (holotype)(USDA).

Material Examined. Brazil: Cruz das Almas, Bahia, ex *Ananas* sp. (Bromeliaceae), 1970, C.H.W. Fletchmann—3 males, 6 females (USPZ).

Remarks. *Tropicoseius braziliensis* Baker & Yunker is closely related to *T. phoreticus* (Fain, Hyland & Aitken), sharing greatly enlarged setae *av2* on tarsi II in males (twice as large as *av3*), a character state typical of species of the group *chiriquensis,* but most likely independently derived in the group *braziliensis.* Females of the 2 species have marginal setae of series *r* and *R* on small platelets. Synapomorphies shared with *T. erioxynon, T.fuentesi,* and *T.phoreticus* include barbed setae on the palpfemur, trochanter, and femur of leg I in both sexes. *T. uniformis* also has barbed setae on leg I, but all palpal setae are smooth.

Tropicoseius phoreticus (Fain, Hyland & Aitken, 1977), new combination

(Fig. 2g)

Rhinoseius phoreticus Fain, Hyland, and Aitken 1977a: 186 (female; type locality: Trinidad, Tumpuna Rd).–Fain, Hyland, and Aitken 1977b: 119, 121, 137, 143–145, figs. 22, 41, 64, 110–111.–Fain 1992: 119, 123, 128, 132, figs. 3, 41.–OConnor, Colwell, and Naeem, 1997: 11–15, figs. 28–37 (male).–Farrier and Hennessey 1993: 48.

Material Examined. Trinidad: Arima Valley, 16 km N. Arima, Andrews Trace, ex *Pitcairnia integrifolia* Ker. (Bromeliaceae), 1-VIII-75, R. K. Colwell—1 male, 1 female; same locality, ex bromeliad, 11-VIII-75, R. K. Colwell—1 female; same locality, ex *Chlorestes notatus notatus* (C. Reichenbach) (Trochilidae), 2-VIII-75, R. K. Colwell—1 female; Arima Valley, Simla Ridge, ex *Glaucis hirsuta insularum* Hellmeyr & Seilern (Trochilidae), 4-III-79—1 male, 1 female; Maracas Bay, ex *Pitcairnia integrifolia* Ker., 29-VIII-80, D. S. Dobkin—2 males, 3 females; **Brazil:** São Paulo, Ilha de Cardoso, ex bromeliad,-IV-88, R. K. Colwell and W. W. Benson—3 males, 2 females.

Remarks. This species is closely related to *T. braziliensis* but is easily distinguished by the unique long, spirally coiled spermatodactyl in males of *T. phoreticus.* This species is redescribed by OConnor, Colwell and Naeem (1995).

Group *wetmorei*

Species in this group share the following synapomorphic character states: (1) capitular setae in male very short, at most half as long as the anterior rostral setae (capitular setae longer or only slightly shorter than the anterior rostral setae in other species of the genus); (2) seta *av1* on femur I in male modified, knoblike; (3) seta *pv* on coxae II in male enlarged, at least 3 times as thick and long as *av.* Moreover, females of all species in the group, bar 1, possess a characteristic maturation pouch in their inseminating apparatus. Males have relatively simple spermatodactyls, usually shorter than the 2nd article of the chelicera, straight or only weakly sinuous, without a stylus. Chelicerae of females have a uni-, rarely bidentate, fixed digit and usually a long mucro, reaching or surpassing the apex of the movable chela.

Tropicoseius erro Baker & Yunker, 1964

(Fig. 2 i and o)

Tropicoseius erro: Baker and Yunker 1964: 108, figs. 109–115, male and female; type locality: Mexico, at Texas quarantine.

Rhinoseius erro: Fain, Hyland, and Aitken 1977b: 119, 123, 137, figs. 25, 49, 68.–Fain 1992: 119–121, 123, 128, 135, fig. 6, 49.–Farrier and Hennessey 1993: 48.

Material Examined. Costa Rica: Heredia Province, La Selva Biological Station, Loop Trail (CCC-CCL), ex *Heliconia sarapiquensis* Daniels & Stiles (Heliconiaceae), 10-IX-80, R. K. Colwell—1 male, 3 females; La Selva Biological Station, SAT 1500 m, ex *Psychotria poeppigiana* Mueller Argoviensis (Rubiaceae), 8-I-89, R. K. Colwell—1 male, 7 females; La Selva Biological Station, CCC 900, ex *Psychotria elata* Sw., 6-I-89, R. K. Colwell—7 females; La Selva Biological Station, Holdridge Trail, ex *Psychotria* sp., 26-VIII-80, R. K. Colwell—3 males, 3 females; La Selva Biological Station, Lindero Occidental, ex *Psychotria* sp., 27-III-71, R. K. Colwell—5 males; La Selva Biological Station, SR 800–1000, ex *Costus scaber* (Costaceae), 28-V-89, R. K. Colwell—1 male, 9 females; La Selva Biological Station, Loop Trail (CCC-CCL), ex *Costus* sp., 10-IX-80, R. K. Colwell—2 females; Parque Nacional Braulio Carrillo, km 26 of Sendero Principal, ex *Psychotria* sp.—1 male, 10 females; Guanacaste Province, Estación Pitilla, ex ?Marantaceae, 1-I-91, C. Moraga—14 males, 21 females; same locality and date, ex ?Bromeliaceae, C. Moraga—1 female; same locality and date, host unknown, C. Moraga—2 females; Estación Pitilla, ex *Costus* sp., 1-I-91, P. Rios—1 male, 1 female; **Colombia:** Antiguia, ex *Phaethornis syrmatophorus* Gould (Trochilidae), 4–23-IV-71, R. B. Waide—1 female.

Remarks. This distinctive species is easily recognized by the features of the female inseminating apparatus, which lacks a maturation pouch in the major duct (Fig. 2o). This is probably the ancestral condition because a similar structure of the apparatus can be observed in more basal species of *Tropicoseius* and most other Melicharini. Chelicerae of the female show a condition intermediate between more basal and more derived species. The

mucro of the movable chela is short, not reaching its apex, a condition typically observed in more basal species, but the fixed digit is unidentate, a condition characteristic for more derived species of the genus (Fig. 2i). Males have a relatively simple, short spermatodactyl and leg chaetotaxy not different from that of the remaining species of the group *wetmorei*.

Tropicoseius eisenmanni Baker & Yunker, 1964

Tropicoseius eisenmanni: Baker and Yunker 1964: 108, figs. 116–130 (male and female; type locality: Panama, Bocas del Toro).–Dusbabek and Cerny 1970: 269.

Rhinoseius eisenmanni: Fain, Hyland, and Aitken 1977b: 120, 123, figs. 15, 45, 73.–Fain 1992: 119, 121, 123, 130, 134, figs. 23, 45.–Farrier and Hennessey 1993: 48.

Remarks. We did not have an opportunity to study the types or any other specimens of this species. However, judging from the original description (Baker and Yunker 1964) and supplementary figures in Fain et al. (1977b), *T. eisenmanni* seems to be most closely related to *T. erro* Baker & Yunker, with which it shares a similar arrangement of opisthoventral setae and the form of the spermatodactyl in the male. The female inseminating apparatus has only a poorly developed, narrow maturation pouch (females of *T.erro* completely lack the maturation pouch). *T. eisenmanni* was originally collected from a hummingbird *Phaethornis guy*. There are no host plant records for this species, but it is likely that *T. eisenmanni* is associated with plants of the families Heliconiaceae or Costaceae.

Tropicoseius wetmorei Baker & Yunker, 1964
(Fig. 2n)

Tropicoseius wetmorei Baker and Yunker 1964: 106, figs. 47–61 (male and female; type locality: Panama, Cerro Punta).

Rhinoseius wetmorei: Lindquist and Evans 1965: 52, fig. 42.–Fain, Hyland, and Aitken 1977b: 109, 120, 121, 137, figs. 14, 43, 66.–Colwell 1979b: 464.–Fain and Hyland 1980: 15.–Ohmer, Fain, and Schuchmann 1991: 484.–Fain 1992: 119, 121, 123, 130, 135, figs. 17, 38.– and Hennessey 1993: 48.

Material Examined. Panama: Chiriquí Province, below Cerro Punta, ex *Heliconia nutans* Woodson (Heliconiaceae), 6-VI-79, W. J. Kress, 79–1089—7 males, 4 females; same locality and date, ex *Heliconia lankesteri-rubra* Daniels & Stiles, W. J. Kress, 70–1090—4 males, 3 females; La Fortuna, Dam Site, ex *Heliconia nutans* Woodson, 13-III-82, W. J. Kress, 82–1355—2 females; Cerro Pate Macho, ex *Heliconia lankesteri-rubra* Daniels & Stiles, 15-III-82, W. J. Kress, 82–1370—10 males, 8 females; **Costa Rica:** San Jose Province, San Isidro del General, ex *Heliconia beckneri* R. R. Smith, 11-VII-76, W. J. Kress, 76–0556—1 female; Heredia Province, Finca La Selva, Sarapiquí, ex *Heliconia imbricata* (Kuntze) Baker, 31-VII-79, W. J. Kress, 79–1101—19 females; La Selva Biological Station, Sendero La Chanchera, ex *Heliconia latispatha* Bentham,-VIII-89, R. K. Colwell—1 female; La Selva Biological Station, SOC 250 & 700, ex *Renealmia cernua* (Swatz ex Roemer & Schultes) Macbride (Zingiberaceae), 26-V-89, R. K. Colwell—3 females; La Selva Biological Station, SAT 1500 m, ex *Psychotria poeppigiana* Mueller Argoviensis (Rubiaceae),-*VIII*-89, R. K. Colwell—1 male, 2 females; La Selva Biological Station, SOC near SLV, ex *Bomarea obovata* (Amaryllidaceae), 26-V-89, R. K. Colwell—3 females; Zona Protectora La Selva (Parque Nacional Braulio Carrillo), elev. 1500 m, ex *Heliconia* sp., 11-IV-86, R. Colwell—1 male, 3 females; Zona Protectora La Selva (Parque Nacional Braulio Carrillo), elev. 2050 m, ex *Heliconia* sp., 13-IV-86, R. Colwell—1 female; Alajuela Province, San Ramon, La Balsa road, ex *Heliconia irrasa* X *imbricata* (Kuntze) Baker, 17-VII-76, W. J. Kress—5 males, 2 females; same locality, ex *Heliconia tortuosa* Griggs, 15-VII-76, W. J. Kress, 76–0599—1 male; Monteverde, Sendero Nuboso, ex *Heliconia tortuosa* Griggs, 28-VI-80, P. Feinsinger—4 males, 2 females; Monteverde, Divide (Brillante), ex *Heliconia* sp., 22-VIII-72, P. Feinsinger—6 males, 4 females; Monteverde, behind Peter Feinsinger's home, ex *Heliconia* sp., 15-III-73, P. Feinsinger—2 females; Monteverde, 24-V-72, G. Powell—12 females; Monteverde, ex *Campylopterus hemileucurus mellitus* Bangs (Trochilidae), 25-IX-72, P. Feinsinger—8 females; Monteverde, ex *Campylopterus hemileucurus mellitus* Bangs, 15-X-72, P. Feinsinger—1 female; Monteverde, ex *Campylopterus hemileucurus mellitus* Bangs, 15-XI-72, P. Feinsinger—1 female; Guanacaste Province, Estación Cacao, ex *Heliconia* sp., 1-I-90, C. Chavez—8 females; Estación Pitilla, ex ?Bromeliaceae, 1-I-91, C. Moraga—1 female; Limon Province, Tortuguero Nat. Park, ex *Heliconia* sp., 1-I-91, J. Solano—18 males, 56 females; same locality, ex ?Acanthaceae—2 males, 4 females; Hitoy Cerere, ex *Heliconia* sp., G. Caballo—14 males, 15 females; **Ecuador:** Zamora Chinchipe, Vilcabamba-Valladolid road, 1 km from Valladolid, elev. 1700 m, ex *Heliconia dielsiana* Loesener, 19-X-89, W. J. Kress, 89–2900—1 male.

Remarks. *Tropicoseius wetmorei* Baker & Yunker is the type species of the genus *Tropicoseius*. It can be easily recognized by the large, bulbous maturation pouch (Fig. 2n), which is possibly homologous with distal parts of the elongate maturation pouches in such species as *T. heliconiae* or *T. bisacculatus*. A structurally similar inseminating apparatus is present in *T. erro*, but the bulbous part is relatively smaller, and in many specimens of that species the part of the major duct below the pouch is slightly dilated. Males have simple, almost straight spermatodactyls.

Tropicoseius bisacculatus (Fain, Hyland & Aitken, 1977), **new combination**
(Fig. 2m)

Rhinoseius bisacculatus Fain, Hyland, and Aitken 1977a: 185 (female; type locality: Brazil, Belem).–Fain, Hyland, and Aitken 1977b: 119, 121, 138, figs. 9, 42,

71, 104, 105.–Colwell 1986a: 487, 491.–Colwell 1986b: 408, 411, 418, 419, 421.–Fain 1992: 119, 123, 129, 132, figs. 15, 37.–Farrier and Hennessey 1993: 47.–OConnor, Colwell, and Naeem 1997: 10–11, figs.18–23 (male).

Material Examined. Tobago (West Indies): Sites A-B, ex *Costus spiralis* (Jacquin) Roscoe (Costaceae), 30-IV-77, P. Feinsinger—6 males, 7 females; **Trinidad:** Arima Valley, 4.4 km E of Cooker Trace, exit on La Laja, ex *Costus scaber,* 7-III-87—2 males, 2 females; Arima Valley, 5 km N. Arima, ridge trail above Simla Research Station, ex *Costus scaber,* 12 Aug. 1975, R. K. Colwell—1 male, 1 female; **Ecuador:** Napo, new road from Cotundo to Coca off Baeza-Tena Rd., 68 km, ex *Heliconia chartacea* Lane ex Barreiros (Heliconiaceae), 27-II-88, W. J. Kress, 88–2364—1 male, 1 female.

Remarks. This species, recently redescribed by OConnor et al. (1997), is most closely related to *T. ochoai* n. sp. Females of the 2 species share a unique structure of the maturation pouch, possibly the most derived within *Tropicoseius.* The pouch is divided into 2 smaller, elongated pouches (Fig. 2m). The proximal pouch is almost certainly a simple dilation of the major duct, but whether the distal pouch is homologous with the atrium of the phytoseiid type of inseminating apparatus (and therefore with maturation pouches in other *Tropicoseius* spp.) is a matter of speculation. The bulbous dilation at the apex of the distal pouch is probably homologous with the pouches in *T. wetmorei* and *T. erro.* Males of *T. bisacculatus* differ from those of *T. ochoai* in having practically all body setae greatly shortened, almost minute, whereas in *T. ochoai* the only shortened setae are those around the ventrianal shield. Also, the legs of *T. bisacculatus* are distinctly more slender and leg setae are always shorter than the width of their respective articles. In *T. ochoai,* the legs are stouter and their setae are long, usually considerably longer than the width of their respective articles.

Judging from the very widely scattered records of *T. bisacculatus* (Belem, Brazil; Napo, Ecuador; Trinidad; Tobago) it seems possible that the species may be distributed broadly in the Amazonian lowlands. See Colwell (1986b) for a historical treatment of the occurrence of this species in Trinidad.

Tropicoseius ochoai, new species
(Fig. 23)

Diagnosis. Dorsal shield of both sexes with narrow lateral incisions, transverse suture sometimes absent; reticulate ornamentation of shield present only on anterolateral regions of shield. Setae of series *s, r, S,* and *R* of male dorsum distinctly longer than setae of series *j, z, J,* and *Z*; ventral setae about male ventrianal shield minute, setae *Zv2* either on shield or soft cuticle; dorsal and lateral setae of female short (about half as long as distance between adjacent setal insertions), subequal. Leg II of male moderately enlarged, weakly curved between tibia and femur; seta *av1* of femur, genu, and tibia knoblike; seta *pv1* on femur thickened, almost spinelike; tarsus III with setae *pv1* and *av2* knoblike. Spermatodactyl short, simple, weakly sinuous; inseminating apparatus of female with 2 distinct (proximal and distal) elongate maturation pouches.

Male. Dorsal shield 480–510 μm long, 282–312 μm wide (measured at level of setae *s4*; 6 specimens), with narrow lateral incisions sometimes connected by a transverse suture; reticulation weak, restricted mainly to antero-lateral regions of shield (Fig. 23a). Dorsal shield with 39–40 pairs of smooth, simple setae, including 20–21 pairs on podonotal and 18–19 pairs on opisthonotal regions; marginal seta *r6* absent; setae of *r* and *R* series on shield, seta *R4* usually on shield but sometimes on soft cuticle. Lateral setae of dorsum generally longer than median pairs: *s3* 55–76 μm, *s4* 54–74 μm, *r2* 45–75 μm, *r3* 40–47 μm, *S1* 50–61 μm, *S2* 53–66 μm, *R1* 61–71 μm, *R2* 60–68 μm, compared with *j2* 13–22 μm, *j3* 19–22 μm, *z2* 25–29 μm, *z4* 26–35 μm, *J1* 19–23 μm, *J2* 16–18 μm; the shortest setae of dorsal shield: *j1* 4–8 μm, *z1* 5–12 μm and *J5* 7–11 μm; the longest: *Z5* 112–133 μm.

Tritosternum with broad, trapezoidal base and slender pilose laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; no reticula discernible on shield. Paragenital setae usually absent but in 1 specimen 1 seta present. Metapodal plates small, elongate. Ventrianal shield narrow, elongately trapezoidal, with setae *Jv1–Jv3, Zv1, Zv2,* para-anal, and postanal setae; seta *Zv2* sometimes on soft cuticle; shield smooth, without ornamentation (Fig. 23b). Ventral setae around ventrianal shield very short (7–14 μm), except *Jv5* (53–72 μm). Peritrema extending anteriad to level of seta *z1*; peritrematic plates united posteriorly with exopodal plates.

Gnathosoma with tectum pointed at apex, its margins smooth. Fixed digit of chelicera unidentate; movable chela edentate, with short, slightly sinuous spermatodactyl, its apex not modified (Fig. 23d). Deutosternum with 7 rows of equally narrow denticles; all rows connected, no rows widened. Rostral setae slender, simple; anterior rostral pairs long (35 μm), posterior exterior pairs shorter than posterior interior pairs (6 μm and 17 μm, respectively); capitular setae simple, short (11 μm). Corniculi slender, with internal margins straight; internal malae very narrow, exceeding tips of corniculi. Setae *al1* and *al2* on palpgenu spatulate, *al* on palpfemur dilated apically (Fig. 23c).

Leg II moderately enlarged, slightly curved ventrally between femur and tarsus; femur, genu, and tibia with seta *av1* stout, knoblike, and seta *pv1* enlarged, almost spinelike; tarsus with setae *av1, av2, pv1,* and *pv2* modified, knoblike (Fig. 23i). Tarsus of leg III with setae *pv1* and *av2* stout, knoblike. Setae of genua and tibiae of legs II and IV long, some of them (*pd1* and *pd2*) twice as long as their respective articles. Coxa I with no

discernible denticles, coxae II–IV with posteriorly convex boss; coxa II with posterior seta large and stout. Leg setation formulas as noted for genus.

Female. Dorsal shield 456–506 μm long, 228–264 μm wide (measured at level of setae *s3*; 12 specimens), with lateral incisions between setae *s6* and *S1*, extending half way to midline of dorsal shield, usually not connected by transverse suture. Reticulate ornamentation poorly developed and absent along midline of shield (Fig. 23e). Dorsal shield with 32 pairs of short, simple setae, including 17 pairs on podonotal and 15 pairs on opisthonotal regions; all marginal setae *r*, *R* and *UR* on soft cuticle; all dorsal setae of similar length (e.g., *j2* 19–22 μm, *j3* 19 μm, *j4* 19–22 μm, *z2* 22–24 μm, *z4* 24–26 μm, except *s1* and *s2* distinctly shorter [9–11 μm]).

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; anterior margin of sternal shield forms 2 distinct lobes with weak ornamentation. Fourth pair of sternal setae and 3rd pair of sternal pores on soft cuticle behind posterior margin of sternal shield; rudimentary endopodal plates sometimes discernible. Anterior hyaline part of genital shield subtriangular, tapered apically; longitudinal ornamentation on posterior part of shield weak. Metapodal plates small, roughly triangular in shape. Anal shield elliptical, ≈1.5 times longer than wide, with poorly developed ornamentation; postanal seta about twice as long as para-anal setae. Ten or 11 posteroventral setae on soft cuticle around anal shield (Fig. 23f). Inseminating apparatus with 2 longitudinal maturation pouches (Fig. 23g), proximal one somewhat longer, with both ends evenly tapering; distal one with bulbous projection; the 2 pouches connected by a short (22–24 μm) section of major duct.

Tectum sharply pointed, shorter and broader than that of male. Fixed digit of chelicera bidentate, movable chela edentate; ventral mucro long, reaching or slightly surpassing apex of movable chela (Fig. 23h). Corniculi more slender than in male; their inner margins parallel.

Second leg not modified; setae of all legs very short but otherwise their arrangement as in male.

Type Material. Costa Rica: Puntarenas Province, Palmar Norte, ex *Heliconia colgantea* Daniels & Stiles (Heliconiaceae), 25-VIII-77, W. J. Kress, 77–0878—1 male (holotype), 1 female (allotype), 3 males and 3 females (paratypes); Osa Peninsula, 5 km NW Tropical Science Center Station, ex *Costus* sp. (Costaceae), 6-III-71, R. K. Colwell—3 males, 13 females (paratypes).

Etymology. This new species is named in honor of Ronald Ochoa (Brigham Young University, Provo, UT), Costa Rican acarologist and valued colleague and friend, who contributed in many ways to the completion of this study.

Remarks. This species is most closely related to *Tropicoseius bisacculatus* (Fain, Hyland & Aitken). Females of the 2 species share a unique structure of the inseminating apparatus, with 2 elongate maturation pouches, of which the proximal one is probably a simple dilation of the major duct, whereas the distal one is possibly homologous to atrium of the phytoseiid type of inseminating apparatus. Males of these 2 species are similar in the structure of the spermatodactyls and share shortened setae around the ventrianal shield. However, the male of *T. ochoai* n. sp. differs in having setae *Jv1–Jv3*, *Jv5*, *Zv1*, and *Zv2* very long. Moreover, *T. ochoai* has normally developed dorsal setae, whereas dorsal setae are all distinctly shortened, almost minute, in *T. bisacculatus*. The 2nd leg of the male of the new species is somewhat stouter than in *T. bisacculatus*, with dorsal setae of the femur, genu, and tibia very long, almost twice as long as width of their respective articles. Females usually have the dorsal suture less distinct than females of *T. bisacculatus*.

Tropicoseius fidelis (OConnor, Colwell & Naeem, 1996), new combination

Rhinoseius fidelis: Colwell 1986b: 408, 409 (nomen nudum).–OConnor, Colwell, and Naeem 1997: 23–27, figs. 58–67 (male and female; type locality: Trinidad, Arima Valley).

Type Material. Trinidad: Arima Valley, 12.8 km N. Arima, La Laja Plantation, ex *Costus arabicus* Linnaeus (Costaceae), 20-VIII-80, D. S. Dobkin—1 female (holotype)(UMMZ); Arima Valley, Blanchisuesse Rd., ex *Costus arabicus* Linnaeus, 23-II-80, R. K. Colwell—1 male (paratype).

Material Examined. Trinidad: Arima Valley, Textel Rd., ex *Costus arabicus* Linnaeus, 7-III-80, R. K. Colwell—1 female; Arima Valley, 100 m down from exit to Cooker Trace, La Laja, ex *Costus arabicus* Linnaeus, 8-III-80, R. K. Colwell—2 males, 1 female; Arima Valley, La Laja Plantation, ex *Costus arabicus* Linnaeus, 20-VIII-80, D. S. Dobkin—1 male, 1 female; Arima Valley, Asa Wright Nature Centre entrance, Blanchisuesse Rd., ex *Costus arabicus* Linnaeus, 14-III-79, R. K. Colwell and S. Naeem—6 males, 17 females; Arima Valley, La Laja Trace, ex *Costus* sp., 8-VIII-75, R. K. Colwell—4 females; Arima Valley, Blanchisuesse Rd., ex *Costus* sp., 23-II-76, R. K. Colwell—1 male; **Brazil:** São Paulo, Ilha de Cardoso, ex *Costus* sp.,-IV-88, R. K. Colwell and W. W. Benson—27 males, 33 females.

Remarks. This recently described species seems to be very closely related to *T. heliconiae* Baker & Yunker. It differs in the larger body size in both sexes and longer opisthosomal and leg setae. The legs in males of *T. fidelis* are generally stouter and their setae are always longer than the width of their respective articles. Also, setae *Jv3* in the male are always on the ventrianal shield, whereas in *T. heliconiae* they are often on soft cuticle.

These 2 species occur sympatrically on Trinidad and possibly in Brazil, but differ significantly in their host preferences. *T. fidelis* lives primarily

in flowers of species of the genus *Costus* (Costaceae), whereas *T. heliconiae* has been collected almost exclusively from flowers of *Heliconia* spp.

Tropicoseius heliconiae Baker & Yunker, 1964
(Figs. 1a, 2l)

Tropicoseius heliconiae: Baker and Yunker 1964: 107, figs. 75–87 (male and female; type locality: unknown [New York quarantine]).

Rhinoseius heliconiae: Fain, Hyland, and Aitken 1977b: 118, 123, 137, figs. 12, 50, 67.–Hyland, Fain, and Moorhouse 1978: 260, 264, 267.–Ohmer, Fain, and Schuchmann 1991: 481.–Fain 1992: 119, 123, 128, 134, fig. 24, 50.–Farrier and Hennessey 1993: 48.

Rhinoseius phaethornis: Fain, Hyland, and Aitken 1977a: 186 (female; type locality: Brazil, Marituba)—**n. syn.**–Fain, Hyland, and Aitken 1977b: 120, 123, 137, 140, 145–149, figs. 11, 47, 72, 112–117, male and female.–Fain 1992: 119, 123, 129, 134, figs. 25, 47.–Farrier and Hennessey 1993: 48.–OConnor, Colwell, and Naeem 1997: 16–20, figs. 34–43.

Rhinoseius mathewsoni: Hyland, Fain, and Moorhouse 1978: 260, 264–267, figs. 9–13 (male and female; type locality: Mexico, Veracruz)- **n. syn.**–Ohmer, Fain, and Schuchmann 1991: 481, 482.–Fain 1992: 119, 123, 129, 134, fig. 54.–Farrier and Hennessey 1993: 48.–OConnor, Colwell, and Naeem 1997: 27.

Rhinoseius spinosus (nomen nudum): Colwell 1986b: 408.

Type Material. ex *Heliconia* sp. (Heliconiaceae) cuttings, origin unknown, at New York quarantine, 7-IX-60, L. Walden & N. Kitazaki—1 female (holotype), 1 male & 1 female (paratypes) (NMNH).

Material Examined. Brazil: Para, Mosquiero Ferry, ex *Phaethornis superciliosus* (Linné) (Trochilidae), 7-II-69, T.H.G. Aitken—2 females (paratypes of *Rhinoseius phaethornis* Fain, Hyland and Aitken); Rio de Janeiro, off highway between Rio de Janeiro and Sao Paulo, 70 km from Rio, 5 km on estrada Passa Tres-Angra dos Reis, elev. 400 m, ex *Heliconia velloziana* L. Emygdio, 31-I-90, W. J. Kress & L. Emygdio, 90–2958—1 female; **Venezuela:** T. F. Amazonas, between Maroa & airstrip, ex *Guacamaya superba* Maguire (Rapateaceae), 1-VII-91, P. Berry, 91–1—3 females; Estado Amazonas, Tobogán de la Selva, elev. 100 m, 35 km SE Puerto Ayacucho, ex *Kunhardtia radiata* Maguire & Steyermark (Rapateaceae), 26-VI-91, P. Berry, 5292—14 males, 40 females; **Trinidad:** Ravine Sable Trace, Vega del Oropóuche, ex *Phaethornis longuemareus* (Lesson), 8-XII-59, T. H. G. Aitken—1 male, 1 female (paratypes of *Rhinoseius phaethornis* Fain, Hyland and Aitken); Arima Valley, Cricket Pitch, Temple Village, ex *Heliconia psittacorum* L. f., 6-III-79, D. S. Dobkin—1 female; Arima Valley, Simla Field Station, ex (Bromeliaceae), 15-III-79—26 males, 27 females; Arima Valley, Simla Trail just behind lab, ex *Glaucis hirsuta insularum* Hellmeyr & Seilern (Trochilidae), 18-II-76, R. K. Colwell—2 females; Waller Field, ex *Heliconia psittacorum* L. f., 8-III-80, D. S. Dobkin—2 males, 2 females; Waller Field, near main rd., ex *Heliconia psittacorum* L. f., 11-III-80, R. K. Colwell—3 males; Arena Forest Reserve, ex *Heliconia psittacorum* L. f., 13-III-87, R. K. Colwell—3 females; milepost 20, Blanchisuesse Rd., ex *Heliconia psittacorum* L. f., 13-III-79, R. K. Colwell—1 female; **Tobago (West Indies):** near plot C, ex unidentified bromeliad, 30-IV-77, P. Feinsinger—3 males, 3 females; Ferry Hill, ex *Bromelia* sp. (yellow-green flowers),-III-79, R. K. Colwell—1 male, 7 females; **French Guiana:** road D21, W Sinnamary, 15 km from turn off, ex *Heliconia richardiana* Miquel, 6-XI-86, W. J. Kress, 86–2087—16 males, 8 females; Highway N 2 between Cayenne and Regina, elev. ca 125 m, ex *Heliconia acuminata* L. C. Richard, 8-X-86, W. J. Kress, 86–2100—1 male, 5 females; **Guyana:** Berbice, New Forest along Ganje River, ex *Heliconia nickeriensis*, 30-III-86, W. J. Kress, 86–1815—1 male, 6 females; **Ecuador:** Napo, new road from Cotundo to Coca off of Baeza-Tena Rd., 68 km from turnoff, ex *Heliconia chartacea* Lane ex Barreiros, 27-II-88, W. J. Kress, 88–2364—1 male; **Mexico:** Veracruz, ex *Amazilia candida* (Meise) (Trochilidae), 17-VIII-63, R. Dickerman—1 female (paratype of *Rhinoseius mathewsoni* Hyland, Fain and Moorhouse); Los Tuxtlas Biological Station, ex *Costus* sp. (Costaceae),-VI-85, R. K. Colwell—2 males; **Costa Rica:** San Jose Province, Carara, Estación Carara, ex *Heliconia* sp., 27-II-90, R. Zunica—4 males, 5 females; Heredia Province, Finca La Selva, successional plots, ex *Heliconia latispatha* Bentham, 30-VIII-80, R. K. Colwell—3 males, 5 females; Finca La Selva, ex *Heliconia sarapiquensis* Daniels & Stiles, 13-IX-80, R. K. Colwell—8 males, 3 females; La Selva Biological Station, SCH at pigsty, 26-V-89, R. K. Colwell—1 female; Puntarenas Province, Osa Peninsula, Rio Aguabuena, ex *Heliconia latispatha* Bentham, 10-II-71, R. K. Colwell—2 males, 4 females; Osa Peninsula, 1 km W. Tropical Science Center Station, ex *Phaethornis superciliosus cephalus* (Bourcier & Mulsant), 7-III-71, R. K. Colwell—1 female; Corcovado National Park, Sirena, ex *Heliconia* sp., G. Fonseca—1 male, 2 females; same locality and host, J. Saberio—5 males, 3 females; Alajuela Province, Monteverde, plot C-6, ex *Amazilia saucerottei hoffmanni* (Cabanis & Heine), 16-X-72, P. Feinsinger—7 females; same locality, ex *Campylopterus hemileucurus mellitus* Bangs (Trochilidae), 25-IX-72, P. Feinsinger—1 female.

Remarks. *Tropicoseius heliconiae* is a widely distributed species, with much intraspecific variation in the length of dorsal and opisthoventral setae, presence of opisthonotal setae *J5* and *Z5*, and in the shape of the male ventrianal shield. Fainet al. (1977a) described *Rhinoseius phaethornis* as differing from *T. heliconiae* in the presence of setae *Z5*. A year later, Hyland et al. (1978) described *R. mathewsoni* and differentiated it from *T. heliconiae* and *R. phaethornis* by the reduced length of some opisthosomal setae in both males and females, poorly developed cuticular network on the dorsal shield in the female, and more oval shape of the female anal shield. After studying type specimens of all 3 species as well as many additional specimens from various hosts and localities, however, it is evident to us

that all forms are conspecific. The length of the opisthoventral setae and all opisthonotal setae *S* in males vary greatly, even among specimens from a single flower. Setae *Jv3* can be either on the ventrianal shield (diagnostic for *T. phaethornis*) or on soft cuticle (diagnostic for *T.heliconiae* and *T.mathewsoni*) in specimens from the same locality, and in some specimens 1 of the paired setae is on the shield whereas the other is on the soft cuticle. Setae *Z5*, the absence of which is supposed to be diagnostic for *T. heliconiae*, are more often present than absent, and there are numerous specimens in which only 1 of the 2 setae is missing (sometimes setae *J5* also are missing). There are localities, however, where individuals with a reduced number of setae are more common (e.g., La Selva Biological Station, Costa Rica). Also the ornamentation of the dorsal shield is subject to great intraspecific variation, as is the shape of the female anal shield. There are no discrete differences in the form of reproductive structures among specimens studied. Hyland et al. (1978) reported new records of *T. heliconiae* from Mexico and, not surprisingly, the specimens were collected from the very same host specimens as the type specimens of their *R. mathewsoni*. We consider *Rhinoseius phaethornis* Fain, Hyland and Aitken, 1977 and *Rhinoseius mathewsoni* Hyland, Fain & Moorhouse, 1978 to be junior synonyms of *Tropicoseius heliconiae* Baker & Yunker, 1964.

Tropicoseius bakeri Dusbabek & Cerny, 1970
(Fig. 24)

Tropicoseius bakeri: Dusbabek and Cerny 1970: 269–272, figs. 1–6; type locality: Cuba, Prov. of Oriente, near Baracoa, Sabanyia–Hunter 1972: 26, 34.
Rhinoseius bakeri: Fain, Hyland, and Aitken 1977b: 101, 121, 137, figs. 19, 46, 74.–Farrier and Hennessey 1993: 47.

Diagnosis. Dorsal shield of both sexes with narrow lateral incisions, transverse suture present but often not complete; reticulate ornamentation of shield best developed in anterolateral regions. Dorsal setae in both sexes comparatively very short, ⅓ to half as long as distance between adjacent setal insertions; ventral setae around male ventrianal shield minute, setae on shield distinctly longer; marginal setae of series *r* and *R* of female on small platelets. Leg II of male moderately enlarged, weakly curved between tibia and femur; seta *av1* of femur, genu and tibia knoblike; seta *pv1* on femur thickened, almost spinelike; tarsus III with setae *pv1* and *av2* knoblike. Both fixed and movable digits of male chelicera edentate; spermatodactyl short, with small subapical dilation and distinctly narrowed apex; inseminating apparatus of female with long, cylindrical maturation pouch with characteristically striated walls.

Male. Dorsal shield 430–465 μm long, 280–310 μm wide (measured at level of setae *s3*; 6 specimens), with narrow lateral incisions usually

connected by a distinct transverse suture; reticulate ornamentation often restricted mainly to antero-lateral regions of shield (Fig. 24a).

Dorsal shield with 37–38 pairs of smooth, simple setae, including 21 pairs on podonotal and 16–17 pairs on opisthonotal regions; marginal setae *r6* absent. Setae of dorsum smooth and simple, generally short (⅓ to half as long as distance between adjacent setal insertions): *j2* 18–20 μm, *j3* 22–26 μm, *z2* 22–26 μm, *z4* 25–30 μm, *J1* 21–24 μm, *J2* 22–26 μm, *s3* 20–22 μm, *s4* 22–26 μm, *r2* 25–28 μm, *r4* 40–48 μm, *S1* 25–29 μm, *S2* 33–38 μm, *R1* 40–45 μm, *R2* 55–60 μm; the shortest setae of dorsal shield: *j1* 8–10 μm, *z1* 12–14 μm and *J5* 10–12 μm; the longest: *Z5* 120–145 μm and *S5* 80–95 μm.

Tritosternum with broad, trapezoidal base and slender, pilose laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; no reticulate ornamentation on shield discernible. Paragenital setae absent. Metapodal plates small, irregular in outline. Ventrianal shield large, subtriangular, with setae *Jv1–Jv3*, *Zv1*, *Zv2* and para-anal and postanal setae; ornamentation present only in anterolateral regions of shield. Ventral setae around ventrianal shield very short (12–24 μm), setae on shield 3–4 times longer than setae on soft cuticle; *Jv5* longer than other setae on soft cuticle (82–90 μm) (Fig. 24b). Peritrema extending anteriad to level of seta *z1*; peritrematic plates not connected with exopodal plates.

Gnathosoma with tectum elongated and pointed apically, with smooth margins. Fixed digit of chelicera edentate; movable chela edentate; spermatodactyl directed anteriad, with small subapical dilation and distinctly narrowed apex (Fig. 24d). Deutosternum with 7 rows of equally narrow denticles; all rows connected, no rows widened. Rostral setae slender, simple; anterior rostral pairs long, posterior exterior pairs shorter than posterior interior pairs; capitular setae simple, short. Corniculi slender, with internal margins weakly incurved; internal malae very narrow, slightly surpassing tips of corniculi. Setae *al1* and *al2* on palpgenu spatulate, *al* on palpfemur dilated apically.

Second leg moderately enlarged, slightly curved ventrally between femur and tarsus; femur and genu with seta *av1* stout, knoblike, and seta *pv1* spinelike; tibia with *av1* knoblike but *pv1* only slightly thicker than remaining tibial setae; tarsus with setae *av1–av3* and *pv1* modified, knoblike (Fig. 24c). Tarsus of leg III with setae *pv1* and *av2* stout, knoblike. Coxa I with no denticles, coxae II–IV with posteriorly convex bosses; coxa II with posterior seta *pv* large and stout (40–42 μm). Setation of legs typical for genus; setae of genua and tibiae of legs II and IV comparatively short, the longest setae (*pd1* and *pd2*) at most as long as width of their respective articles.

Female. Dorsal shield 490–510 μm long, 300–315 μm wide (measured at level of setae *s3*; 12 specimens), with narrow lateral incisions between setae *s6* and *S1*, usually connected by transverse suture. Reticulate

ornamentation well-developed but somewhat less pronounced in middle part of podonotal region of shield (Fig. 24e). Dorsal shield with 33 pairs of short, simple setae, including 18 pairs on podonotal and 15 pairs on opisthonotal regions; marginal setae *r2* on shield, remaining *r*'s, *R* 's and *UR*'s on soft cuticle, but each seta on small chitinous platelet; all dorsal setae of similar length: *j2* 18–20 μm, *j3* 20 μm, *j4* 20–21 μm, *z2* 18–20 μm, *z4* 22–24 μm, *s1* 22–24 μm, *s2* 18–20 μm.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; anterior margin of sternal shield forms 2 distinct lobes with weak reticulate ornamentation. Fourth pair of sternal setae and 3rd pair of sternal pores on soft cuticle behind posterior margin of sternal shield. Anterior hyaline part of genital shield broadly triangularly rounded, widened; longitudinal ornamentation on posterior part of shield weak. Metapodal plates small, irregular in outline. Anal shield elliptical, ≈1.5 times longer than wide, with poorly developed reticulate ornamentation; postanal seta about twice as long as para-anal setae (Fig. 24f). Eight to 10 posteroventral setae on soft cuticle around anal shield. Inseminating apparatus with long, cylindrical maturation pouch (100–120 μm), with characteristically striated walls (Fig. 24g); atrium and calyx separated from pouch by short, narrow section of major duct.

Tectum sharply pointed, shorter and broader than in male; fixed digit of chelicera unidentate, movable chela edentate; corniculi more slender than in male; their inner margins parallel.

Second leg not modified; setae of all legs very short but otherwise their arrangement as in male.

Material Examined. Mexico: Nayarit, San Blas dump, ex bromeliad w/ red bracts & yellow flowers, 25-XII-77, A. J. Heyneman & B. Hallet—3 males, 7 females; same locality, ex terrestrial bromeliad, 5-I-78, A. J. Heyneman & B. Hallet—3 males, 2 females; same locality, ex *Amazilia rutila diluta* van Rossem (Trochilidae), 25-XII-77, A. J. Heyneman & B. Hallet—3 females; same data, ex *Cyanthus latirostris magicus* (Mulsant & Verreaux) (Trochilidae—2 males, 2 females; Tamalipas, Rancho Cielo, ex *Campylopterus curvipennis curvipennis* (Lichtenstein) (Trochilidae), 16-VII-73, R. K. Colwell—2 deutonymphs, 3 females.

Remarks. *Tropicoseius bakeri* Dusbabek & Cerny, 1970 was originally described on the basis of 5 females from the nasal cavity of the hummingbird *Chlorostilbon ricordii ricordii* (Gervais) from Cuba. Females from the Mexican localities listed above are indistinguishable from the Cuban types, as described by Dusbabek and Cerny (types not seen). Given the level of endemicity of the Cuban biota, study of males of Cuban origin may eventually reveal the Mexican specimens to be a distinct species. Meanwhile, a Mexican male is described above for the 1st time.

This species is most closely related to *T. naeemi* n. sp. The 2 species share a similar structure of the female inseminating apparatus, with a long maturation pouch with distinctly striated walls. Male chelicerae in the 2 species have edentate digits and spermatodactyls with distinctly narrowed, slightly bent apices. *T. bakeri* can be distinguished from *T. naeemi* by the marginal setae of series *r* and *R* in the male on the dorsal shield (on soft cuticle in *T. naeemi*), opisthoventral seta *Jv3* in the male on the shield (on soft cuticle in *T. naeemi*), reticulate ornamentation on the posterior part of the female dorsal shield (striated ornamentation in *T. naeemi*), and the atrium of the female inseminating apparatus separated from the maturation pouch by a short, narrow section of the major duct (maturation pouch merging with the atrium in *T. naeemi*).

Tropicoseius naeemi, new species
(Figs. 25–26)

Diagnosis. Dorsal shield of both sexes with distinct lateral incisions connected by transverse suture; ornamentation in males restricted to anterolateral region of shield, in females distinct over entire shield, in opisthonotal region consisting of transverse, parallel striations. Dorsal setae in both sexes short, subequal (about half as long as distance between adjacent setal insertions); setae *r4–r6* and all *R*'s in male on soft cuticle. Ventrianal shield of male with setae *Jv1–Jv2* and *Zv1–Zv2* in addition to anal setae; setae *Jv3* on soft cuticle. Leg II of male moderately enlarged, weakly curved between tibia and femur; seta *av1* of femur, genu and tibia knoblike; seta *pv1* on femur thickened, almost spinelike; tarsus III with setae *pv1* and *av2* knoblike. Both fixed and movable digits of male chelicera edentate, in female fixed digit unidentate; spermatodactyl short, weakly downcurved and with its apex narrow and somewhat bent. Spermatheca with large, elongate maturation pouch slightly widened in its proximal part, with striated walls.

Male. Dorsal shield 661–667 μm long, 307–360 μm wide (measured at the level of setae *s3*; 3 specimens), with lateral incisions between setae *s6* and *S1* distinctly surpassing level of setae *z6*, connected by transverse suture; weak reticulate ornamentation restricted to anterolateral region of shield (Fig. 25a). Podonotal part of shield somewhat longer than opisthonotal one, shield widest in opisthonotal region, at level of setae *J2*. Dorsal shield with 34 pairs of smooth, centrally dilated setae, including 19 pairs on podonotal and 15 on opisthonotal regions; marginal setae *r4–r6* and *R1–R5* on soft cuticle. Most dorsal setae relatively short (23–38 μm); *Z5* somewhat thicker and noticeably longer (128–135 μm) than remaining dorsal setae; setae *J5* longer than *j1* (16–17 and 11 μm, respectively)

Tritosternum typical for genus, with trapezoidal base and slender, tapering pilose laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; paragenital setae absent. Metapodal plates comparatively small, irregular in shape. Ventrianal shield narrow, without discernible reticulation (Fig. 25b); setae *Jv1–Jv2* and *Zv1–Zv2* on shield, setae *Jv3* on soft cuticle;

Jv5 about as long as postanal seta (63–83 μm). All remaining ventral setae short (25–34 μm). Peritrema extending anteriad to level of setae *z1*.

Gnathosoma with tectum narrowly tapering to sharp point, with smooth margin. Fixed digit of chelicera edentate; movable chela edentate, with short (50–56 μm), weakly downcurved spermatodactyl directed anteriad, its apex noticeably bent (Fig. 26e). Deutosternum with 7 transverse rows of denticles, all connected, none widened. Rostral setae simple, slender; capitular setae very short, less than half as long as anterior rostral setae (5–7 and 29 μm, respectively). Corniculi slender, their inner margins slightly convergent; internal malae extending to tip of corniculi. Setae *al1* and *al2* on palpgenu spatulate.

Coxa of leg I without denticles. Leg II only slightly enlarged, weakly curved ventrally between femur and tarsus; posterior seta of coxa distinctly thicker and longer than anterior one (41–43 and 11 μm, respectively); femur with seta *av1* thick, knoblike; seta *av1* of genu and tibia enlarged, knoblike; tarsus with setae *av1–av3* and *pv1* enlarged, knoblike (Fig. 26d). Tarsus III with setae *pl1* and *av2* enlarged, knoblike; *av3* unmodified. Small bosses present on coxae of legs II–IV. Leg setation as noted for genus.

Female. Dorsal shield 614–649 μm long, 301–330 μm wide (measured at the level of setae *s3*; 6 specimens), with distinct, narrow lateral incisions between setae *s6* and *S1* clearly surpassing level of setae *z6* and connected by transverse suture. Ornamentation distinct over entire shield (less distinct in anterolateral region), in opisthonotal region ornamentation consists of parallel, widely spaced striations (Fig. 26a).

Dorsal shield with 32 pairs of smooth, simple setae, including 17 pairs on podonotal and 15 pairs on opisthonotal regions; marginal setae *r*'s, *R*'s and *UR*'s on soft cuticle laterally; dorsal setae short, collectively subequal (23–45 μm).

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores, shield not ornamented. Fourth pair of sternal setae and 3rd pair of sternal pores on soft cuticle behind posterior margin of sternal shield. Genital shield with anterior hyaline part broadly rounded, its posterior part weakly reticulate, slightly widened behind genital setae. Paragenital setae absent. Metapodal plates small, triangular. Anal shield about twice as long as wide, weakly reticulate (Fig. 26b). Eleven pairs of opisthogastric setae on soft cuticle around anal shield, setae *Jv5* 88–101 μm long. Inseminating apparatus with large, elongate maturation pouch, 354–413 μm long and 18–24 μm wide, slightly widened in proximal region; in most specimens walls of pouch striated (Fig. 26c).

Tectum with pointed apex but somewhat shorter than that of male. Fixed digit of chelicera unidentate, movable chela edentate; mucro short, reaching half of movable chela. Corniculi more slender than in male; their inner margins parallel.

Leg chaetotaxy as in male, except no setae modified on leg II and leg III.

Etymology. Named in honor of Shahid Naeem (Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN), loyal collaborator and friend, without whose efforts this study could not have been done.

Type Material. Martinique (West Indies): ex *Heliconia* sp. (Heliconiaceae), 4-VII-76, P. Feinsinger—1 male (holotype), 1 female (allotype), 2 males, 1 female (paratypes); ex *Eulampis jugularis* (Linné)(Trochilidae), 1-VII-76, P. Feinsinger—11 females (paratypes).

Remarks. This new species is most closely related to *Tropicoseius bakeri* Dusbabek & Cerny, known from Cuba and Mexico (for a differential diagnosis see remarks for *T. bakeri*). *T. naeemi* is the only species of the *wetmorei* group that has the ventrianal shield of the male reduced such that setae *Jv3* are on soft cuticle. Ornamentation of the opisthonotal region of the dorsal shield in females of *T. naeemi* is very characteristic, resembling that present in distantly related *T. phoreticus* (Fain, Hyland & Aitken.).

In our collection, there are hummingbird flower mites from the neighboring island of Guadeloupe, West Indies, collected from *Heliconia bihai* (Heliconiaceae), that closely resemble the new species. The ornamentation and setation of their dorsal shields are identical to these of *T. naeemi* and the spermathecas have similar (but not identical) structure. Because the Guadeloupe specimens are all females, they are not included in the type series.

Tropicoseius analis (Fain & Hyland, 1980), **new combination**
(Figs. 2p, 27)

Rhinoseius analis Fain and Hyland 1980: 23, figs. 31–33 (type locality: Antioquia, Colombia).–Ohmer, Fain, and Schuchmann 1991: 481.

Diagnosis. Dorsal shield of both sexes with narrow lateral incisions, transverse suture usually absent; reticulate ornamentation of shield well-developed, but usually more distinct in females than in males. Setae of series *s, r, S,* and *R* of male dorsum distinctly thicker and longer than setae of series *j, z, J,* and *Z*; dorsal and lateral setae of female very short, subequal. Male ventrianal shield large, covering most of opisthoventral region; metapodal plates fused with shield; female anal shield typical for genus, slightly elongated. Spermatodactyl short, weakly sinuous, with apex spirally twisted; inseminating apparatus of female with long, tubular maturation pouch.

Male. Dorsal shield 510–540 μm long, 300–340 μm wide (measured at level of setae *s3*; 6 specimens), with narrow lateral incisions rarely connected by a transverse suture; reticulation distinct but restricted mainly to antero-lateral regions of shield (fig. 27a). Dorsal shield with 41 pairs of smooth, simple setae, including 21 pairs on podonotal and 20 pairs on

opisthonotal regions; marginal seta *r6* absent. Setae of series *s, r, S* and *R* of dorsum generally longer than setae of series *j, z, J* and *Z*: *s3* 50–55 μm, *s4* 65–75 μm, *r2* 60–72 μm, *r3* 45–50 μm, *S1* 63–70 μm, *S2* 67–75 μm, *R1* 87–92 μm, *R2* 75–82 μm, compared with *j2* 25–27 μm, *j3* 20–24 μm, *z2* 20–24 μm, *z4* 32–35 μm, *J1* 19–20 μm, *J2* 15–18 μm; the shortest setae of dorsal shield: *j1* 5–7 μm, *z1* 6–8 μm, and *J5* 10–12 μm; *Z5* the longest (115–130 μm).

Tritosternum with broad, trapezoidal base and slender pilose laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; no reticulate ornamentation on shield discernible. Paragenital setae absent. Ventrianal shield large, covering most of opisthoventral region, with setae *Jv1–Jv3, Zv1, Zv2* and para-anal and postanal setae; shield smooth, without ornamentation; metapodal plates fused with shield (Fig. 27b). Peritrema extending anteriad to level of seta *z1*; peritrematic plates free, not connected with exopodal plates.

Gnathosoma with tectum pointed at apex, its margins smooth. Fixed digit of chelicera uni- or edentate; movable chela edentate; spermatodactyl short, slightly sinuous, its apex spirally twisted (Fig. 27e). Deutosternum with 7 equally narrow rows of denticles; all rows connected. Rostral setae slender, simple; anterior rostral pairs long (20 μm), posterior exterior pairs shorter than posterior interior pairs (7 μm and 11 μm, respectively); capitular setae simple, short (9 μm). Corniculi slender, with internal margins straight, parallel; internal malae narrow, reaching or slightly surpassing tips of corniculi (Fig. 27c). Setae *al1* and *al2* on palpgenu spatulate, *al* on palpfemur dilated apically.

Leg II stout, slightly curved ventrally between femur and tarsus; coxa II with posterior seta large and stout; femur, genu and tibia with seta *av1* stout, knoblike, and seta *pv1* spinelike; tarsus with setae *av1–av3* and *pv1* modified, knoblike (Fig. 2p). Tarsus of leg III with setae *pv1* and *av2* stout, knoblike. Coxa I with no denticles, coxae II–IV with posteriorly convex bosses. Setation formulas of legs as noted for genus; setae of genua and tibiae of legs II and IV relatively long, some of them (*pd1* and *pd2*) about as long as width of their respective articles.

Female. Dorsal shield 520–555 μm long, 267–275 μm wide (measured at level of setae *s3*; 10 specimens), with lateral incisions between setae *s6* and *S1*, extending to level of setae *z6*, usually not connected by transverse suture (Fig. 27f). Reticulate ornamentation well-developed over entire shield. Dorsal shield with 32 pairs of short, simple setae, including 17 pairs on podonotal and 15 pairs on opisthonotal regions; all marginal setae *r, R* and *UR* on soft cuticle; all dorsal setae of similar length: *j2* 20–24 μm, *j3* 18–20 μm, *j4* 23–25 μm, *z2* 24–27 μm, length of *j1, z1,* and *J5* as in male.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; anterior margin of sternal shield forms 2 distinct lobes with

weak reticulate ornamentation; 4th pair of sternal setae and 3rd pair of sternal pores on soft cuticle behind posterior margin of sternal shield. Anterior hyaline part of genital shield narrowly rounded, widened; longitudinal ornamentation of posterior part of shield weakly developed. Metapodal plates small, roughly triangular in shape. Anal shield elliptical, about twice as long as wide, with weakly developed reticulate ornamentation; postanal seta about twice as long as para-anal setae; setae *J5* slightly longer and thicker than postanal seta (Fig. 27g). Nine to 10 posteroventral setae on soft cuticle around anal shield. Inseminating apparatus with long (82 μm), tubular maturation pouch (Fig. 27h).

Tectum sharply pointed, somewhat shorter and broader than in male; fixed digit of chelicera unidentate, movable chela edentate; mucro clearly surpassing apex of movable chela (Fig. 27d); corniculi more slender than in male, their inner margins parallel.

Second leg not modified; setae of all legs very short but otherwise their arrangement as in male.

Material Examined. Panama: El Llano—Carti Rd., ex *Heliconia lutea* Kress (Heliconiaceae) 20-VIII-83, W. J. Kress, 83–1562—1 male, 1 female; Cerro Jefe, ex *Heliconia lutea* Kress, 20–22-VIII-83, W. J. Kress, 83–1574—2 males, 5 females; **Costa Rica:** Puntarenas Province, Osa Peninsula, Pacific Rd. 8 km SW Tropical Science Center Station, ex *Heliconia ?bihai* (L.) L., 10-III-71, R. K. Colwell—3 males, 8 females; Osa Peninsula, 1 km W Tropical Science Center Station, ex *Phaethornis superciliosus cephalus* (Bourcier & Mulsant) (Trochilidae), 7-III-71, R. K. Colwell—2 females.

Remarks. This species was originally described (Fain and Hyland 1980) from the single male holotype collected in Antioquia, Colombia, from the hummingbird *Phaethornis superciliosus.* Here we describe the female for the 1st time and redescribe the male. *Tropicoseius analis* is the only member of the genus that has the metapodal plates fused with the ventrianal shield. Males of this species show a possibly highly derived structure of the chelicera, with the most pronounced reduction of dentition. Most specimens examined have both fixed and movable digits of the chelicera edentate, although in one specimen a minute tooth on the fixed digit is present. Similar reduction of the dentition of the male chelicera can be observed in *T. bakeri* Dusbabek & Cerny and *T. naeemi* n. sp. *T. analis* shares a similar structure of the spermatodactyl (having a spirally twisted apex) with such species as *T. kressi* n. sp. and *T. trinitatis* (Fain, Hyland & Aitken).

Tropicoseius trinitatis (Fain, Hyland & Aitken, 1977), **new combination**

Rhinoseius trinitatis: Fain, Hyland, and Aitken 1977a: 186 (female; type locality: Trinidad, Vega de Oropouche).–Fain, Hyland, and Aitken 1977b: 120, 121,

137, 149.–Colwell 1986b: 408, 409, 411.– 1990: 131–138.–Heyneman, A. J. et al.1991: 463, 465, 477.–Fain 1992: 119–120, 123, 130, 132, figs. 20, 43.–Farrier and Hennessey 1993: 49.–OConnor, Colwell, and Naeem 1996: 4–10, figs. 3–17 (male).

Material Examined. Trinidad: Arima Valley, .8 km up from Bridge C6.9, Blanchisseuse Rd, ex *Heliconia hirsuta* L. f. (Heliconiaceae), 15-II-79, R. K. Colwell—8 males, 8 females; St. Georges, Blanchisseuse, Arima Rd., ex *Heliconia hirsuta* L. f., 5-IV-86, W. J. Kress, 86–1879—2 males, 1 female; Arima Valley, Upper Tripp Trace (Jujube Tree Trace), ex *Heliconia hirsuta* L. f., 23-II-79, R. K. Colwell—1 male; Arima Valley, Cooker Trace, La Laja Trace, ex *Heliconia hirsuta* L. f., 4-VIII-75, R. K. Colwell—1 male, 1 female; Arima Valley, La Laja Trace, ex *Heliconia hirsuta* L. f., 7-III-87—2 males; Arima Valley, Andrews Trace, ex *Heliconia hirsuta* L. f., 1-VIII-75, R. K. Colwell—2 males, 4 females; Arima Valley, Andrews Trace, ex *Heliconia hirsuta* L. f., 1-VIII-75, R. K. Colwell—2 males, 5 females.

Remarks. This species was recently redescribed by OConnor et al. (1997) who described a male for the first time. It is closely related to *T. kressi, T. klepticos,* and *T. venezuelensis,* from which it can be distinguished by the opisthonotal setation in males, in which the lengths of setae of the *S* series increase toward the end of the opisthosoma, *S5* being at least 4 times longer than *S1*. Also *Z5* and *Jv5* are very long, almost flagelliform. Features of the female inseminating apparatus and the spermatodactyl in males are generally similar to those in *T. kressi, T. venezuelensis* and *T. klepticos.* All 4 related species occur in the tropical lowlands and feed exclusively on flowers of *Heliconia* spp. (Heliconiaceae). (Note: The host plant of *T. trinitatis* in Trinidad that was identified as *Heliconia trinidatis* in Colwell (1986b) and Dobkin (1984, 1987, 1990) is in fact *H. hirsutis* L. f.

Tropicoseius kressi, new species
(Fig. 28)

Diagnosis. Dorsal shield of both sexes with narrow lateral incisions connected by transverse suture; in both sexes reticulate ornamentation distinct over entire shield. Setae on dorsal shield of male short (≈½ to ⅔ as long as distances between adjacent setal insertions) except *Z5, S4,* and *S5* noticeably longer and thicker than remaining dorsal setae; in female all dorsal setae short. Leg II in male moderately enlarged, with seta *av* of femur, genu, and tibia knoblike; setae *pv* of coxa and *pv1* of femur thickened, almost spinelike. Tarsus III with setae *pv1* and *av2* knoblike. Spermatodactyl with apex spirally twisted apically; inseminating apparatus of female with long, tubulous maturation pouch. Peritrema in both sexes reaching level of setae *z1*.

Male. Dorsal shield 438–456 μm long, 246–279 μm wide (measured at level of setae *s3*; 12 specimens), with narrow lateral incisions between setae *s6* and *S1,* extending ≈⅓ of the way to the midline of the dorsal shield and connected by distinct transverse suture; reticulate ornamentation well-developed over entire shield (Fig. 28a). Dorsal shield with 34 pairs of smooth, simple setae, including 19 pairs on podonotal and 15 pairs on opisthonotal shields; marginal setae *r5, r6,* and *R1–R6* on soft cuticle. Lateral setae of opisthosoma and setae *Z5, S4* and *S5* distinctly longer and thicker than median dorsal setae: *Z5* 118–134 μm, *S4* 70–72 μm, *S5* 75–77 μm compared with *J1* 17–20 μm, *J2* 12–16 μm, *Z1* 17–19 μm, *Z2* 17–18 μ, *Z3* 16–18 μm, *S1* 17–19 μm, *S2* 19–25 μm.

Tritosternum with short, trapezoidal base and slender pilose laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; no reticulate ornamentation on shield. Paragenital setae absent. Metapodal plates irregular and variable in shape, comparatively small. Ventrianal shield large, narrowing toward posterior margin; setae *Jv1–Jv3, Zv1, Zv2,* para-anal, and postanal setae on shield (rarely, setae *Zv2* on soft cuticle); reticulate ornamentation of shield with weak or absent (Fig. 28b). Peritrema extending anteriad to the level of seta *z1*; peritrematic plates not connected with exopodal plates.

Gnathosoma with tectum pointed at apex, its margins smooth. Fixed digit of chelicera unidentate; movable chela edentate, with short, slightly curved spermatodactyl, its apex spirally twisted (Fig. 28d). Deutosternum with 7 rows of denticles; all rows connected, no rows widened. Rostral setae slender, simple; anterior rostral setae long (30 μm), posterior interior setae longer than posterior exterior setae (20 μm and 7 μm, respectively); capitular setae simple, short (8 μm). Corniculi slender, their internal margins slightly convex; internal malae evenly tapering and reaching tips of corniculi. Setae *al1* and *al2* on palpgenu spatulate, *pl* on palpfemur dilated apically.

Second leg moderately enlarged and curved ventrally between femur and tarsus; all setae always shorter than width of their corresponding articles; femur, genu, and tibia with seta *av1* stout, knoblike; tarsus with setae *av1–av3* and *pv1* modified, knoblike; setae *pv1* of femur thickened, spinelike (Fig. 28c). Tarsus of leg III with setae *pv1* and *av2* stout, knoblike. Coxa I with no denticles; coxa II–IV with posteriorly convex bosses; coxa II with posterior seta large and stout. Setation formulas of legs I, II, III and IV typical for genus.

Female. Dorsal shield 456–480 μm long, 264–276 μm wide (measured at level of setae *s3*; 12 specimens), lateral incisions between setae *s6* and *S1,* extending ⅓ to ½ way to midline of dorsal shield, transverse suture always present. Reticulate ornamentation dense and distinct over entire shield (Fig. 28f). Dorsal shield with 32 pairs of short, simple setae, including 17 pairs on podonotal and 15 pairs on opisthonotal regions; all setae *r, R,* and *UR* on soft cuticle laterally; setae on dorsal shield almost uniform in length (shorter than half the lengths between adjacent setal insertions)

Tritosternum with base noticeably longer than in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; its anterior margin forms 2 distinct lobes; 4th pair of sternal setae and 3rd pair of sternal pores on soft cuticle behind posterior margin of shield. Anterior hyaline part of genital shield narrowly rounded, with convex sides; posterior part of shield distinctly widened behind genital setae. Metapodal plates small, usually triangular in shape. Anal shield obovate, ≈1.5 times longer than wide, with poorly developed reticulate ornamentation; distance between anal shield and posterior part of genital shield small, distinctly less than half width of anal shield; postanal seta more than twice as long as para-anal setae (Fig. 28g). Nine posteroventral setae on integumental area around anal plate. Inseminating apparatus with long (58–62 μm) and narrow (3–4 μm) maturation pouch (Fig. 28h).

Tectum as in male but shorter; fixed digit of chelicera unidentate, movable chela edentate; mucro almost reaching apex of chela (Fig. 28e). Corniculi more slender than in male; their inner margins parallel.

Second leg not modified, without spine- or knoblike setae; tarsus III with no modified setae; setation of the remaining legs as in male.

Type Material. Panama: Pipeline Road near Gamboa, ex *Heliconia vaginalis* Bentham (Heliconiaceae), 30-VIII-80, W. J. Kress, 80–1256—1 male (holotype), 1 female (allotype), 13 males and 21 females (paratypes).

Etymology. This species is named in honor of W. John Kress (Department of Botany, Smithsonian Institution, Washington, DC), authority on the taxonomy and biology of Heliconiaceae, collector of specimens of this new species and thousands of other specimens of hummingbird flower mites in preserved, determined floral material generously made available to this study.

Remarks. *Tropicoseius kressi* n. sp. is most closely related to *T. trinitatis* (Fain, Hyland & Aitken). The 2 species share a similar form of the male spermatodactyl with spirally twisted apices, setae of the series *R* in male on soft cuticle, small distance between the genital and anal shields in the female, and a similar structure of the female inseminating apparatus, with long, tubulous maturation pouch. The new species can be distinguished easily from *T. trinitatis* by short setae of the *S* series in the male; these setae are very long, almost flagelliform in *T. trinitatis.*

Tropicoseius venezuelensis Baker & Yunker, 1964

Tropicoseius venezuelensis Baker and Yunker 1964: 106, figs. 62–74 (male and female; type locality: Venezuela, at New York quarantine).

Rhinoseius venezuelensis: Fain, Hyland, and Aitken 1977b: 119, 123, 137–138, 145, figs. 10, 51, 69.–Fain 1992: 118–121, 123, 130, 135, figs. 19, 51.–Farrier and Hennessey 1993: 49.

Type Material. Venezuela: (at New York quarantine), ex *Heliconia* sp. (Heliconiaceae), 10-IV-59, W. Costello et al.—1 female (holotype) (NMNH); **Panama:** Ft. Clayton, Canal Zone, ex *Heliconia* sp., 30-VII-61, C. E. Yunker—1 female (paratype).

Material Examined. Panama: Cocle, El Cope, beyond Sawmill, ex *Heliconia ignescens* Daniels & Stiles, 23-IV-80, W. J. Kress,—2 females; **Costa Rica:** Puntarenas Province, vicinity of Golfito, ex *Heliconia latispatha* Bentham, 13-VII-76, W. J. Kress, 76–0587—1 female; **Guyana:** Berbice, New Forest, along Ganje River, ex *Heliconia stricta* Huber, 30-III-86, W. J. Kress, 86–1813—14 males, 9 females; **Ecuador:** Napo, new road from Catundo to Coca off of Baeza-Tena road, 68 km from turnoff, ex *Heliconia chartacea* Lane ex Barreiros, 27-II-88, W. J. Kress, 88–2364—10 males, 28 females.

Remarks. *Tropicoseius venezuelensis* is closely related to *T. klepticos,* and there is a possibility that the 2 forms are, in fact, conspecific. Males of the 2 species are practically indistinguishable, having identically shaped spermatodactyls and identical opisthosomal and leg chaetotaxy. However, there are discrete differences between various populations in the structure of the female inseminating apparatus. Females from populations in Panama and several localities in Costa Rica (Puntarenas, ex *Heliconia latispatha*), Guyana, and Ecuador (Napo, ex *Heliconia chartacea*) have maturation pouches distinctly longer than the remaining part of the major duct, a condition identical to that observed in the type specimens (described from flowers collected in Venezuela). In *T. klepticos,* in contrast, although the size of the maturation pouch is similar to that in *T. venezuelensis,* the remaining part of the major duct is at least as long as the pouch or often longer. For this reason the 2 forms are treated here as distinct species.

Tropicoseius klepticos (OConnor, Colwell & Naeem, 1996), **new combination**

(Fig. 2k)

Rhinoseius klepticos, (nomen nudum) Colwell 1986b: 408, 409, 411, 413.–OConnor, Colwell, and Naeem 1996: 27–31, figs. 68–77 (male and female; type locality: Trinidad, Arima Valley).

Type Material. Trinidad: Arima Valley, ridge trail above Simla Research Station, 5 km N. Arima, ex *Heliconia spathocincinata* Aristeguieta (Heliconiaceae), 3-VIII-75, R. K. Colwell—1 female (holotype), 1 male (paratype) (UMMZ).

Material Examined. Trinidad: Toco-Matelot Rd., Shark River, ex *Heliconia bihai* (L.) L., 17-III-87, R. K. Colwell—2 males, 4 females; Simla Biol. Reserve, ex *Heliconia bihai* (L.) L., 8-III-87, R. K. Colwell- -1 male; **Ecuador:** Napo, Jatun Satcha Biological Reserve, across Rio Napo from Misahaulli, 1900 ft, ex *Heliconia standleyi* Macbride, 28-II-88, W. J. Kress,

Pacific Rd., ex *Eutoxeres aquila salvini* Gould, 9-III-72, R. K. Colwell—4 females.

Remarks. This species is widely distributed and quite variable in features of the female inseminating apparatus, shape of the anal shield, and ornamentation of shields. Fain and Hyland (1980) described *R. waidei* on the basis of female specimens, some of which were collected from the same bird carrier as *R. eutoxeres,* another, very similar new species described in their paper. Presence on the same bird does not necessarily mean that the mites came from the same flower but certainly increases the probability. They claimed that the 2 species were closely related to *T. fairchildi* but could be distinguished by a number of characters. We examined types of both *R. waidei* and *R. eutoxeres* and found that the characters on the basis of which they were considered distinct species fit well into range of intraspecific variation of *T. fairchildi.* We studied a large series of specimens of this species from various localities and hosts and no discrete morphological differences among or within populations could be found. The anal shield in females, although generally slightly longer than wide, quite frequently is wider than long or as long as wide, even among specimens collected from the same flower. Ornamentation of the dorsal shield also is subject to great intraspecific variation and is possibly a function of age (freshly molted individuals tend to have poorly discernible ornamentation); we have specimens in which the anal shield is wider than long (a diagnostic character for *R. waidei*) but the dorsal shield has no discernible ornamentation. Although the shape and length of the maturation pouch are generally relatively invariant characters among *Tropicoseius* spp., some specimens of *T. fairchildi* collected from a single flower exhibited quite a degree of variation and a few had the pouch as narrow as the one observed in the type series of *R. eutoxeres* (3.6–4 μm). The "conical ventrolateral spine" on palpfemur (seta *pv*), which was supposed to be one of the diagnostic characters of *R. eutoxeres,* is often enlarged in *T. fairchildi.* For these reasons we are convinced that the 3 forms are conspecific and *Rhinoseius waidei* Fain & Hyland and *Rhinoseius eutoxeres* Fain & Hyland should be considered junior synonyms of *Tropicoseius fairchildi* Baker & Yunker.

Tropicoseius fairchildi is one of the few species of hummingbird flower mites that occur within a great altitudinal range. Specimens of this species were collected from sea level (Panama) up to 2,300 m a. s. l. (Ecuador). Like the very closely related *T. colombiensis,* they feed exclusively on flowers of the genus *Heliconia* (Heliconiaceae).

Tropicoseius colombiensis (Fain & Hyland, 1980), **new combination** (Fig. 1 c and d)

Rhinoseius colombiensis Fain and Hyland 1980: 15, 21, 23, figs. 20, 23, 25–27, 35 (male and female; type locality: Colombia, Antioquia).–Ohmer, Fain, and Schuchmann 1991: 481.–Fain 1992: 119–120, 123, 128, 134, figs. 21, 56.

Material Examined. Nicaragua: Zelaya, 32 km W of Rama, ex *Heliconia curtispatha* Petersen (Heliconiaceae), 6-VII-77, W. J. Kress, 77–0759—1 male, 4 females; **Costa Rica:** Puntarenas Province, Corcovado Nat. Park, Sirena, ex *Heliconia* sp., 1-I-90, G. Fonseca—1 female; same locality and host, J. Saberio—4 males, 3 females; Guanacaste Province, Santa Rosa Nat. Park, Playa Naranjo, ex *Mansoa hymenaea* (A.DC.) Gentry (Bignoniaceae), E. Alcazar—3 females; **Ecuador:** Morona Santiago, 4 km S of San Juan de Bosco, elev. 1300 m, ex *Heliconia peteriana* Abalo and G. L. Morales, 17-X-89, W. J. Kress, 89–2886—2 males, 2 females; Morona Santiago, 20 km from San Juan de Bosco along the road to Gualaquiza, elev. 1500 m, ex *Heliconia pastazae* L. Anderss., 17-X-89, W. J. Kress, 89–2888—1 male, 6 females; **Colombia:** Chocó, vicinity of El Siete, Bolivar-Quibdo road, ex *Heliconia combinata* Abalo and G. L. Morales, 8-VII-86, W. J. Kress, 86–2043—1 male.

Remarks. *Tropicoseius colombiensis* is most closely related to *T. fairchildi* Baker & Yunker but can be distinguished by a very broad anal shield in the female, the width of which is distinctly larger than the width of posterior margin of the genital shield (Fig. 1c). Also, the ventrianal shield in males is large, with the lateral margins roughly parallel (narrowing posteriad in *T. fairchildi*). The 2 species seem to feed exclusively on flowers of *Heliconia* spp. (Heliconiaceae) and occur at relatively high altitudes.

Tropicoseius perezgloriae (Wiese and Fain, 1993), **new combination**

Rhinoseius perezgloriae Wiese and Fain 1993: 96–98, figs. 22–24 (type locality: Colombia Valle de Cauca).

Remarks. We did not have an opportunity to examine any specimens of this species, described recently on the basis of 3 females collected from the hummingbird *Eutoxeres aquila.* As pointed out by Wiese and Fain (1993), *T. perezgloriae* seems to be most closely related to *T. fairchildi,* sharing a relatively large anal shield in the female and a spermatheca with a long, tubular maturation pouch. It is likely that this species is affiliated with flowers of the genus *Heliconia* (Heliconiaceae).

Tropicoseius adsimilis (Fain & Hyland, 1980), **new combination**

Rhinoseius adsimilis Fain and Hyland 1980: 15, 23, figs. 37–38 (female; type locality: Colombia, Antioquia).–Ohmer, Fain, and Schuchmann 1991: 481.–Fain 1992: 119, 123, 132, figs. 11, 55.

Type Material. Colombia: Antioquia, ex *Eutoxeres aquila* (Bourcier) (Trochilidae), 10–15-V-71, R. B. Waide), 1 female (paratype) (IRSNB).

Remarks. This species is known only from 4 female specimens collected from hummingbird carriers and therefore is not included in our cladistic analysis of the genus. Fain and Hyland (1980) point out its similarity

to *Rhinoseius eutoxeres* Fain & Hyland (here considered conspecific with *Tropicoseius fairchildi* Baker & Yunker), but in fact the species is probably more closely related to *T. analis* (Fain & Hyland), being very similar in the proportions of dorsal and anal shields (although the anal shield in *T. analis* is more elongated), and similar in the shape of the anal shield and the structure of the inseminating apparatus. *T. adsimilis* most likely feeds on flowers of *Heliconia* spp. (Heliconiaceae).

Tropicoseius chlorestes (Fain, Hyland & Aitken, 1977), new combination

Rhinoseius chlorestes Fain, Hyland, and Aitken 1977a: 185 (female; type locality: Belem, Para, Brazil).–Fain, Hyland, and Aitken 1977b: 121, 138, 140–142, figs. 13, 48, 70, 106, 107.–Fain 1992: 119–120, 123, 130, 132, figs. 16, 48.

Type Material. Brazil: Para, Belem, APEG Forest, Station A (IPEAN), ex *Chlorestes notatus* (C. Reichenbach) (Trochilidae), 8-X-69, T. H. G. Aitken & T. E. Lovejoy—1 female (paratype) (IRSNB).

Remarks. This species is known from only 3 females and therefore is not included in our cladistic analysis. It appears that *T. chlorestes* is related to such species as *T. venezuelensis, T. klepticos* and *T. heliconiae,* sharing a similar form of the inseminating apparatus. The major duct in *T. chlorestes* is wider in its proximal part than in these other species. There are no host plant records for *T. chlorestes,* but it most likely it feeds on flowers of either Heliconiaceae or Costaceae.

Genus *Rhinoseius* Baker & Yunker, 1964

Rhinoseius Baker and Yunker 1964: 103 type species: *Rhinoseius tiptoni* Baker and Yunker, 1964.–Lindquist and Evans 1965: 5, 19–21, 25, 30, 51–53.–Hunter 1972: 26.–Colwell 1973: 737, 738, 743–747, 753, 756, 757.–Colwell et al. 1974: 447.–Fain, Hyland, and Aitken 1977b: 101, 102, 107–109, 111, 113, 115, 135.–Krantz 1978: 128.–Hyland, Fain, and Moorhouse 1978: 260.–Fletchmann and Johnston 1978: 165.–Colwell and Naeem 1979: 485,486, 489, 490.–Colwell 1979: 461–463, 465–467.–Fain and Hyland 1980: 15.–Micherdzinski and Lukoschus 1980: 65, 77.–Luteyn 1983: 41.–Stiles 1983: 593.–Dobkin 1984: 245, 250, 252.–Dobkin 1985: 536.–Colwell 1985: 58–59.–Naeem, Dobkin, and OConnor 1985: 338.–Henderson 1985: 67, 70.–Colwell 1986a: 475–477, 487.–Colwell 1986b: 407, 409, 412, 415, 418, 423.–Dobkin 1990: 131, 137.–Colwell et al. 1991: 455, 456, 458.–OConnor, Colwell, and Naeem 1991: 348.–Ohmer, Fain, and Schuchmann 1991: 481, 484.–Lindquist and Wu 1991: 900, 901.–Christiansen, Colwell, and Kaliszewski 1992: 98, 102.– Farrier and Hennessey 1993: 47.–OConnor, Colwell, and Naeem 1997: 1.

Diagnosis. Dorsal shield of male either entire, laterally incised, or completely divided; that of female always with distinct lateral incisions; opisthonotal setae *J1, J2, J4, Z2, Z3,* and *Z4* of male or only some of them often hypertrophied; both sexes always lack setae *z3* and *s6* on podonotal region, and sometimes lack setae *z1* on podonotal and/or *J3, Z4,* and *S1* on opisthonotal region; *j1* always longer than *J5*; opisthonotal setae *J5* in female always, and in male usually, accompanied by bundle of microspinules. Genital shield of female with anterior hyaline part usually distinctly incised, rarely truncated; genital setae on soft cuticle adjacent to genital shield. Endopodal and exopodal plates absent in both sexes, rarely rudimentary endopodal plates present in male; peritrematic plates reduced, especially around stigmas. Leg II of male usually not greatly enlarged; *av1* on femur II slightly to greatly enlarged, *pv1* and *pv2* spinelike or not modified; *av1* on tibia II, and *pv1* and *pv2* of tarsus II thickened; no modified setae on tarsus III. Setal formula of genua I–IV: 13–11–9–9; that of tibia: 13–10–8–9; setae *pl2* missing from tibia III and IV. Gnathosoma with tectum broadly rounded or crenulate; corniculi in male with inner margins clearly divergent, often slightly bilobed, those of females with inner margins parallel; pilus dentilis on fixed digit of chelicera modified into hyaline lobe; male spermatodactyl short, straight and directed posteroventrad, sometimes with apical lobiform projection. Female inseminating apparatus with conspicuous basal dilation (infundibulum) and short, simple sperm duct.

Male. *Dorsum.* Dorsal shield either entire (Fig. 29a) or with shallow lateral incisions between setae *s5* and *S1,* or completely divided into podonotal and opisthonotal shields (Fig. 33a); ornamentation of shield restricted to anterolateral regions or shield smooth. Dorsal shield with 25–30 pairs of setae. Setae *3* and *s6* absent in all species; *z1, J3, Z4,* and *S1* absent in some species. In some species opisthonotal setae *J2, J4, Z2, Z3* and *Z4* (Fig. 31a) or only *J1* and *J2* hypertrophied, spinelike (Fig. 35 a and b); sometimes podonotal *z4* and *s4* or opisthonotal *J2–J4, Z2–Z3* long and thickened, almost clublike; *Z5* sometimes modified, clublike; setae of *z, s, r, S,* and *R* series (or only some of them) in some species strongly elongated, flagelliform; *J5* very short, usually accompanied by bundle of microspinules; podonotal setae *j1* always distinctly longer than opisthonotal *J5.* Marginal setae of *r* and *R* series on soft cuticle but occasionally *r2* and *r3* on shield. Peritrema usually shortened, reaching level of setae *s1,* but sometimes only level of setae *s2*; narrow vestiges of peritrematic plates usually present between levels of setae *r3* and *r5* but sometimes reduced to barely discernible vestiges around stigmas.

Venter. Sternogenital shield not modified, with 5 pairs of sternal setae and 3 pairs of pores; no paragenital setae; endopodal and exopodal plates absent, rarely rudimentary endopodal plates present. Ventrianal shield either very large, covering most of opisthoventral region, with most of opisthoventral setae and a pair of more or less developed posterior processes near anal opening (Fig. 35 d and e); or divided into a true anal shield with paraanal and postanal setae, and strongly reduced ventral shield with 0–4 pairs

of setae (Fig. 29b); metapodal plates present but usually very small. Structure of opisthosomal setae subject to great inter- and intraspecific variability, ranging from normal to highly modified, flagelliform.

Gnathosoma. Tectum short, anterior margin convex or crenulate (serrate). Deutosternum with 7 rows of equally, moderately wide denticles; all rows connected. Capitular setae as long or only slightly shorter than anterior rostral pairs; corniculi with their inner margins clearly divergent, often slightly bilobed; *al* on palpfemur, and *al1* and *al2* on palpgenu spatulate, rarely the latter 2 unmodified; apotele on palptarsus 2-tined. Fixed digit of chelicera bi- or tridentate; pilus dentilis modified into hyaline lobe; movable chela edentate; with short, almost straight, or more or less incurved spermatodactyl, always directed ventrad or posteroventrad, and sometimes with small apical or subapical lobiform projection.

Legs. Coxae I with 1 or more convex rows of small denticles. Leg II usually not appreciably stouter than remaining pairs; seta *pv* on coxa usually not thickened, rarely stout, spinelike; *av1* on femur either not modified or knoblike or strongly enlarged, spinelike; *av1* on tibia not modified, rarely slightly thicker then rest of tibial setae; *pv1* and *pv2* on tarsus never modified (i.e., never spine- or knoblike); all setae always shorter than width of their respective articles; setae of tarsus III never modified (Fig. 2a); coxa IV usually with more or less developed posterior spur (Fig. 33b). Setation of genua of legs I, II, III, IV, respectively 13–11–9–9; that of tibia 13–10–8–9; setae *pl2* absent on tibiae III and IV.

Female. *Dorsum.* Dorsal shield with distinct lateral incisions reaching or exceeding level of setae *z6,* never connected by transverse suture (Fig. 32a); setae *s6* always absent; setae *z1, J3,* and *Z4* sometimes absent; all marginal setae *r*'s and *R*'s on soft cuticle laterally; most dorsal setae short, subequal. Podonotal setae *j1* always longer than opisthonotal setae *J5*; *J5* accompanied by a bundle of microspinules. Peritrema usually shortened, reaching level of setae *s1,* but sometimes only level of setae *s2*; vestiges of peritrematic plates present between levels of setae *r3* and *r5.*

Venter. Anterior margin of sternal shield weakly convex or shallowly incised but never with distinct anterior lobes; shield with 3 pairs of sternal setae and 2 pairs of pores, 4th pair of setae and 3rd pair of pores on soft cuticle behind shield. Genital shield with anterior hyaline part distinctly incised (Fig. 32b), less often truncated; posterior part of shield either broadly rounded or distinctly widened, with its hind margin truncated; genital setae on soft cuticle adjacent to genital shield; endopodal and exopodal plates absent. Anal shield usually roughly circular, rarely longer than wide; shield as broad as or narrower than posterior margin of genital shield; metapodal plates very small, elongate. Inseminating apparatus usually well sclerotized, with enlarged infundibulum; major duct thin, relatively short (Fig. 36c); other components of apparatus not discernible.

Gnathosoma. Tectum usually shorter than on male, convex or crenulate (serrate). Corniculi more slender than in male, their inner margins parallel; fixed digit of chelicera bidentate, rarely with 3–4 small teeth (Fig. 2e), movable chela edentate; ventroproximal mucro on movable chela reaching or surpassing its apex.

Legs. Coxae I with 1 or more convex rows of small denticles. Leg II not modified, all setae normal. Setation of legs as noted for male.

Species Included:

Group *rafinskii*

Rhinoseius tiptoni Baker & Yunker, 1964
Rhinoseius pastorae Wiese & Fain, 1993
Rhinoseius ucumariensis Wiese & Fain, 1993
Rhinoseius luteyni n. sp.
Rhinoseius rafinskii Micherdzinski & Lukoschus, 1980
Rhinoseius nadachowskyi Wiese & Fain, 1993

Group *richardsoni*

Rhinoseius caucaensis Ohmer, Fain & Schuchmann, 1991
Rhinoseius haplophaedia Ohmer, Fain & Schuchmann, 1991
Rhinoseius androdon Fain & Hyland, 1980
Rhinoseius richardsoni Hunter, 1972
Rhinoseius antioquiensis Fain & Hyland, 1980

Remarks. The genus *Rhinoseius* Baker & Yunker is well-defined by the following apomorphic character states: (1) exopodal and endopodal plates absent in both sexes (rudimentary endopodal plates present in males of 1 species), (2) female genital setae on soft cuticle adjacent to the genital shield, (3) peritrematic plates reduced around stigmas, (4) podonotal setae *s6* absent in both sexes, (5) opisthonotal setae *J5* in the female accompanied by bundle of microspinules, (6) setae *pl2* absent on tibia IV in both sexes, and (7) female inseminating apparatus with a large infundibulum. In addition to these unique character states, most species of this genus are characterized by the anterior hyaline part of the genital shield in females with angular incision.

Rhinoseius is undoubtedly most closely related to 2 other (of 3 described) genera of melicharine mites associated with flowers—*Tropicoseius* Baker & Yunker, and *Xanthippe* Naskrecki & Colwell. Derived character states shared with *Tropicoseius* include edentate movable chela of chelicerae, fixed chela devoid of multiple teeth at the base, enlargement of the 2nd leg in males, modification of the seta *av* on femur and genu II into thick spines or knobs, and all marginal setae of series *r* and *R* in females on soft cuticle lateral to the dorsal shield. The last character also is shared

with what appears to be the most basal genus of the three, *Xanthippe,* with which *Rhinoseius* shares a similar form of the spermatodactyl and corniculi in males.

Two groups of species can be distinguished within the genus *Rhinoseius,* each characterized by several morphological and ecological traits. Both lineages apparently independently developed several specialized features, the most prominent being the spinelike, hypertrophied dorsal setae in males. Females in both groups have the anterior hyaline part of the genital shield incised, except for the most basal species in each group (*R. tiptoni* and *R. caucaensis*), in which the shield is truncated anteriorly. Certain species in each group also independently lost podonotal setae *z1* and opisthonotal setae *J3.*

Group *rafinskii*

All species in the group *rafinskii* are characterized by division of the ventrianal shield in males into separate ventral and anal shields, and by the dorsal shield in males entire, without lateral incisions. The 4th coxae in both sexes are simple, without posterior spurs (with the exception of *R. nadachowskyi,* where the spurs are present but are smaller than those in species of the group *richardsoni*).

Rhinoseius tiptoni Baker & Yunker, 1964
(Fig. 2e)

Rhinoseius tiptoni Baker & Yunker 1964: 103–104, figs. 1–15 (male and female; type locality: Panama, Cerro Punta).–Lindquist and Evans 1965: 22, 52.–Fain, Hyland, and Aitken 1977b: 109, 117, 122, 136, figs. 27, 33, 57.–Fain and Hyland 1980: 15.–Micherdzinski and Lukoschus 1980: 77.–Ohmer, Fain, and Schuchmann 1991: 481, 483–484.–Fain 1992: 119–121, 123, 127, 132, figs. 10, 31.–Wiese and Fain 1993: 70, 77, 78.–*Rhinoseius tiptoni,* Farrier and Hennessey 1993: 49.

Material Examined. Costa Rica: Heredia Province, Cariblanca, Roadside, ex *Besleria* sp.7-I-89, R. K. Colwell—7 males, 4 females; Pueblo Nuevo, Rio Negro Ford, ex Gesneriaceae, 8-II-71, R. K. Colwell—1 male, 3 females; La Selva Biological Station, CC 2400, ex *Besleria robusta* Donn. Sm., B. Loiselle—1 male; Finca La Selva Biological Station, S boundary, ex *Heliconia trichocarpa* Daniels & Stiles (Heliconiaceae), 30-VIII-80, R. K. Colwell—1 male; La Selva Biological Station, CC 2400, ex *Besleria robusta* Donn. Sm.,, R. K. Colwell—1 male, 1 female; La Selva Biological Station, ex *Columnea purpurata* (Gesneriaceae), 10-I-90, R. K. Colwell—1 male; Angel Falls, ex *Columnea* sp., 23-III-71—1 male; Puntarenas Province, San Vito de Java, Cloud Forest, ex *Phaethornis guy coruscus* Bangs (Trochilidae), 16-III-71, R. K. Colwell—2 males; San Vito de Java, Cloud Forest, ex Gesneriaceae (yellow-orange flowers), 12-III-71, R. K. Colwell—1 male; San Vito de Java, 1 km W Field Station, ex unidentified floral host, 11-III-71, R. K. Colwell—1 female; San Vito de Java, Las Cruces, ex *Dalbergaria florida* (Wiehler) Morton (Gesneriaceae), 27-II-75, J. Utley—1 male, 2 females; same locality, ex *Columnea* sp., 22-II-75, J. Utley—4 males; San Vito de Java, ex *Columnea* sp., 11-III-71, R. K. Colwell—1 male, 1 female.

Remarks. *Rhinoseius tiptoni* is one of the most basal species of the genus, retaining several plesiomorphic character states shared with basal species of the sister genus, *Tropicoseius.* These include an unmodified genital shield in the female (no incision on the hyaline part of the shield), a relatively very long major duct of the inseminating apparatus with a poorly developed infundibulum, and the fixed digit of the female chelicera with 3–4 small teeth (Fig. 2e). The closest relative of *R. tiptoni* seems to be *R. pastorae* Wiese & Fain, from which it differs in having characteristically modified opisthonotal setae *z4* and *s4* in the male, strongly shortened setae around the anal shield, a distinctly shorter spermatodactyl, and an unmodified genital shield in the female.

Although the original description of the species (Baker & Yunker 1964) depicts a male with opisthoventral setae *Zv1* on soft cuticle, almost all males in our collection have these setae on the ventral shield. Therefore, in our cladistic analysis, *Zv1* is coded as on the shield.

This is the only species of the genus that has not been collected from flowers of the family Ericaceae. Apparently, it feeds primarily on Gesneriaceae.

Rhinoseius pastorae Wiese & Fain, 1993

Rhinoseius pastorae Wiese and Fain 1993: 77–82, figs, 6–10 (male and female; type locality: Colombia, Cordilliera Central).

Material Examined. Ecuador: Napo, elev. 2500 m, ex *Alloplectus dielsii* (Mansf.) Wiehl (Gesneriaceae), 18-VI-85, B. Stein, 3083—1 male, 2 females; Napo, Rd. to Puyo, 0°27′S, 77°51′W, elev. 1830 m, 9.5 km S Beza, ex *Ceratostema peruvianum* Gmelin (Ericaceae), 16-X-92, J. L. Luteyn, 14697—1 male.

Remarks. This recently described species bears some resemblance to *R. tiptoni,* and like *R. tiptoni* still shows some character states that we believe are ancestral within the genus *Rhinoseius.* These include a relatively strongly enlarged leg II in males, with setae *av* on the femur and *av3* on the tarsus strongly enlarged and spinelike, as well as an unmodified spermatodactyl devoid of the subapical lobe. *R. pastorae* can be distinguished easily from *R. tiptoni* by the presence of flagelliform opisthoventral setae in males and distinctly longer spermatodactyls. Although the drawings that accompany the original description (Wiese and Fain 1993) depict a female

with the anterior part of its genital shield rounded, both female specimens in our collection have genital plates distinctly incised anteriorly. Otherwise our specimens agree fully with this description.

Rhinoseius pastorae was originally described from flowers considered to be an unidentified species of Bromeliaceae.

Rhinoseius luteyni, new species
(Figs. 29–30)

Diagnosis. Dorsal shield of male entire, with no lateral incisions; that of female with lateral incisions between setae *z6* and *Z1*; ornamentation of shield well-developed only in antero-lateral region. Male podonotal setae *j3–j6* and *z5–z6*, and opisthonotal *J5* (sometimes also *J1*) short; remaining dorsal setae either long and flagelliform or thickened, fusiform; setae *z3*, *s6*, *J3*, *Z4*, and *S1* absent in both sexes; dorsal setae of female short, subequal. Ventrianal shield of male divided into rudimentary, transverse ventral shield, and roughly circular anal shield; opisthoventral setae short, except for flagelliform *Jv4*, *Jv5*, and *Zv3*. Second leg in male only slightly stouter than remaining legs; seta *av* of femur only slightly thickened, *pv1* and *pv2* of femur knoblike; *av* and *pv* of genu spinelike; *av2* and *av3* of tarsus with enlarged, bulbous bases. Genital shield of female with anterior hyaline part distinctly incised; posterior part distinctly reticulate. Spermatodactyl directed posteroventrad, straight, with subapical lobiform projection; inseminating apparatus of female with small infundibulum.

Male. Dorsal shield 484–549 μm long, 280–301 μm wide (measured at level of setae *s3*; 5 specimens), entire, without lateral incision. Reticulate ornamentation of shield well-developed only in antero-lateral region of shield (Fig. 29a). Dorsal shield with 29 pairs of setae, including 17 pairs on podonotal and 12 pairs on opisthonotal shield; podonotal setae *z3* and *s6* absent, *j1* long (23–28 μm); some podonotal setae short: *j3* 7–9 μm, *j4* 11–12 μm, *j5* 11–14 μm, *j6* 11–12 μm, *z5* 16–23 μm, *z6* 11–25 μm; other podonotal setae long: *j2* 42–50 μm, *z2* 41–52 μm, *z4* 50–86 μm, *s3* 56–79 μm, *s4* 65–90 μm; opisthonotal setae *J3*, *Z4*, and *S1* absent; *J1* shorter than other opisthonotal setae (17–32 μm); lateral opisthonotal setae long, flagelliform: *S2* 68–152 μm, *S3* 97–153 μm, *R1* 97–108 μm, *R2* 90–106 μm; other opisthonotal setae long, thickened, fusiform : *J2* 52–65 μm, *Z2* 59–72 μm, *Z3* 62–77 μm; *J5* simple, not accompanied by microspinules.

Tritosternum with broad, trapezoidal base and long, broadly spaced laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; ornamentation discernible only in its posterior region. Paragenital setae absent. Metapodal plates small, elongate. Ventrianal shield divided into rudimentary, transverse ventral shield, with setae *Jv2* and *Zv1*, accompanied by 2 small, transverse platelets; and roughly circular anal shield that bears only para-anal and postanal setae; all remaining ventral setae on soft cuticle

around anal shield. Ventral setae *Jv1–Jv3*, and *Zv1–Zv2* short, subequal; remaining 3 pairs of opisthoventral setae (*Jv4*, *Jv5*, *Zv3*) long, and flagelliform (Fig. 29b). Peritrema extending almost to level of setae *s1*; peritrematic plates reduced to narrow vestiges around stigmas.

Gnathosoma with tectum short, broadly rounded apically. Fixed digit of chelicera bidentate; movable chela edentate; spermatodactyl directed posteriad, 68–72 μm long, with small subapical lobe (Fig. 30e); apical part of spermatodactyl curved inward, as seen ventrally (Fig. 30d). Rostral setae slender, simple; anterior rostral pairs long (25–27 μm), posterior exterior pairs shorter than posterior interior pairs (14–16 μm and 28–29 μm, respectively); capitular setae simple, somewhat shorter than anterior rostral pair (16–23 μm). Corniculi with their inner margins divergent. Setae *al1* and *al2* on palpgenu widened apically, but not distinctly spatulate; *al* on palpfemur spatulate; *d3* on palpfemur enlarged, spinelike.

Second leg not greatly enlarged, slightly curved ventrally between femur and tarsus; seta *av* of femur only slightly thickened, *pv1* and *pv2* of femur knoblike; *av* and *pv* on genu spinelike; setae of tibia not modified; setae *av2* and *av3* of tarsus with bulbous bases and acute apices (Fig. 29c). Tarsus of leg III with no modified setae. Coxa I with 2 external and 3 internal rows of denticles; coxae II–IV with no discernible bosses; coxa IV not modified. Setation of legs as noted for genus.

Female. Dorsal shield 560–575 μm long, 277–289 μm wide (measured at level of setae *s3*; 5 specimens), with distinct lateral incisions between setae *z6* and *Z1*, not connected by transverse suture. Reticulate ornamentation best developed in lateral regions of shield (Fig. 30a). Dorsal shield with 28 pairs of short, simple setae, including 16 pairs on podonotal and 12 pairs on opisthonotal regions; setae *z3* and *s6* of podonotal region, and setae *J3*, *Z4*, and *S1* of opisthonotal region absent; podonotal setae *j1* short (16–20 μm); most dorsal setae generally short (6–20 μm), with *Z5* the longest (32–47 μm), and *J5* very short (6 μm), accompanied by a bundle of microspinules; all setae of series *r* and *R* on soft cuticle.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; anterior margin of sternal shield truncated, with no ornamentation. Fourth pair of sternal setae and 3rd pair of sternal pores on soft cuticle behind posterior margin of sternal shield. Anterior hyaline part of genital shield widened and with deep angular incision; reticulate ornamentation of posterior part of shield distinct; setae *st5* on soft cuticle beside shield. Metapodal plates small, elongate. Anal shield roughly circular, with poorly developed ornamentation; postanal seta about twice as long as paraanal setae (Fig. 30b). Seven to 9 posteroventral setae on soft cuticle around anal shield. Inseminating apparatus with relatively small infundibulum and short, threadlike spermiduct (34–45 μm) (Fig. 30c).

Tectum shorter than in male, smooth; corniculi with inner margins straight, parallel; fixed digit of chelicera bidentate, movable chela edentate;

mucro reaching apex of chela (Fig. 30f); *d3* on palpfemur not modified. Second leg not modified; setae of all legs short but otherwise their arrangement as in male.

Type Material. Ecuador: Cotopaxi National Park, 8 km SE Pan American Junction, ex *Castilleja* sp. (Scrophulareaceae), 11-VIII-76, R. K. Colwell—male (holotype), female (allotype), 10 males, 16 females (paratypes); Napo, Slacedo-Napo rd., elev. 2926 m, 0°55′S 78°30′W, ex *Psammisia incana* Luteyn (Ericaceae), 23-XI-89, J. L. Luteyn, 13393—2 males, 1 female (paratypes).

Etymology. This new species is named in honor of James L. Luteyn (The New York Botanical Garden, Bronx, NY), authority on the taxonomy and biology of neotropical Ericaceae, collector of this species and thousands of other specimens of hummingbird flower mites in preserved, determined floral material generously made available to this study.

Remarks. *Rhinoseius luteyni* n. sp. is most closely related to the recently described *R. ucumariensis* Wiese & Fain from Colombia, with which it shares the absence of setae *J3* in both sexes. The 2 species share with *R. rafinskii* Micherdzinski & Lukoschus and *R. nadachowskyi* Wiese & Fain the presence of a characteristic triangular, subapical lobe on the spermatodactyls. All 4 species also are characterized by seta *av* on male femur II either not modified or only slightly enlarged. *R. luteyni* n. sp. can be distinguished from other species of the genus by long, flagelliform setae of series *z, s, r, S,* and *R* in males, as well as setae *j2, J2, J4, Z2, Z3,* and *Z5* thickened, and fusiform. Females of the new species can be distinguished from those of *R. ucumariensis* by the proportions of the dorsal shield. In the new species, the opisthonotal region of the shield is only slightly shorter than the podonotal one, whereas in *R. ucumariensis* the podonotal region is at least 1.4 times longer than the opisthonotal one.

Rhinoseius ucumariensis Wiese & Fain, 1993

Rhinoseius ucumariensis Wiese and Fain 1993: 70–75, 77–78, figs. 1–5 (male and female; type locality: Colombia, Cordilliera Central).

Material Examined. Peru: Amazonas, Chachapoyas, elev. 3000 m, ex *Centropogon argutus* Wimmer (Campanulaceae), 4-II-85, B. Stein, 2080—1 male, 1 female; Amazonas, 19km SW Leimebamba, 6°45′S, 77°48′W, elev. 3020 m, along rd. to Balsas, ex *Vaccinium mathewsii* Sleumer (Ericaceae), 13-II-85, J. L. Luteyn, 11382—2 males, 1 female; **Ecuador:** Napo, elev. 3200 m, ex *Siphocampylus ecuadoriensis* Wimmer (Campanulaceae), 18-VI-85, B. Stein, 3085—4 males, 6 females; halfway between Papallacta and Borja, elev. 2438 m, ex Ericaceae, 9-II-(coll. P. Feinsinger—3 males, 1 female; Pan American Hwy, Santa Rosa Turns, 15 km S Quito, ex *Siphocampylus giganteus* (Cavanilles) G. Don, 12-VIII-76, R. K. Colwell—1 male, 14 females; Cañar, 7–9 km NE Pindilíg toward Rivera, 2°35′S, 78°49W, elev. 3000–3200 m, ex *Siphocampylus scandens* (H. B. K.) G. Don, 19-I-85, J. L. Luteyn, 11106—3 males, 4 females; Carchi, Tulcán-El Caramelo rd., 0°45′N, 77°40′W, elev. 3300 m, 27 km E Panamerican Hwy., ex *Siphocampylus ecuadoriensis* Wimmer, 10-I-85, J. L. Luteyn, 10953—1 male.

Remarks. This species is closely related to *R. luteyni* n. sp. but can be easily distinguished by the set of characters listed in the remarks under the description of the new species. Males of *R. ucumariensis* can also be recognized by having setae on the podonotal region of the dorsal shield distinctly longer than those on the opisthonotal region. It is interesting to note that a similar tendency can be observed in some species of the genus *Proctolaelaps* associated with hummingbird-pollinated flowers (e.g., *P. jurgatus* OConnor, Colwell & Naeem).

Rhinoseius ucumariensis was originally described from flowers of an unidentified species of Gesneriaceae.

Rhinoseius rafinskii Micherdzinski & Lukoschus, 1980

Rhinoseius rafinskii Micherdzinski and Lukoschus 1980: 65–78, figs. 1–10 (male and female; type locality: Ecuador, Volcán Cotopaxi).–Fain 1992: 117–119, 123, 127, 132.–Wiese and Fain 1993: 70, 78, 82.

Type Material. Ecuador: Volcano Cotopaxi, ex *Vaccinium corymbosum* (Ericaceae), elev. ≈ 4000 m, 24 -XI-75, J. Rafinski—1 female (paratype) (FMNH); **Venezuela:** La Carbonera, Cordil de Merida, ex undet. Liliaceae, 2-X-75, J. Rafinski—2 males, 1 female, 2 larvae (paratypes) (FMNH).

Remarks. This is probably one of the most highly derived species of the genus; closely related to the recently described *R. nadachowskyi* Wiese and Fain. It is characterized by an entire male dorsal shield, opisthonotal setae in male spinelike and moved anteriad, division of the male ventrianal shield into ventral shield with setae *Jv1–Jv2* and *Zv1–Zv2* (only *Jv1* and *Zv1* on shield in *nadachowskyi*), the presence of a subapical, lobiform projection on the spermatodactyl, and incised anterior, hyaline part of the genital shield (a character omitted in the original description); and the absence of opisthonotal setae *z4* and *s1* in the female.

Typically for the genus, *R. rafinskii* occurs at high elevations and is associated with flowers of Ericaceae, although some specimens were collected also from *Puya* sp. (Bromeliaceae) and unidentified species of Liliaceae (Micherdzinski and Lukoschus 1980).

Rhinoseius nadachowskyi Wiese & Fain, 1993
(Figs. 31–32)

Rhinoseius nadachowskyi Wiese and Fain 1993: 82–84, figs. 11–12 (male; type locality: Colombia, Cordillera Central, Parque de Ucumari, in valley of Río Otún).

Diagnosis. Dorsal shield of male entire, without lateral incisions; that of female with distinct lateral incisions between setae *z6* and *Z1*; reticulate ornamentation of shield well-developed in anterolateral regions only. Podonotal setae straight and simple, setae *z1, z3, s6,* and *S1* absent in both sexes, in female also *J3* and *Z4* absent; in male opisthonotal setae *J2, J4, Z2,* and *Z3* strongly thickened, spinelike; dorsal and lateral setae of female short, subequal. Peritrema shortened, reaching level of seta *s2*. Ventrianal shield of male divided into small, transverse ventral shield with setae *Jv1* and *Zv1* and roughly circular anal shield; opisthoventral setae short, some of them slightly thickened. Second leg of male only slightly enlarged; femur with setae *pv1* and *pv2* spinelike, distinctly larger than slightly thickened *av*; genu and tibia with setae *av* and *pv* thickened, spinelike; tarsus with setae *av2* and *av3* spinelike; coxae IV in both sexes with small posterior spurs. Genital shield of female with hyaline anterior part distinctly incised. Spermatodactyl directed posteroventrad, with small subapical lobe; inseminating apparatus of female with bulbous infundibulum and short spermiduct.

Male. Dorsal shield 432–492 μm long, 240–300 μm wide (measured at level of setae *s3*; 12 specimens), entire, without lateral incisions; reticulate ornamentation distinct in anterolateral region (Fig. 31a). Dorsal shield with 29–30 pairs of setae; setae *z1, z3* and *s6* absent; *j1* relatively long (22–24 μm); opisthonotal setae *J2, J4, Z2, Z3* and *Z4* strongly thickened, spinelike, their lengths as follows: *J2* 68–75 μm, *J4* 51–66 μm, *Z2* 62–70 μm, *Z3* 66–73 μm, and *Z4* 66–77 μm; *J5* minute, accompanied by microspinules; opisthonotal setae *J3* and *S1* absent. All remaining dorsal setae not modified, straight, and simple.

Tritosternum with broad, trapezoidal base and slender, pilose laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; reticulate ornamentation poorly developed. Paragenital setae absent. Metapodal plates usually small, roughly circular or elongate. Ventrianal shield divided into small, transverse ventral shield, with setae *Jv1* and *Zv1* (1 or both setae *Zv1* sometimes on soft cuticle), and roughly circular anal shield, bearing only para-anal and postanal setae; all remaining ventral setae on soft cuticle around anal shield (Fig. 31b). Peritrema short, reaching level of setae *z4*; peritrematic plates reduced to narrow vestiges around stigmas.

Gnathosoma with tectum short, broadly rounded anteriorly. Fixed digit of chelicera tridentate; movable chela edentate; spermatodactyl directed posteroventrad, short, straight, and with small, lobiform subapical projection; apex of spermatodactyl slightly bent (Fig. 31e). Deutosternum with 7 equally narrow rows of denticles; all rows connected. Rostral setae slender, simple; anterior rostral pairs long (29 μm), posterior exterior pairs shorter than posterior interior pairs (11 μm and 25 μm, respectively); capitular setae simple, about as long as anterior rostral pair (23–25 μm). Corniculi short, outwardly curved and bilobed apically; internal malae narrow, reaching tips of corniculi (Fig. 31c). Setae *al1* and *al2* on palpgenu, and *a1* on palpfemur spatulate.

Second leg only slightly enlarged, weakly curved ventrally between femur and tarsus; femur with setae *pv1* and *pv2* spinelike, distinctly larger than only slightly thickened *av*; genu and tibia with setae *av* and *pv* thickened, spinelike; tarsus with setae *av2* and *av3* spinelike (Fig. 32d). Tarsus of leg III with no modified setae. Coxa I with 2 external and 3 internal rows of denticles; coxae II–IV with no discernible bosses; coxae IV with small posterior spurs. Setation of legs as noted for genus.

Female. Dorsal shield 510–672 μm long, 273–312 μm wide (measured at level of setae *s3*; 8 specimens), with lateral incisions between setae *z6* and *Z1*, surpassing level of setae *z6* and not connected by transverse suture. Reticulate ornamentation restricted to anterolateral regions of shield (Fig. 32a). Dorsal shield with 28–29 pairs of short, simple setae, including 15 pairs on podonotal and 13–14 pairs on opisthonotal regions; setae *z1, z3,* and *s6* of podonotal region and setae *Z4* and *S1* of opisthonotal region absent (rarely *Z4* present); most dorsal setae generally subequal, with *Z5* the longest (18–26 μm); *J5* the shortest (13–18 μm), accompanied by microspinules.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; anterior margin of sternal shield convex, without lobes; reticulate ornamentation poorly discernible, restricted to its anterior part or absent. Fourth pair of sternal setae and 3rd pair of sternal pores on soft cuticle behind posterior margin of sternal shield. Anterior hyaline part of genital shield widened and with deep angular incision; longitudinal ornamentation of posterior part of shield distinct. Metapodal plates small, elongate, in some specimens 1 or both plates absent. Anal shield roughly circular, with poorly developed ornamentation; postanal seta about twice as long as para-anal setae (Fig. 32b). Nine to 11 pairs of posteroventral setae on soft cuticle around anal shield. Inseminating apparatus with large, bulbous infundibulum and short, threadlike spermiduct.

Tectum shorter than in male, crenulate or smooth (Fig. 32c); corniculi with inner margins straight, parallel; fixed digit of chelicera tridentate, movable chela edentate but with a small hump; mucro reaching or surpassing apex of chela (Fig. 31d).

Second leg not modified; coxae IV with small posterior spurs; setae of all legs very short but otherwise their arrangement as in male.

Material Examined. Colombia: Putumayo, Pasto-Sibundoy rd., 3015–3130m, km 33–34, ex *Plutarchia angulata* A. C. Smith (Ericaceae), 25-I-75, J. L. Luteyn, 5020—1 male; same locality, km 33–36 E Pasto, ex *Plutarchia angulata* A. C. Smith, 20-II-79, J. L. Luteyn, 6786—2 females; **Venezuela:** Merida Province, Trail from La Negrita to the Boqueron of Quebrada de Las Canas, elev. 2990–3300 m, ex *Cavendishia ruiz-teranii* Luteyn (Ericaceae), 31-X-78, J. L. Luteyn, 6099—32 males and 36 females;

Ecuador: Cotopaxi, Latacunga-Quevedo rd., 0°58′S, 78°56′W, 274–3350m, 3–14km E Pilaló, ex *Sphyrospermum buxifolium* Poeppig & Endlicher (Ericaceae), 4-IV-92, J. L. Luteyn, 14400—1 male, 1 female; Loja, Loja-Vilcabamba Rd., 4°8′S, 79°13′W, 2160m, 29 km N Vilcabamba, ex *Macleania puberula* Bentham (Ericaceae), 24-X-92, J. L. Luteyn, 14712—1 male, 1 female; Pichincha, Calacalí-Nanegalito Rd., 0°6′N, 78°30′W, elev. 1800 m, 1 km SE Nanegalito, ex *Thibaudia floribunda* H. B. K. (Ericaceae), 17-XI-92, J. L. Luteyn, 14787—4 males, 1 female; Zamora/Chinchipe, Vilcabamba-Valladolid, 4°30′S, 79°8′W, 2470–2560m, 21.3–24.6 km S Yananga, ex *Ceratostema reginaldi* (Sleumer) A. C. Smith (Ericaceae), 23-X-92, J. L. Luteyn, 14708—7 males, 3 females.

Remarks. This species, recently described on the basis of 2 male specimens by Wiese and Fain (1993), is closely related to *R. rafinskii* Micherdzinski & Lukoschus. The 2 species are characterized by the presence of several pairs of highly modified, spinelike setae on the male opisthonotum. A superficially similar, but independently derived condition can be observed in 2 species of the *richardsoni* group, *R. richardsoni* Hunter & *R. antioquiensis* Fain & Hyland. However, in these 2 species the modified, spinelike setae are probably homologous with setae *J1* and *Z1* in females, whereas in *R. rafinskii* and *R. nadachowskyi* the modified dorsal setae are most likely homologous with setae *J2–J4* and *Z2–Z4* of the female. Although there are no observations revealing the function of the modified setae in males of the 2 species of the *rafinskii* group, it is not unlikely that they play a similar, self-defensive role as do analogous setae in *R. richardsoni* (Colwell 1973).

Rhinoseius nadachowskyi can be distinguished from *R. rafinskii* by the higher number of the modified setae in the male (5 versus 4 pairs), a stronger reduction in size of the ventral shield in the male, and the absence of opisthonotal setae *Z4* in the female. Also, the opisthoventral setae surrounding the anal shield in the male are usually thicker and shorter than the corresponding setae in males of *R. rafinskii.*

Group *richardsoni*

Species in this group are characterized by a large ventrianal shield in males that covers most of the opisthosomal venter, the absence of opisthonotal setae *J3* in females, and the presence of large posterior spurs on coxae IV in both sexes. The dorsal shield in males is either completely divided into podonotal and opisthonotal shields, or marked by deep lateral incisions. Females of all species have a dorsal shield typical for the genus, with lateral incisions between the level of setae *z6* and *Z1.*

Rhinoseius caucaensis Ohmer, Fain & Schuchmann, 1991

Rhinoseius caucaensis Ohmer, Fain, and Schuchmann 1991: 481, 484–489, figs. 1–13 (male and female; type locality: Colombia, Depto. Valle de Cauca).—Fain 1992: 120, 123, 127, 133, fig. 30.

Type Material. Colombia: Bajo Calima, Depto. Valle del Cauca (04°08′N, 77°04′W), pluvial lowland forest, elev. 50 m, ex *Amazilia rosenbergi* (Boucard) (Trochilidae), C. Ohmer—1 male, 1 female (paratypes)(IRSNB).

Remarks. *Rhinoseius caucaensis* is one of the basal species of the genus, retaining several plesiomorphic character states that include a female genital shield with its hyaline part not incised but rounded, a condition typical for other Melicharini. Also, the male dorsal shield is undivided (all other species of the *richardsoni* group have completely divided shields), and the opisthonotal setae are unmodified. Interestingly, this species has opisthonotal setae *Z5* serrated, a character state that among other hummingbird flower mites is present only in females of *T. erioxynon* and *T. fuentesi* n spp.. There is little doubt that this is a case of an independent derivation of the character state (homoplasy).

There are no host plant records for this species, but most likely it feeds on plants of the family Ericaceae. However, its closest relatives, *R. haplophaedia, R. androdon, R. richardsoni,* and *R. antioquiensis,* are associated primarily with the genera *Cavendishia* and *Macleania.*

Rhinoseius haplophaedia Ohmer, Fain & Schuchmann, 1991 (Figs. 33–34)

Rhinoseius haplophaedia Ohmer, Fain, and Schuchmann 1991: 481, 489–490, figs. 14–18 (female; type locality: Colombia, La Planada).-Fain 1992: 120, 123, 127, 132, fig. 28.

Diagnosis. Dorsal shield of male completely divided into separate podonotal and opisthonotal shields, that of female with deep, characteristically downcurved incisions between setae *z6* and *Z1.* Reticulate ornamentation of male shields best developed in their antero-lateral regions, female shield without discernible reticulation. Dorsal setae *s6, z3, J3,* and *Z4* absent in both sexes; setae *Z5* in both sexes thickened, usually with slightly dilated apices. Ventrianal shield of male large, with setae *Jv1–Jv3* and *Zv1–Zv3.* Coxae II in both sexes characteristically impressed along posterior edge; coxae IV in both sexes with posterior spurs. Second leg in male not greatly enlarged; seta *av* on femur, large, spinelike, located on small chitinous protuberance; setae *av* of genu knoblike; *av2* and *av3* of tarsus knoblike. Genital shield of female with anterior hyaline part distinctly incised. Spermatodactyl directed posteriad, straight; inseminating apparatus of female poorly discernible, with small, bulbous infundibulum and short, threadlike sperm duct.

Male. Dorsal shield 584–596 μm long, 295–307 μm wide (measured at the level of setae *s3*; 5 specimens), completely divided into separate podonotal and opisthonotal shields between levels of setae *z6* and *Z1.* Reticulate ornamentation of shields most distinct in antero-lateral regions (Fig.

33a). Dorsal shield with 30 pairs of setae, including 17 pairs on podonotal and 13 pairs on opisthonotal shield; podonotal setae *z3* and *s6* absent, *j1* relatively long (34–39 μm); dorsal setae generally short: *j2* 14 μm, *j3* 17–18 μm, *j4* 17–23 μm, *j5* 18–25 μm, *j6* 25–34 μm, *z2* 14–20μm, *z4* 25 μm, *z5* 23–25 μm, *z6* 28–34 μm; opisthonotal setae *J3* and *Z4* absent; *J5* short (9–11 μm), simple; *Z5* the longest (65–75 μm), thickened and usually with slightly dilated apices.

Tritosternum with broad, trapezoidal base and long, broadly spaced laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; weak ornamentation discernible only in its posterior region. Paragenital setae absent. Metapodal plates small, elongate. Ventrianal shield large, with irregular lateral margins, with setae *Jv1–Jv3, Zv1–Zv3,* and anal setae; setae *Jv4–Jv5, Zv4–Zv5, Sv1–Sv2,* and *UR*'s on soft cuticle around shield (Fig. 33b). Peritrema slightly surpassing level of setae *s1*.

Gnathosoma with tectum short, deeply serrated anteriorly (Fig. 33e). Fixed digit of chelicera tridentate; movable chela edentate; spermatodactyl directed posteriad, 99–104 μm long, straight and simple (Fig. 33c). Rostral setae slender, simple; anterior rostral pairs only slightly longer than capitular setae simple. Corniculi short, outwardly curved. Setae *al1* and *al2* on palpgenu widened apically, spatulate; *al* on palpfemur spatulate.

Second leg not greatly enlarged, curved ventrally between femur and tarsus; seta *av1* on femur enlarged, spinelike, situated on small chitinous protuberance; *av1* on genu enlarged, knoblike, *av1* on tibia unmodified; setae *av2* and *av3* of tarsus knoblike (Fig. 33d). Tarsus of leg III with no modified setae. Coxa I with one external and 2 internal rows of denticles; coxae II characteristically impressed along posterior edge (Fig. 33d); coxae IV with large posterior spurs; coxae II–IV with no discernible bosses. Leg setation as noted for genus.

Female. Dorsal shield 720–726 μm long, 330–354 μm wide (measured at the level of setae *s3*; 4 specimens), with distinct, characteristically downcurved lateral incisions between setae *z6* and *Z1* slightly surpassing level of setae *z6,* never connected by a transverse suture. Shield smooth, with no discernible ornamentation (Fig. 34a). Dorsal shield with 29 pairs of short, simple setae, including 16 pairs on podonotal and 13 pairs on opisthonotal regions; setae *z3* and *s6* of podonotal region, and setae *J3* and *Z4* of opisthonotal region absent; podonotal setae *j1* 18 μm long; most dorsal setae generally short (21–25 μm); *Z5* the longest (61 μm), thickened and with slightly dilated apices; *J5* minute (11 μm), accompanied by a bundle of microspinules.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; anterior margin of sternal shield truncated, with no ornamentation. Fourth pair of sternal setae and 3rd pair of sternal pores on soft cuticle behind posterior margin of sternal shield. Anterior hyaline part of genital shield widened and with shallow angular incision, posterior part of

shield behind setae *st5* distinctly widened and usually accompanied by a pair of small, transverse platelets; longitudinal ornamentation of shield weak, restricted to its posterior part; setae *st5* on soft cuticle beside shield. Metapodal plates small, elongate. Anal shield elliptical, nearly straight-sided, slightly longer than wide; postanal seta ≈1.5 times as long as para-anal setae (Fig. 34b). Nine to 18 posteroventral pairs of setae on soft cuticle around anal shield, some setae often missing from one or both sides of ventral region. Inseminating apparatus poorly discernible, with bulbous infundibulum and short, threadlike sperm duct.

Tectum shorter than in male, smooth or weakly serrated; corniculi more slender than in male, with inner margins straight, parallel; fixed digit of chelicera tridentate, movable chela edentate, mucro short, not reaching half of movable chela.

Second leg not modified; leg setation as in male; coxae II characteristically impressed along posterior edge; coxae IV with large posterior spurs.

Type Material. Colombia: Depto. Narino, La Planada (forest reserve) (00°54′N, 77°47′W), elev. 1000 m, ex *Haplophaedia lugens* (Gould) (Trochilidae), 21-III-89, C. Ohmer 1 female (paratype)(IRSNB).

Material Examined. Ecuador: Napo-Pastaza, Baeza-Tena rd., 2030–2175, 1–5 km SE Cosanga, ex *Cavendishia pseudospicata* Sleumer (Ericaceae), 6-IV-78, J. L. Luteyn, 5674—13 males, 9 females; Pichincha, Calacalí-Nanegalito Rd., 0°6′N, 78°30′W, elev. 1800 m, ≈ 23km NW Calacalí, ex *Macleania* cf. *ericae* (Ericaceae), 17-XI-92, J. L. Luteyn, 14789—1 male; same locality, ex *Macleania coccoloboides* x cf. *ericae,* J. L. Luteyn, 8474—3 males; Nono-Tandayapa Rd., 0°1′S, 78°38′W, 1830m, ≈ 20.8 km W Nono, ex *Disterigma pentandrum* Blake (Ericaceae), 18-XI-92, J. L. Luteyn, 14791—2 males; Nono-Pto. Quito Rd., 0°4′S, 78°N, 1650–1900m, km 59, ex *Macleania stricta* A. C. Smith, 15-XI-89, J. L. Luteyn, 13339—2 males, 1 female; Pichinga, Antigua-Sto. Domingo, 1800–1900m, Carr. Antigua-Sto. Domingo, km 72–74, ex *Anthopterus verticillatus* Luteyn (Ericaceae), 3-IV-78, J. L., 5650—3 males, 6 females.

Remarks. This species was originally described on the basis of 2 female specimens collected from nasal cavities of the hummingbird *Haplophaedia lugens* from La Planada, Colombia (Ohmer et al. 1991). Here we describe the male for the 1st time and redescribe the female. This species is most closely related to *R. antioquiensis* Fain & Hyland, *R. richardsoni* Hunter and *R. androdon* Fain & Hyland. These species share a completely divided dorsal shield and a well-developed, large ventrianal shield in males. Dorsal setae *J1* and *Z1* in males of *R. haplophaedia* and *R. androdon* retain the plesiomorphic, unmodified condition, whereas in the 2 remaining species these setae are highly modified and spinelike. Unique apomorphies of *R. haplophaedia* include thickened setae *Z5* that usually have slightly dilated apices, seta *av* on the femur of the 2nd legs in males situated on a

prominent well-sclerotized protuberance, and coxae II in both sexes with characteristically impressed posterior edges.

Like most species of the genus, *R. haplophaedia* is found at middle to high elevations in flowers of the family Ericaceae.

Rhinoseius androdon Fain & Hyland, 1980

Rhinoseius androdon Fain and Hyland 1980: 15, 17, 19, figs. 2, 5, 10–12, 15 (male and female; type locality: Colombia, Antioquia).–Ohmer, Fain, and Schuchmann 1991: 481, 482, 489, 490, 492.– Fain 1992: 119, 123, 127, 133, figs. 12, 27.

Material Examined. Colombia: Chocó, Río Fujiado, affluent of Rio San Juan, 4°36′N, 76°54′W, ex *Cavendishia coccinea* A. C. Smith (Ericaceae), 7 Apr. 1979, J. L. Luteyn, 4787—9 males, 1 female.

Remarks. This species was originally described from specimens collected in Antioquia, Colombia, from the hummingbird *Androdon equatorialis.* Along with closely related *R. richardsoni, R. antioquiensis,* and *R. haplophaedia,* this species is characterized by a completely divided dorsal shield in the male. With *R. antioquiensis* and *R. richardsoni* it also shares the presence of a pair of posterior processes on the ventrianal shield. Unlike these 2 species, however, male opisthonotal setae show the plesiomorphic, unmodified condition. Typically for the genus, *R. androdon* occurs at high elevations on flowers of the family Ericaceae.

Rhinoseius richardsoni Hunter, 1972
(Figs. 2a, 35–36)

Rhinoseius richardsoni Hunter 1972: 26–30, figs. 1–2 (male and female; type locality: Costa Rica, Cerro de la Muerte).–Colwell 1973: 743–745,748–750.–Fain, Hyland, and Aitken 1977b: 101, 109, 117, 122, 136, 150, figs. 16, 34, 56.–Colwell 1979: 463, 466.–Fain and Hyland 1980: 15, 17.–Micherdzinski and Lukoschus 1980: 77–78.–Colwell 1983: 768.–Colwell 1986b: 408, 409, 413.–Ohmer, Fain, and Schuchmann 1991: 489, 490, 492, 493.–Farrier and Hennessey 1993: 49.

Rhinoseius panamensis Fain, Hyland, and Aitken 1977a: 186 (male; type locality: Panama, Chiriquí Province, Cerro Punta)—**n. syn.**–Fain, Hyland, and Aitken 1977b: 109, 113, 122, 136, 150–151, figs. 118–121.–Fain and Hyland 1980: 15, 17.–Micherdzinski and Lukoschus 1980: 77.–Ohmer, Fain, and Schuchmann 1991: 481, 490–493, figs. 19–25.

Diagnosis. Dorsal shield of male completely divided into podonotal and opisthonotal shields; that of female with lateral incisions between setae *z6* and *Z1*; reticulate ornamentation restricted to anterolateral regions of shield, that of female distinct over entire shield. Podonotal setae straight and simple, setae *z1, z3, s6, J3* and *Z4* absent in both sexes, setae *J2, J4,*

Z2, and *Z3* absent only in male; opisthonotal setae *J1* and *Z1* of male strongly thickened, spinelike, often with spiral pattern; *Z5* and *S5* straight and moderately thickened to strongly enlarged, spinelike and with spiral pattern; dorsal and lateral setae of female short (about half as long as distance between adjacent setal insertions), subequal. Ventrianal shield of male large, with a pair of posterior processes; opisthoventral setae straight and moderately elongated to distinctly flagelliform. Genital shield of female with hyaline anterior part distinctly incised. Spermatodactyl short, almost straight to weakly incurved, directed posteroventrad; inseminating apparatus of female with large, bulbous infundibulum and threadlike spermiduct.

Male. Dorsal shield 460–500 μm long, 260–295 μm wide (measured at level of setae *s3*; 15 specimens), completely divided into podonotal and opisthonotal shields; reticulate ornamentation discernible only in anterolateral regions of podonotal shield (Fig. 35a and b). Dorsal shields with 27–29 pairs of setae, including 16–17 pairs on podonotal and 11–12 pairs on opisthonotal shields; setae *z1, z3* and *s6* absent, *j1* long (34–40 μm); *J1* and *Z1* strongly modified, thick and spinelike, often with spiral pattern (length 60–67 μm, width 8–11 μm), opisthonotal setae*J2–J4* and *Z2–Z4* absent, *J5* minute, accompanied by bundle of microspinules; *Z5* and *S5* variable, short and moderately thickened (Fig. 35a) to strongly enlarged, spinelike with spiral pattern (Fig. 35b), their size, respectively: length 71–100 and 63–89 μm, width at base 4–11 μm; intermediate forms are common (Fig. 35c).

Tritosternum with broad, trapezoidal base and comparatively short, slender pilose laciniae. Sternogenital shield with 5 pairs of setae and 3 pairs of pores; reticulate ornamentation usually easily discerned over entire shield. Paragenital setae absent. Metapodal plates usually small, elongate. Ventrianal shield large, trapezoidal; setae *Jv1–Jv5, Zv1–Zv5,* para-anal and postanal setae on shield, or setae *Jv3* or *Jv4* sometimes on soft cuticle; ventrianal shield with a pair of more or less developed chitinous processes at level of para-anal setae; reticulate ornamentation distinct over entire shield. All ventral setae vary greatly among specimens in their length and structure, from comparatively short and not appreciably thickened (Fig. 35d) to long and flagelliform with distinctly thickened bases (Fig. 35e). Specimens with all setae of intermediate length and thickness often occur. Peritrema extending anteriad to level of seta *z2,* but in some specimens only to level of seta *z4.*

Gnathosoma with tectum short, crenulated anteriorly. Fixed digit of chelicera unidentate; movable chela edentate, with short, almost straight to distinctly incurved spermatodactyl directed posteroventrad (Fig. 36e). Deutosternum with 7 rows of equally narrow denticles; all rows connected. Rostral setae slender, simple; anterior rostral pairs long, posterior exterior pairs shorter than posterior interior pairs; capitular setae simple, about as long as anterior rostral pair. Corniculi short, with internal margins divergent;

internal malae very narrow, distinctly exceeding tips of corniculi. Setae *al1* and *al2* on palpgenu spatulate, *al* on palpfemur dilated apically.

Second leg not greatly enlarged, very slightly curved ventrally between femur and tarsus; femur and genu with seta *av1* small but stout, knoblike, and seta *pv1* spinelike; tibia with no modified setae; tarsus with setae *av1* and *av2* modified, knoblike (Fig. 36f). Tarsus of leg III with no modified setae (Fig. 2a). Coxa I with one external and one internal rows of denticles; coxae II–IV with no discernible bosses; coxae IV with large posterior spurs. Setation of legs typical for genus.

Female. Dorsal shield 520–560 μm long, 260–295 μm wide (measured at level of setae *s3*; 15 specimens), with deep lateral incisions between setae *z6* and *Z1* reaching to level of setae *z6,* never connected by a transverse suture. Reticulate ornamentation distinct over entire shield (Fig. 36a). Dorsal shield with 27–28 pairs of short, simple setae, including 15 pairs on podonotal and 12–13 pairs on opisthonotal regions; setae *z1, z3,* and *s6* of podonotal region, and setae *J3* and *Z4* of opisthonotal region absent; most dorsal setae of similar length (12–26 μm), except for somewhat longer *j1* (27–32 μm), *j2* (38–42 μm), *z2* (40–44 μm), and *s3* (30–35 μm); *J5* minute (5–7 μm), accompanied by microspinules.

Tritosternum as in male. Sternal shield with 3 pairs of setae and 2 pairs of pores; anterior margin of sternal shield convex, without lobes; reticulate ornamentation weak, restricted to its anterior part. Fourth pair of sternal setae and 3rd pair of sternal pores on soft cuticle behind posterior margin of sternal shield. Anterior hyaline part of genital shield widened and with broadly angular incision; longitudinal ornamentation of posterior part of shield distinct. Metapodal plates small, elongate, in some specimens 1 or both plates absent. Anal shield oval, with poorly developed ornamentation; postanal seta about twice as long as para-anal setae (Fig. 36b). Eight to 11 pairs of posteroventral setae on soft cuticle around anal shield. Inseminating apparatus with large, bulbous infundibulum and long, threadlike spermiduct (Fig. 36c), its distal part sometimes indiscernible.

Tectum shorter than in male, crenulate, rarely smooth; fixed digit of chelicera unidentate, movable chela edentate; mucro short, reaching about halfway of chela (Fig. 36d).

Second leg not modified; setae of all legs very short but otherwise their arrangement as in male.

Material Examined. Costa Rica: San Jose Province, Cerro de La Muerte, ex *Macleania rupestris* (H.B.K.) A.C. Smith (Ericaceae), 8-VIII-76, R. K. Colwell—6 females; Cerro de la Muerte, Salsipuedes, 27-III-71, R. K. Colwell—2 females; Cerro de la Muerte, Georgina Hill site 2, ex *Centropogon talamancensis* Wilbur (Campanulaceae), 23-I-71, R. K. Colwell—5 females; Cerro de la Muerte, Log Bank, bagged transplant Cerro, 20-I-71, R. K. Colwell—3 females; Cerro de la Muerte, Salsipuedes, ex *Bomarea* sp. (Amaryllidaceae), 27-III-71, R. K. Colwell—1 male, 2 females; Cerro de la Muerte, Georgina Hill site 2, ex *Eugenes fulgens spectabilis* (Lawrence) (Trochilidae), 16-I-71, R. K. Colwell—1 female; same locality, ex *Panterpe insignis* Cabanis & Heine (Trochilidae), 27-III-71, R. K. Colwell—4 females; Alajuela Province, Monteverde, Station Rd., 24-VIII-80, R. K. Colwell—1 male, 3 females; Monteverde, ex *Macleania* sp., 22-VIII-72, P. Feinsinger—1 male, 2 females; Monteverde, ex *Doryfera ludovicae veraguensis* Salvin (Trochilidae), 16-X-72, P. Feinsinger—2 males, 4 females; Monteverde, ex *Campylopterus hemileucurus mellitus* Bangs (Trochilidae), 22-I-73, P. Feinsinger—2 females; same carrier and locality, 15-XI-72, P. Feinsinger—2 females; Irazu, ex *Macleania* sp., 27-III-71, R. K. Colwell—5 females; Heredia Province, Parque Nacional Braulio Carrillo-Barva, ex Ericaceae, 6-VI-90 (voll. A. Fernandez—34 males, 111 females; Parque Nacional Braulio Carrillo-Barva, ex Gesneriaceae, 6-VI-90 (voll. A. Fernandez—1 male; San Rafael, road to Parque Nacional Braulio Carrillo, ex *Cavendishia* sp. (Ericaceae), 7-I-89, R. K. Colwell—12 males, 23 females; Parque Nacional Braulio Carrillo, Quebrada Cascante, elev. 700 m camp, ex Ericaceae—4 males, 4 females; Parque Nacional Braulio Carrillo-Barva, ex Ericaceae, 6-I-90, A. Fernandez—5 males, 17 females; **Panama:** Chiriquí, Cerro Horqueta, 1700–1800m, along a ridge, eastern side, ex *Symphysia floccosa* (L. Wms.) L. Wms.(Ericaceae), 24-V-73, J. L. Luteyn, 3756—1 male, 1 female; **Colombia:** Antioquia, Yarumal-Valdivia Road, 10 km N. of Yarumal, elev. 2135 m, ex *Cavendishia subamplexicaulis* A. C. Smith, 22–23-III-79, J. L. Luteyn, 7065—2 males, 6 females; 25 km N Yarumal, 7°1′N, 75°35′W, 1525–1830, 2 km W PanAm Hwy. toward Fermin de Br., ex *Macleania stricta* A. C. Smith, 22-V-88, J. L. Luteyn, 1214—2 males, 2 females; Valle, Mpio. El Cairo, Correg. Boquerón, 4°45′N, 76°20′W, 2000–2200m, Vereda Amarillas, Serr. de los Paraguas, ex *Psammisia* n. sp.? (Ericaceae), 14-V-88, J. L. Luteyn, 12327—1 male, 4 females; **Ecuador:** Napo-Pastaza, Baeza-Tena rd., elev. 2030–2175 m, 1–5 km SE Cosanga, ex *Cavendishia ?cuatrecasasii* A. C. Smith, 6-IV-78, J. L. Luteyn, 5677—1 male; Pichincha, Quito-Sto. Domingo new road, 0°20′S, 78°55′W, elev. 1000–1830 m, 26–56 km E Sto. Domingo, ex *Macleania sleumeriana* A. C. Smith, 27-X-92, J. L. Luteyn, 14719—9 males, 22 females; Morona-Santiago, SW of military checkpoint in Limon (= General L. Plaza Gutierrez), 59.1 km SW of Mendez, 2°58′S, 78°25′W, elev. 2150 m, ex *Cavendishia nobilis* Lindley var *capitata* (Bentham) Luteyn, 27 X 1988, Dorr & Barnett, 5907—4 males, 4 females. **Venezuela:** T. F. Amazonas, between Maroa & airstrip, in sabaneta, elev. ca. 125 m, ex *Guacamaya superba* Maguire (Rapateaceae), 1-VII-91, P. Berry, 91–2—1 male.

Remarks. *Rhinoseius richardsoni* is a very conspicuous, highly derived species, easily recognizable by the modified opisthonotal setae *Z1* and *J1* in males (a character shared with *R. antioquiensis*) and the absence of podonotal setae *z1* in both sexes. It shows considerable intraspecific variation in regard to both length and form of many opisthonotal and opistho-

ventral setae. Setae *Z5* and *S5* vary from moderately thick and blunt to strongly enlarged and spinelike, often with a spiral pattern. Opisthoventral setae also range from relatively short and unmodified to very long, almost flagelliform. There is no correlation between the form of setae and body size. Fain et al. (1977b), on the basis of a single male, described a new species, *Rhinoseius panamensis,* which merely represents a heteromorphic form of *R. richardsoni.* Both forms frequently occur in a single flower and intermediate forms are not uncommon. Therefore, we regard *R. panamensis* Fain, Hyland & Aitken a junior synonym of *R. richardsoni* Hunter.

Rhinoseius richardsoni is probably the most common and widespread species of the genus. It has been collected from a wide range of host plants but it seems that, typically for the genus, it prefers plants of the family Ericaceae. Like other species of *Rhinoseius* it occurs predominantly at high elevations.

Rhinoseius antioquiensis Fain & Hyland, 1980

Rhinoseius antioquiensis Fain and Hyland 1980: 15, 17, figs. 1, 4, 7–9, 14 (male and female; type locality: Colombia, Antioquia).–Ohmer, Fain, and Schuchmann 1991: 481, 482, 489.–Fain 1992: 119–120, 123, 127, 133, fig. 29.

Type Material. Colombia: Antioquia, ex *Androdon aequatorialis* Gould (Trochilidae), 4–22-VIII-71, R. B. Waide), 1 female (paratype); Antioquia, ex *Chalybura urochrysia* (Gould) (Trochilidae), 11–14-V-71, R. B. Waide), 1 male (paratype).

Material Examined. Colombia: Antioquia, Uramita-Peque rd., 1400m, 2–5km above Uranta (Las Juntas), ex *Cavendishia lindauiana* Hoer. (Ericaceae), 29-III-79, J. L. Luteyn, 7166—5 males, 14 females; **Ecuador:** Pastaza, Puyo-Tena Rd., elev. 1050–1100 m, ex *Cavendishia palustris* A. C. Smith, 2-V-92, J. L. Luteyn, 14587—1 male.

Remarks. This species is most closely related to *R. richardsoni* but differs in having opisthonotal setae *Z5* flagelliform in males (they are spinelike in *R. richardsoni*), podonotal setae *z1* present in both sexes, and longer peritremes (reaching the level of setae *j2*).

Key to Species of Genera *Rhinoseius* and *Tropicoseius*

The following species are not included in the key because either no specimens of those species were examined or the species are known from only 1 sex: *T. changensis, T. bellavistensis, T. carlosalberti, T. adsimilis, T. chlorestes, T. eisenmanni,* and *T. perezgloriae.*

1. Tibiae III and IV lacking seta *pl2* (8 and 9 setae, respectively); dorsal shield lacking seta *s6*; tarsus III of males without modified setae; spermatodactyl directed posteroventrally; anterior, hyaline part of female genital shield truncated or emarginated, rarely broadly rounded (**genus *Rhinoseius***) 2

   Tibiae III and IV with seta *pl2* present (9 and 10 setae, respectively); seta *s6* on dorsal shield always present; tarsus III of males with seta *av2* always, and *pv1* and *av3* usually, knoblike; spermatodactyl directed anteriorly, but sometimes its distal portion bent; anterior, hyaline part of female genital shield rounded or tapered (**genus *Tropicoseius***) 12

2. Ventrianal shield in males transversely divided into separate ventral and anal shields (Fig. 29b); dorsal shield of male entire, with no lateral incisions; coxa IV in both sexes unmodified, rarely with rudimentary posterior spur (**group *rafinskii***) 3

   Ventrianal shield in males entire (Fig. 33b); dorsal shield of male with lateral incisions or divided into separate podonotal and opisthonotal shields; coxa IV in both sexes with posterior spur (**group *richardsoni***) 8

3. Seta *av1* on femur II in males strongly enlarged, spurlike; spermatodactyl simple, without apical projection 4
   Seta *av1* on femur II in male simple, not enlarged (Fig. 29c); spermatodactyl with apical or subapical projection (Fig. 30e) 5
4. Seta *Zv1* in male on ventral shield; opisthoventral setae in male short; opisthonotal setae *z4* and *s4* in male much thicker and longer than remaining dorsal setae; anterior, hyaline part of female genital shield not incised ..... (Fig. 2e) ***R. tiptoni*** Baker & Yunker
   Seta *Zv1* in male on soft cuticle; most of opisthoventral setae in male flagelliform; opisthonotal setae *z4* and *s4* in male unmodified; anterior, hyaline part of female genital shield distinctly incised .. .. ***R. pastorae*** Wiese & Fain
5. Opisthonotal setae *J3* in female absent; opisthonotal setae *J*'s in male not enlarged 6
   Opisthonotal setae *J3* in female present; at least some opisthonotal setae *J*'s and *Z*'s in male enlarged, spinelike (Fig. 31a) 7
6. Opisthonotal setae *J2, J4, Z2, Z3,* and *Z5* in male thickened, fusiform (Fig. 29a); opisthonotal region of dorsal shield in female about as long as podonotal region of dorsal shield (Fig. 30a) ... . (Figs. 29–30) ***R. luteyni*** Naskrecki & Colwell, n. sp.
   Opisthonotal setae *J2, J4, Z2, Z3,* and *Z5* in male not thickened; podonotal region of dorsal shield in female at least 1.4 times longer than opisthonotal one ..... ***R. ucumariensis*** Wiese & Fain
7. Setae *Jv2* and *Zv2* in male on ventral shield; male with 4 pairs of modified, spinelike setae; setae *Z4* in females present .... ***R. rafinskii*** Micherdzinski & Lukoschus
   Setae *Jv2* and *Zv2* in male on soft cuticle (Fig. 31b); male with 5 pairs of modified, spinelike setae (Fig. 31a); setae *Z4* in females absent ..... (Figs. 31–32) ***R. nadachowskyi*** Wiese & Fain
8. Dorsal shield of male with lateral incisions; setae *Zv3* in male on soft cuticle; anterior, hyaline part of female genital shield broadly rounded; seta av1 on femur II in male greatly enlarged, spurlike ..... ***R. cauacaensis*** Ohmer, Fain & Schuchmann
   Dorsal shield of male divided into separate podonotal and opisthonotal shields (Figs. 33a, 35a and b); setae *Zv3* in male on ventrianal shield (Fig. 33b); anterior, hyaline part of female genital shield truncated or incised (Fig. 34b); seta av1 on femur II in male moderately enlarged, knoblike 9
9. Opisthonotal setae *Z5* in both sexes thickened and with slightly dilated apices (Figs. 33a, 34a); coxae II in both sexes with deeply impressed posterior edge; seta av on femur II in male situated on prominent protuberance (Fig. 33d); ventrianal shield of male without posterior processes; seta *av1* on tibia II in male enlarged, spinelike ..... (Figs. 33–34) ***R. haplophaedia*** Ohmer, Fain & Schuchmann

   Opisthonotal setae *Z5* in neither sex modified; coxae II in both sexes with typically rounded posterior edge; seta av on femur II in male not situated on a protuberance; ventrianal shield of male with a pair of posterior processes; seta *av1* on tibia II in male not modified 10
10. Opisthonotal setae in male short, unmodified; no modified, spinelike setae on dorsal shield in male ..... ***R. androdon*** Fain & Hyland
    Opisthonotal setae in male flagelliform or thickened; opisthonotal setae *Z1* and *J1* in male enlarged, spinelike 11
11. Podonotal setae *z1* in both sexes present; setae *Z5* in male flagelliform ..... ***R. antioquiensis*** Fain & Hyland
    Podonotal setae *z1* in both sexes absent; setae *Z5* in male thickened, spinelike (Fig. 35 a and c) .... (Figs. 2a, 35–36) ***R. richardsoni*** Hunter
12. Tectum rounded (Fig. 3f); leg II in males very stout, genu II wider than long, at least 3 times as wide as that of leg I (**group *chiriquensis***) 13
    Tectum tapering to a point, sometimes its apex bifurcated or serrated; genu of leg II in males longer than wide, at most twice as wide as that of leg I 22
13. Setae *Z5* in both sexes, and *r3* in male, longer and thicker than remaining opisthonotal setae, with distinctly dilated apices (Figs. 17a, 18a); spermatodactyl without stylus but with small, subapical lobe (Fig. 16c) .... (Figs. 16–18) ***T. berryi*** Naskrecki & Colwell, n. sp.
    Setae *r3* and *Z5* unmodified in both sexes; spermatodactyl always with stylus 14
14. Seta *pv1* on tarsus III in male normal, not spine- or knoblike; dorsal shield of male usually entire, without lateral incisions (rarely incisions present) 15
    Seta *pv1* on tarsus III in male modified, knoblike; dorsal shield of male always with lateral incisions 17
15. Apex of spermatodactyl simple, not hooklike; ventral shield of male reduced to small anal shield, resembling that of female; posterior part of male sternogenital shield reduced so that setae *st5* on soft cuticle (Fig. 4b); opisthonotal part of female dorsal shield at most with weak incisions at the level of setae *S3–S5* (Fig. 5a) .... (Figs. 2b, 3–5) ***T. chazdonae*** Naskrecki & Colwell, n. sp.
    Apex of spermatodactyl strongly modified, hooklike; ventrianal shield of male sometimes reduced in its anterior part but at least setae *Jv1* and *Jv2* on shield; setae *st5* in male always on sternogenital shield; opisthonotal part of female dorsal shield with distinct, irregular incisions at the level of setae *S3–S5*. 16

16. Apex of fixed digit of chelicera of male characteristically elongated (Fig. 9c); main arm of spermatodactyl twisted outwards (Fig. 9d); incisions at the level of setae *S3-S5* in female well-developed (Fig. 10a) ..... (Figs. 9–10) ***T. steini*** Naskrecki & Colwell, n. sp.
    Apex of fixed digit of chelicera of male not modified (Fig. 6c); main arm of spermatodactyl not twisted outwards (Fig. 6b); incisions at the level of setae *S3–S5* in female poorly developed (Fig. 8a) ..... (Figs. 6–8) ***T. cervus*** Naskrecki & Colwell, n. sp.
17. Apex of spermatodactyl downcurved, hooklike; seta av1 on tibia II of male enlarged, spinelike. ..... (Figs. 1b, 6e) ***T. colwelli*** Hunter
    Apex of spermatodactyl straight; seta *av1* on tibia II of male unmodified 18
18. Seta *av3* on tarsus III in male not enlarged or knoblike (Fig. 2c) .. 19
    Seta *av3* on tarsus III in male enlarged, knoblike (Fig. 2d) 20
19. Femur II of male with a prominent chitinous protuberance; teeth on fixed digit of male chelicera very widely spaced, distance between the 1st and 2nd tooth larger than width of fixed digit (Fig. 12e) ..... (Figs. 11–12) ***T. kaliszewskii*** Naskrecki & Colwell, n. sp.
    Femur II of male without chitinous protuberance; teeth on fixed digit of male chelicera closely spaced. .... ***T. chiriquensis*** Baker & Yunker
20. Anterior part of podonotal region of dorsal shield in both sexes with dense, parallel striations .... (Fig. 6 f and g) ***T. ornatus*** (Fain & Hyland)
    Dorsal shield without parallel striations. 21
21. Apex of spermatodactyl blunt, stylus reaching or surpassing the apex; dorsal setae in male usually long, reaching or surpassing distances between adjacent setal insertions .... (Fig. 2d) ***T. peregrinator*** Baker & Yunker
    Apex of spermatodactyl pointed, stylus not reaching the apex (Fig. 13c); dorsal setae in male short, not reaching adjacent setal insertions (Fig. 14a) .... (Figs. 13–15) ***T. rowelli*** Naskrecki & Colwell, n. sp.
22. Seta *ad* on trochanter I in both sexes serrated; seta *av1* on femur I in male not modified; seta *pv* on coxa II in male not appreciably thicker than *av* (Fig. 20d); opisthoventral setae in male usually very long, flagelliform (**group *braziliensis***) 23
    Seta *ad* on trochanter I in both sexes smooth; seta *av1* on femur I in male enlarged, knoblike; seta *pv* on coxa II in male at least 3 times as thick and long as *av* (Fig. 2p); opisthoventral setae in male short, unmodified (only in *T. trinitatis* flagelliform) (**group *wetmorei***) 27

23. Dorsal shield divided into 2 separate, podonotal and opisthonotal dorsal shields (Fig. 19a); coxa I in both sexes with one or more rows of denticles (Fig. 19b). 24
    Dorsal shield with lateral incisions but not divided into 2 separate shields; coxa I in both sexes without rows of denticles. 25
24. Opisthonotal setae *S1* absent in both sexes; apex of spermatodactyl forming a superficial loop, with a small subapical lobe (Fig. 19c and d); dorsal setae *pd1* and *ad1* on femur II in male smooth (Fig. 20d). ..... (Figs. 19–20) ***T. erioxynon*** Naskrecki & Colwell, n. sp.
    Opisthonotal setae *S1* present in both sexes; apex of spermatodactyl sometimes bent but never forming a loop, and without a subapical lobe; dorsal setae *pd1* and *ad1* on femur II in male serrated (Fig. 21d). ..... (Figs. 21–22) ***T. fuentesi*** Naskrecki & Colwell, n. sp.
25. Spermatodactyl about as long as 2nd segment of chelicera; setae *ad1* and *pd* on palpfemur in female smooth; anterolateral regions of the podonotal part of the dorsal shield in female with dense, parallel striations. .... (Fig. 2 c and h) ***T. uniformis*** (Fain, Hyland & Aitken)
    Spermatodactyl distinctly longer than 2nd segment of chelicera; setae *ad1* and *pd* on palpfemur in female serrated; dorsal shield of female without parallel striations 26
26. Spermatodactyl very long, spirally coiled; coxa IV in both sexes with small posterior spur .... (Fig. 2g) ***T. phoreticus*** (Fain, Hyland & Aitken)
    Spermatodactyl about as long as 2nd segment of chelicera, bent but not spirally coiled; coxa IV without posterior spur. .... (Fig. 2f) ***T. braziliensis*** Baker & Yunker
27. Spermatheca of female without a maturation pouch (Fig. 2o); mucro on female chelicera short, not reaching apex of movable chela (Fig. 2i) ..... (Fig. 2 i and o) ***T. erro*** Baker & Yunker
    Spermatheca with a maturation pouch (Fig. 2k and n); mucro on female chelicera long, reaching or surpassing apex of movable chela (Fig. 2j). 28
28. Setae *ad1, pd1,* and *pd2* on femur I in female thickened, spinelike; anal shield of female wider than posterior part of genital shield (Fig. 1c); genu of leg IV in female stout, at most as long as wide 29
    Setae *ad1, pd1,* and *pd2* on femur I in female simple, not thickened; anal shield of female narrower than posterior part of genital shield (Fig. 23f), if equal than anal shield distinctly longer than wide; genu of leg IV in female slender, at least twice as long as wide 30
29. Anal shield of female only slightly wider than posterior part of genital shield, and usually somewhat longer than wide; lateral mar-

gins of ventrianal shield in male narrowing posteriad. .... (Fig. 2j) ***T. fairchildi*** Baker & Yunker

Anal shield of female distinctly wider than posterior part of genital shield, always wider than long (Fig. 1c); lateral margins of ventrianal shield of male parallel .... (Fig. 1 c and d) ***T. colombiensis*** (Fain & Hyland)

30. Female maturation pouch of various shapes but never very long, its distal part bent under right angle (Fig. 2 l and m); apex of spermatodactyl straight, simple (Fig. 23d) 31

Female maturation pouch very long, at least 8 times as long as wide, its distal part not bent under right angle (Fig. 2k); apex of spermatodactyl either twisted (Fig. 27e) or with a small subapical dilatation (Fig. 24d) 35

31. Spermatheca with a single, bulbous maturation pouch (Fig. 2n); opisthoventral setae on soft cuticle around ventrianal shield in male decidedly shorter than setae on shield .... (Fig. 2n) ***T. wetmorei*** Baker & Yunker

Spermatheca with either a single, elongate or 2 separate maturation pouches; opisthoventral setae on ventrianal shield and soft cuticle in male of similar length 32

32. Spermatheca with 2 separate maturation pouches (Fig. 2m) 33

Spermatheca with one maturation pouch (Fig. 2l). 34

33. Dorsal setae of male minute, shorter than half the distance between adjacent setal insertions; opisthoventral setae *Jv1–Jv3, Jv5, Zv1,* and *Zv2* of male short, about as long as half the distance between adjacent setal insertions .... (Fig. 2m) ***T. bisacculatus*** (Fain, Hyland & Aitken)

Dorsal setae of male relatively long, most of them at least as long as half the distance between adjacent setal insertions; opisthoventral setae *Jv1–Jv3, Jv5, Zv1,* and *Zv2* of male distinctly longer than the distance between adjacent setal insertions (Fig. 23b) ... . (Fig. 23) ***T. ochoai*** Naskrecki & Colwell, n. sp.

34. Dorsal shield of female 527–562 μm long, that of male 527–603 μm long; opisthoventral setae *Jv3* of male always on ventrianal shield ..... ***T. fidelis*** (Oconnor, Colwell & Naeem)

Dorsal shield of female 491–509 μm long, that of male 480–530 μm long; opisthoventral setae *Jv3* of male usually on soft cuticle. ..... (Figs. 1a, 2l) ***T. heliconiae*** Baker & Yunker

35. Apex of spermatodactyl sometimes with small subapical dilatation but never twisted; walls of maturation pouch striated (Fig. 24g) 36

Apex of spermatodactyl clearly bent and twisted; walls of maturation pouch smooth (Fig. 27h) 37

36. Marginal setae of series *r* and *R* in male on dorsal shield (Fig. 24a); opisthoventral setae *Jv3* in male on ventrianal shield (Fig. 24b); ornamentation of posterior part of female dorsal shield reticulate (Fig. 24e). ..... (Fig. 24) ***T. bakeri*** Dusbabek & Cerny

Marginal setae of series *r* and *R* in male on soft cuticle; opisthoventral setae *Jv3* in male on soft cuticle (Fig. 25b); ornamentation of posterior part of female dorsal shield striated (Fig. 26a). .... (Figs. 25–26) ***T. naeemi*** Naskrecki & Colwell, n. sp.

37. Marginal setae of series *R* in male on soft cuticle; distance between genital and anal shields in female shorter than half the width of anal shield 38

Marginal setae of series *R* in male on dorsal shield; distance between genital and anal shields in female longer than half the width of anal shield. 39

38. Lengths of setae of *S* series in male increasing greatly toward end of opisthosoma, *S5* at least 4 times longer than *S1*; setae *Z5* in male at least 3 times as long as postanal seta, almost flagelliform ..... ***T. trinitatis*** (Fain, Hyland & Aitkens)

Lengths of setae of *S* series in male only moderately increasing toward end of opisthosoma, *S5* at most 3 times as long as *S1* (Fig. 28a); setae *Z5* in male at most twice as long as postanal seta, never flagelliform. ..... (Fig. 28) ***T. kressi*** Naskrecki & Colwell, n. sp.

39. Metapodal plates of male merged with ventrianal shield (Fig. 27b) . ..... (Figs. 2p, 27) ***T. analis*** (Fain & Hyland)

Metapodal plates of male separated from ventrianal shield. 40

40. Maturation pouch of female inseminating apparatus distinctly longer than remaining part of major duct. .... ***T. venezuelensis*** Baker & Yunker

Maturation pouch of female inseminating apparatus at most as long as remaining part of major duct .... (Fig. 2k) ***T. klepticos*** (OConnor, Colwell & Naeem)

Discussion

Although a full analysis of the evolutionary implications of our findings will appear elsewhere, we offer here a preliminary historical interpretation of the reconstructed phylogeny of sister genera *Rhinoseius* and *Tropicoseius* (Fig. 39). Table 5 summarizes, by mite species, the biological origin of all specimens studied for this monograph, plus the origin of all other specimens for which the biological source has been reported by other workers. Two preliminary comments are needed to set the stage for this discussion. First, recall that neither host information nor biogeographical information was included among the characters used to reconstruct the mite phylogeny. Second, in this discussion, we consistently refer to *Rhinoseius* in Baker & Yunker's original sense, as indicated in the cladogram (Fig. 39) and in the systematic sections of this monograph.

The most striking and immediate inference that arises from a comparison of the cladogram (Fig. 39) with the data of Table 5 is that mites of this lineage are quite conservative with regard to host plant affiliation, at least at the level of host plant genera and families. A summary of the host affiliation data of Table 5 is mapped on the cladogram in Fig. 40.

Consider, first, the genus *Rhinoseius.* With the single exception of *R. tiptoni,* every species in the genus *Rhinoseius* for which host plant records exist has been collected from plants of the family Ericaceae. In contrast, none of the species of the genus *Tropicoseius* is known from ericads, except for a single specimen of *T. steini* n. sp. collected from *Ceratostema peruvianum.* Within *Rhinoseius,* species of the *richardsoni* group are known almost exclusively from ericads, whereas several members of the sister group *rafinskii* are somewhat less restricted, with some species found also in Gesneriaceae

(*R. tiptoni* is known only from this family), Bromeliaceae, Campanulaceae, and Scrophulariaceae. Clearly, the most parsimonious hypothesis of origin for the genus *Rhinoseius* is that the ancestor of the group occupied an ericaceous host.

Consider, 2nd, the genus *Tropicoseius*. According to our phylogenetic hypothesis (Fig. 37), the *chiriquensis* group is the most basal lineage in this genus. Among those species in the *chiriquensis* group for which adequate host plant records exist, all are affiliated with plants of the family Campanulaceae, several species almost exclusively so. (The 5 species not known from campanulaceous hosts—*T. peregrinator, T. berryi, T. kaliszewskii, T. bellavistensis,* and *T. carlosalberti*—are known either from a single collection or from very few individuals.) Non-campanulaceous hosts of species in this group form almost exactly the same list of plant families as the non-ericaceous affiliations of wayward *Rhinoseius* species—Gesneriaceae, Bromeliaceae, and Scrophulariaceae. Among the 5 species of the *chiriquensis* group not known from any campanulaceous host, some may have made definitive host shifts. *T. kaliszewskii* is known only from the very small and geographically restricted Amazonian family Rapateaceae (Liliales). *T. berryi* is the only hummingbird flower mite (of any genus) known from a species of the species-rich and widespread genus *Fuchsia* (Onagraceae). In spite of the fact that most *Fuchsia* species are pollinated by hummingbirds, no other species of the genus (or family) is known to support hummingbird flower mites in spite of persistent efforts to find mites in flowers of these plants. In spite of these cases, the most parsimonious hypothesis of origin for the *chiriquensis* group is clearly an ancestral affiliation with campanulaceous hosts.

All known species of *Rhinoseius* are restricted to tropical latitudes, whereas *Tropicoseius* species reach both the latitudinal and altitudinal limits for hummingbird flower mites (Table 5). In the New World tropics, hummingbird-pollinated species of the family Ericaceae are restricted largely to cool montane and high montane regions (Luteyn 1989). Thus, if *Rhinoseius* originated in an ericaceous host, that host was almost certainly a tropical montane species. Likewise, the hummingbird-pollinated Campanulaceae (with the exception the north temperate species *Lobelia cardinalis,* which lacks hummingbird flower mites) are almost exclusively tropical and montane in distribution. Moreover, ericaceous and campanulaceous hosts often grow side by side in the same habitats in tropical montane regions and are visited by the same hummingbirds (see, for example, Colwell 1973). Taking these facts and inferences into account, we propose a montane tropical origin for the *Rhinoseius-Tropicoseius* clade as a whole.

Among known taxa, the genus *Xanthippe* is the most probable sister group of this clade. Although the 2 known species of *Xanthippe* are from the tropical lowlands, they are known (albeit in considerable abundance) from only a single collection (Naskrecki and Colwell 1995). Thus, the geographical and host distribution of this genus needs much more investigation before

anything useful can be inferred with regard to the host, carrier or dispersal agent, and biogeography of the common ancestor of *Xanthippe* and the *Rhinoseius-Tropicoseius* clade.

Returning, now, to the genus *Tropicoseius,* the next most basal lineage after the *chiriquensis* group is the *braziliensis* group. All 5 species of this group are found in hosts of the family Bromeliaceae, at least 2 of the species exclusively so, based on known records. Other hosts include plants in the families Campanulaceae (a link with the *chiriquensis* group), Amaryllidaceae, and Rubiaceae (*Psychotria* = *Cephaelis*). Recall that at least 1 species in the *chiriquensis* group and 1 in the *rafinskii* (*Rhinoseius*) group also have been collected from bromeliads, foreshadowing a probable host shift into bromeliads in the ancestor of the *braziliensis* group. At least 2 species in this group (*T. erioxynon* and *T. fuentesi*) occupy the flowers of *Puya* spp. (Bromeliaceae). This plant genus co-occurs throughout the Andean highlands in the same habitats as mite hosts in the family Campanulaceae (*Lobelia, Centropogon,* and *Siphocampylus*) as well as Ericaceae. This suggests a tropical highland origin of the *braziliensis* group with subsequent spread into lowland bromeliads.

Within *Tropicoseius,* the *wetmorei* group, which includes the most derived species, is primarily affiliated with plants of the genus *Heliconia* (Heliconiaceae). This species-rich plant genus (200–250 species) is restricted to the tropical lowlands and lower montane elevations. New World *Heliconia* species are exclusively hummingbird pollinated (Berry and Kress 1991). Within the *wetmorei* group, the most basal species (*T. erro*) and the clade comprising *T. fidelis, T. heliconiae, T. bisacculatus, T. ochoai,* and *T. wetmorei* show a pronounced affiliation with the genus *Costus* (Costaceae) as well as with *Heliconia,* suggesting that an affiliation with *Costus* may have preceded a definitive shift to *Heliconia.* Plants of these 2 genera grow side by side in early successional habitats and often are pollinated by the same hermit hummingbirds (subfamily Phaethorninae) (Colwell 1986a). The 8 species in the *wetmorei* group that are known exclusively from *Heliconia* form a clade of their own.

In summary, speciation in the genera *Rhinoseius* and *Tropicoseius* clearly manifests a high degree of conservatism with regard to host affiliation at the plant generic and familial level. Nonetheless, Table 5 documents numerous cases of polyphagy at this level, with mites occupying not only a typical host for their species group but also unrelated plants, often those characteristically occupied by sister clades of mites. Presumably, such cases of polyphagy set the evolutionary stage for definitive host shifts such as those that must have taken place between the major clades within *Rhinoseius* and *Tropicoseius.* In addition, there are candidate cases for definitive host shifts at the level of apical species—*T. kaliszewskii* from Campanulaceae to Rapateaceae, *T. berryi* from Campanulaceae to Onagraceae, *R. tiptoni* from Ericaceae to Gesnericeae (although further sampling could change this picture). Perhaps these species may become the ancestors of new radiations of hummingbird flower mites.

Acknowledgments

We are grateful to many colleagues and institutions for their collaboration and assistance. For his many contributions to this project over a period of 20 yr, we express our gratitude to Shahid Naeem (Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN). For tireless intellectual and practical guidance of all kinds, we thank E. E. Lindquist (Agriculture and Agri-Food Canada, Ottawa, Canada) and the late M. Kaliszewski (Brigham Young University, UT). Ronald Ochoa (Brigham Young University) contributed to the success of this project in myriad ways when the future seemed most in doubt. For their many intellectual contributions to research on hummingbird flower mites and for their generosity in collecting material that has found its way into this study, we are especially grateful to D. S. Dobkin, P. Feinsinger, and A. J. Heyneman. For cooperation and facilitation of work in the field we thank R. Gámez and J. Jiménez (Instituto Nacional de Biodiversidad, Costa Rica), the Organization for Tropical Studies (Costa Rica), Simla Biological Station (Trinidad, W.I.), and others too numerous to name. For offering generous access to fluid-preserved plant material in their institutional or personal collections, we thank P. E. Berry (Missouri Botanic Garden, St. Louis, MO); W. J. Kress (Department of Botany, Smithsonian Institution, Washington, DC); J. L. Luteyn (The New York Botanical Garden, Bronx, NY); P.J.M. Maas (Rijksuniversiteit Utrecht, Utrecht, The Netherlands); and B. A. Stein (The Nature Conservancy, Arlington, VA). For plant identifications, we are grateful to the botanists just mentioned, as well as B. Hammel (Missouri Botanical Garden, St. Louis, MO); and J. Richards (Florida International University, Miami, FL). For field collections of mites on our behalf we are grateful to

W. W. Benson, R. L. Chazdon, S. A. Cunningham, E. R. Fuentes, B. Hallet, J. H. Hunt, B. Loiselle, R. Levin, F. Ortiz, G. Powell, C.H.F. Rowell, J. Utley, and the parataxonomists of the Instituto Nacional de Biodiversidad (Costa Rica): A. Fernandez, C. Chavez, C. Moraga, G. Caballo, G. Fonseca, J. Saberio, J. Solano, and P. Rios. For the prompt and generous loan of types and other specimens we thank A. Fain (Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium), C.H.W. Flechtmann (Universidad de São Paulo, São Paulo, Brazil), E. E. Lindquist (Agriculture and Agri-Food Canada, Ottawa, Canada), B. Oconnor (University of Michigan, Ann Arbor, MI), and R. L. Smiley (USDA–ARS, Beltsville, MD). For their work in the painstaking task of preparing and sorting specimens, we are grateful to J. Bloszyk, M. Lentell, S. Naeem, R. Morales, R. Ochoa, N. Oconotrillo, and M. Paniagua. This work would have been impossible without the generous financial assistance of the National Science Foundation (awards DEB-7812038, BSR 86–04929, BSR-8906228, and BSR-9025024 to R.K.C.) the Universities of California and Connecticut, the Organization for Tropical Studies, and the Ford Foundation. We express special gratitude to R. Baumann and to the Office of Grants and Contracts at Brigham Young University for their flexibility and generosity in helping to see this project through to completion.

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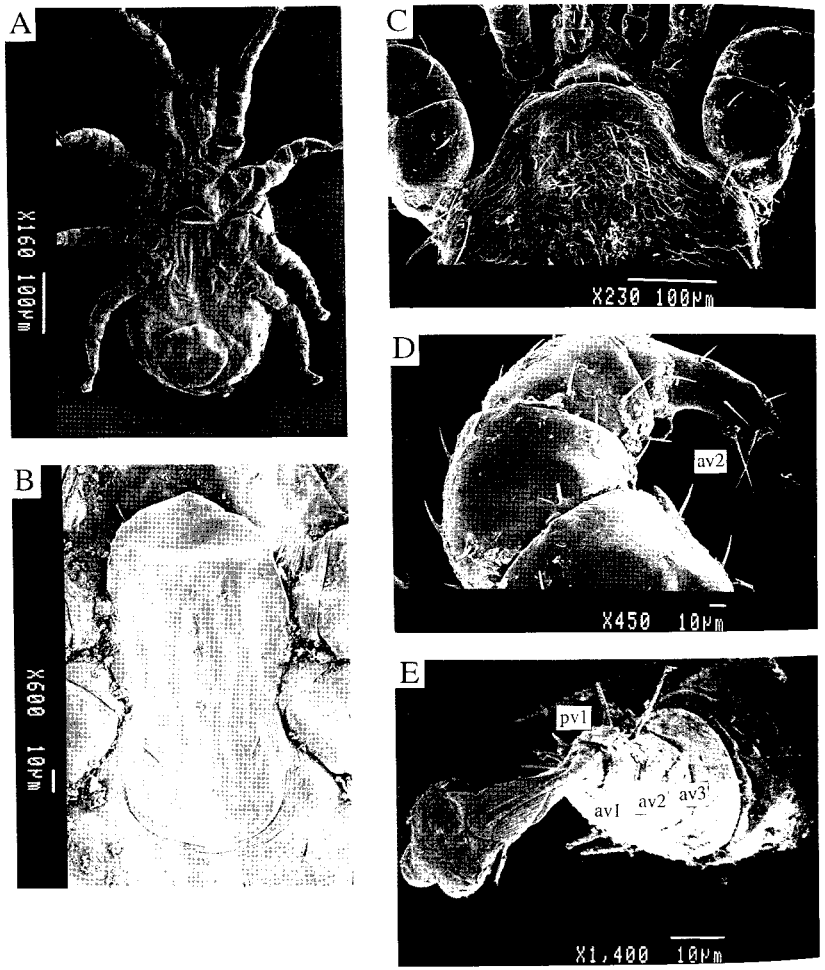

Fig. 1. Diagnostic characters of *Tropicoseius* spp.: (a) female venter (b) *T. colombiensis,* genital shield (c) anterior part of male body (d) *T. colwelli,* male leg II (e) *T. heliconiae,* male tarsus III.

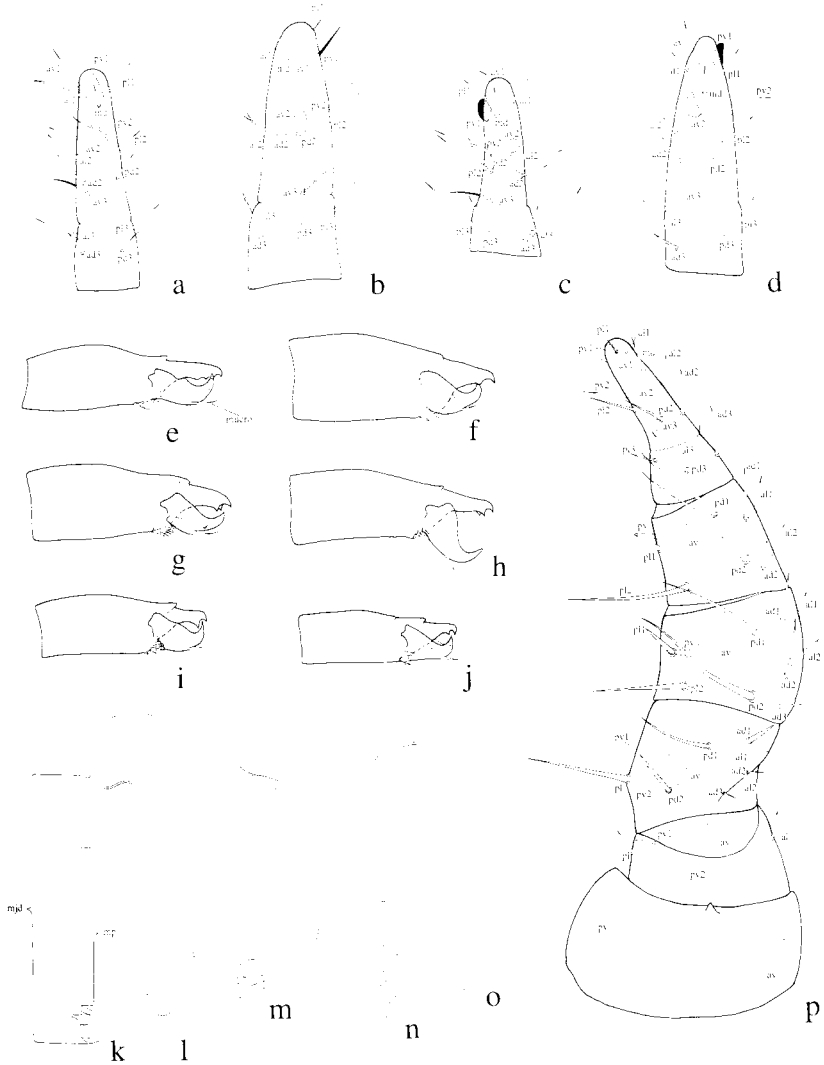

Fig. 2. Diagnostic characters of *Tropicoseius* and *Rhinoseius* spp. (a–d): male III tarsi (excluding pretarsus): (a) *R. richardsoni* (b) *T. chazdonae* n. sp. (c) *T. uniformis* (d) *T. peregrinator* (e–j): female chelicerae, lateral (antiaxial) views: (e) *R. tiptoni* (f) *T. braziliensis* (g) *T. phoreticus* (h) *T. uniformis* (i) *T. erro* (j) *T. fairchildi* (k–o) spermathecae: (k) *T. klepticos* (l) *T. heliconiae* (m) *T. bisacculatus* (n) *T. wetmorei* (o) *T. erro* (p) male leg II (excluding pretarsus), *T. analis.* Abbreviations: mjd, major duct, mp, maturation pouch.

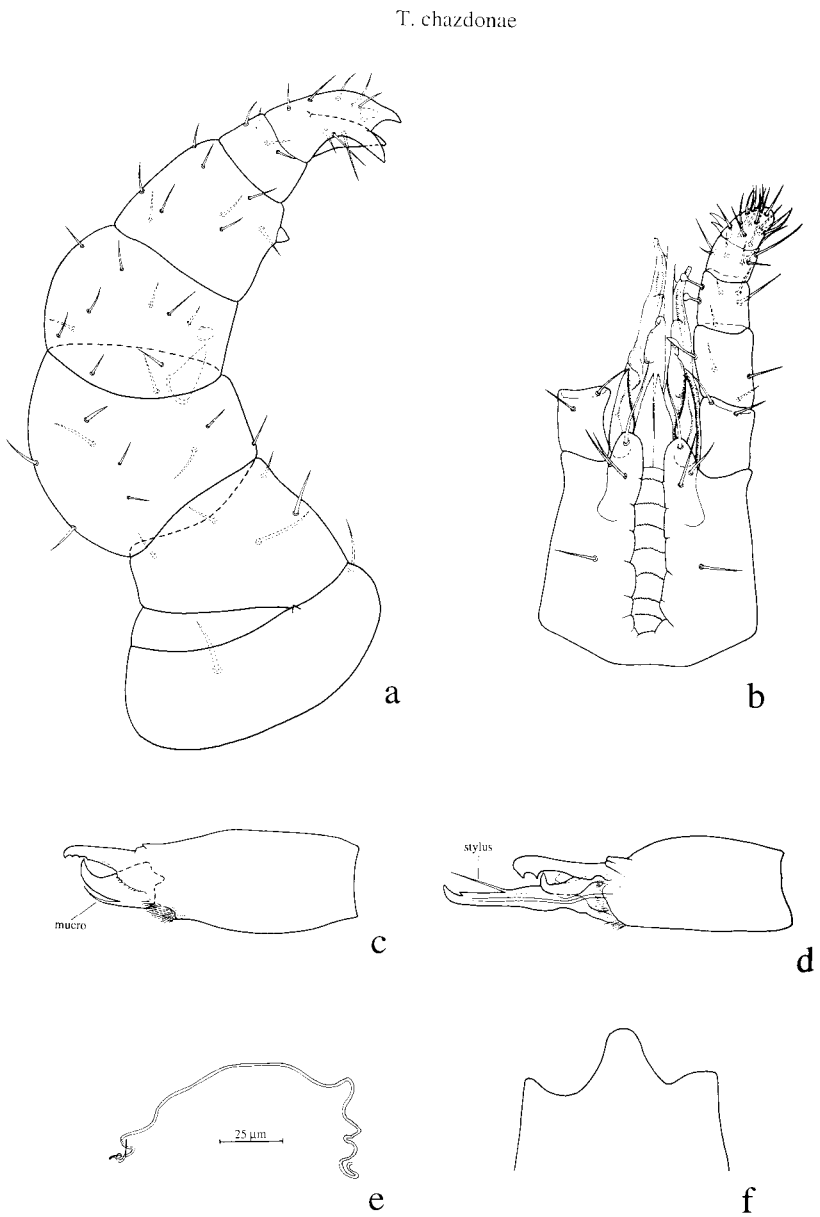

Fig. 3. *Tropicoseius chazdonae.* (a) Leg II (excluding pretarsus), male (b) Venter of gnathosoma, male (c) Female chelicera, lateral view (d) Male chelicera, lateral view (e) Spermatheca (f) Male tectum.

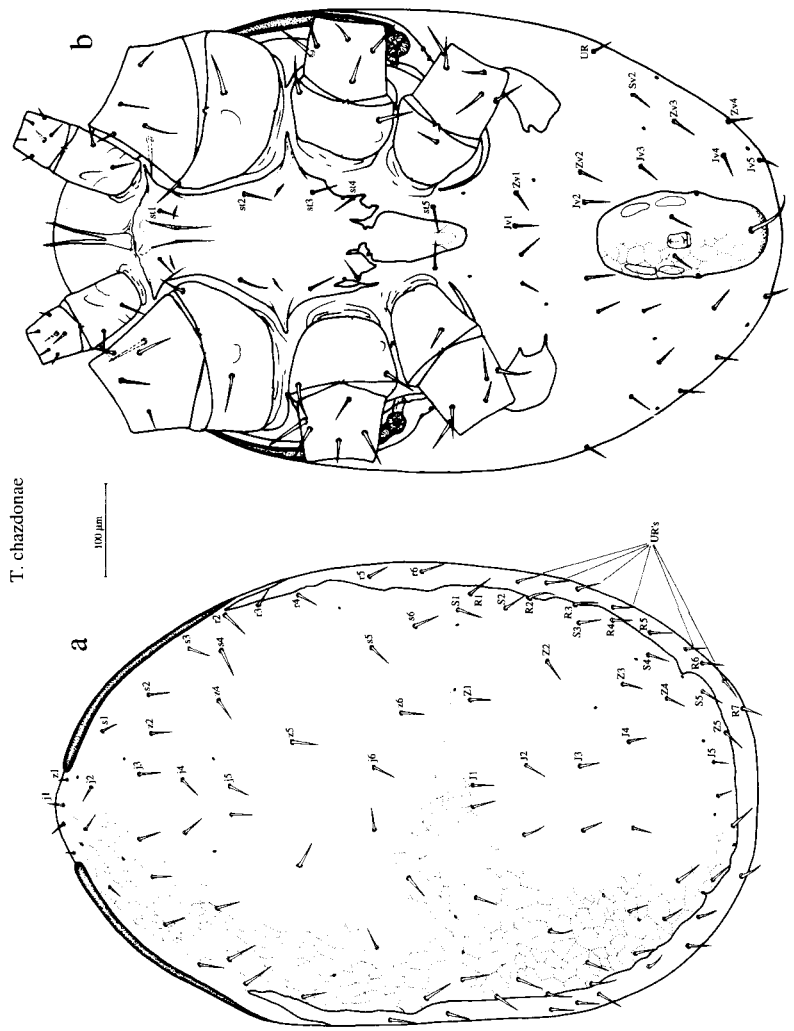

Fig. 4. *Tropicoseius chazdonae,* male. (a) Idiosomal dorsum (b) Idiosomal venter.

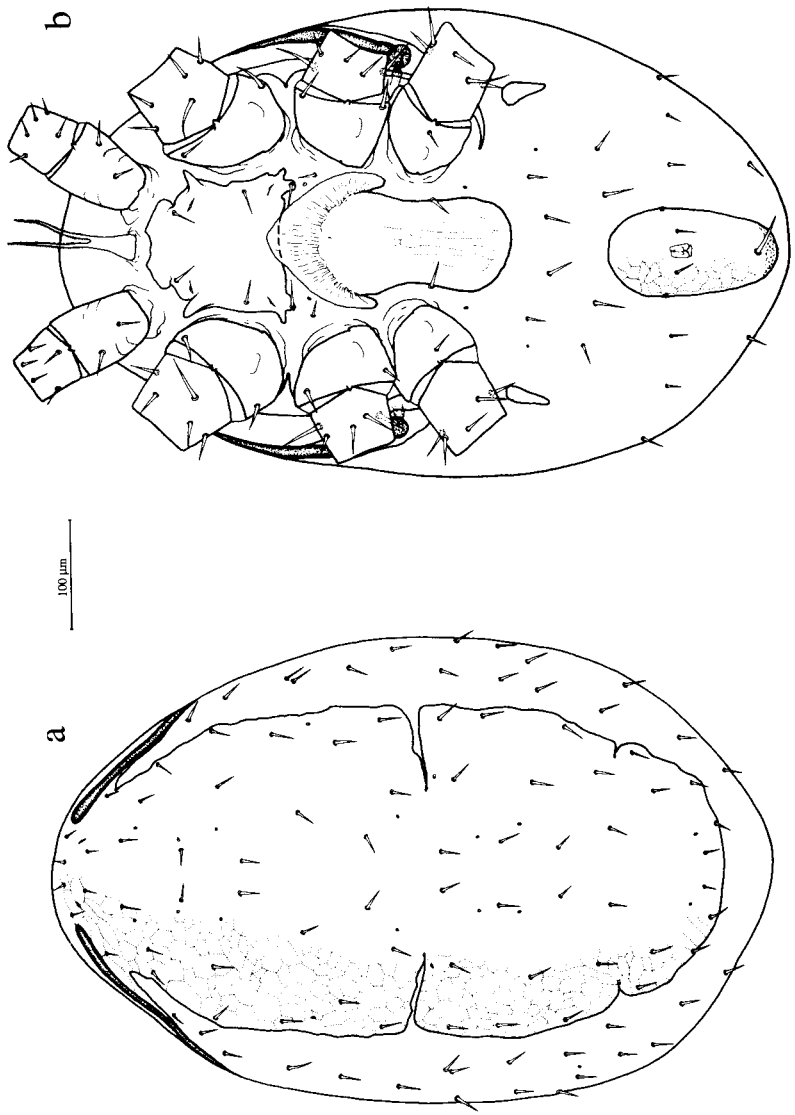

Fig. 5. *Tropicoseius chazdonae*, female. (a) Idiosomal dorsum (b) Idiosomal venter.

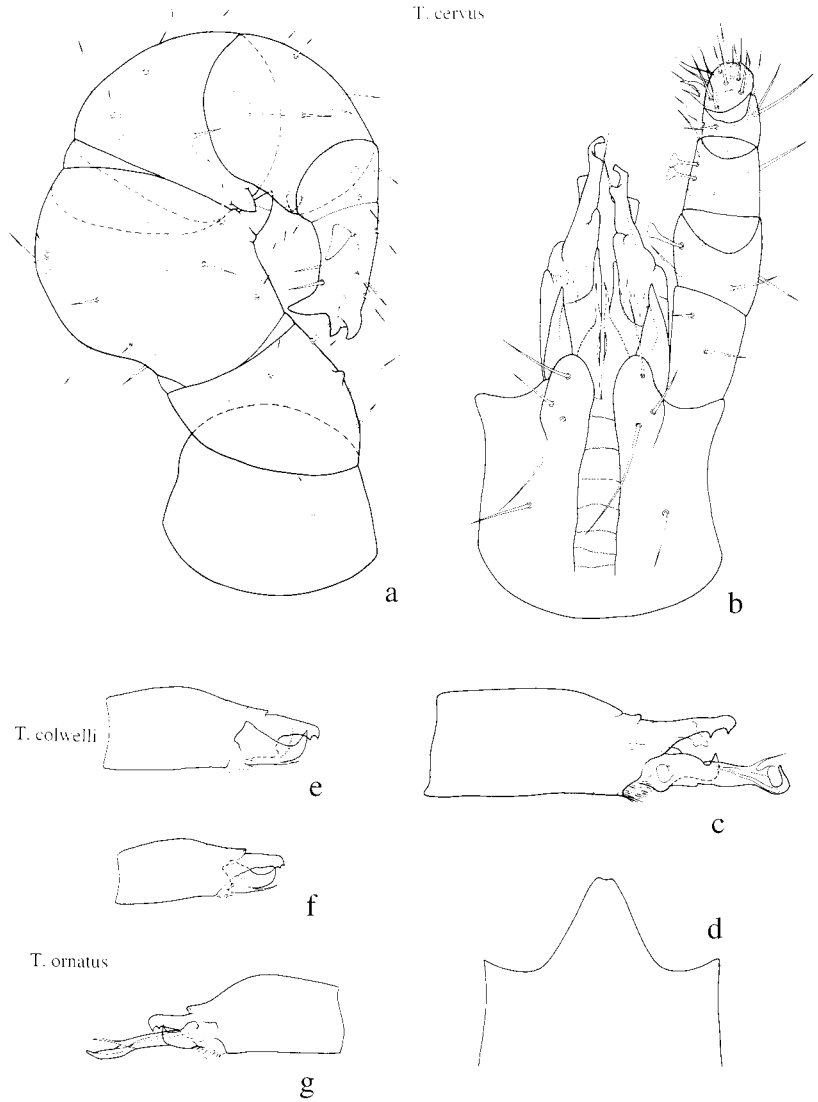

Fig. 6. (a–d): *Tropicoseius cervus.* (a) Leg II (excluding pretarsus), male (b) Venter of gnathosoma, male (c) Male chelicera, lateral view (d) Male tectum (e) *T. colwelli,* female chelicera, lateral view (f) Female chelicera, lateral view (g) *T. ornatus,* male.

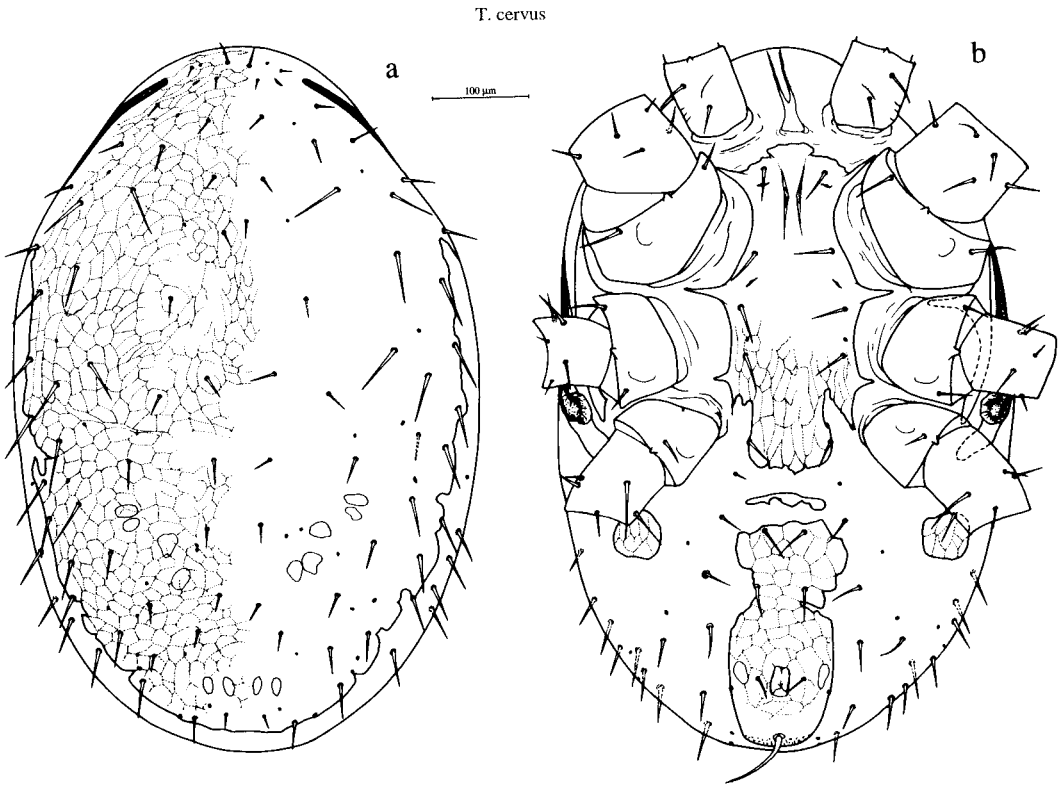

Fig. 7. *Tropicoseius cervus,* male. (a) Idiosomal dorsum (b) Idiosomal venter.

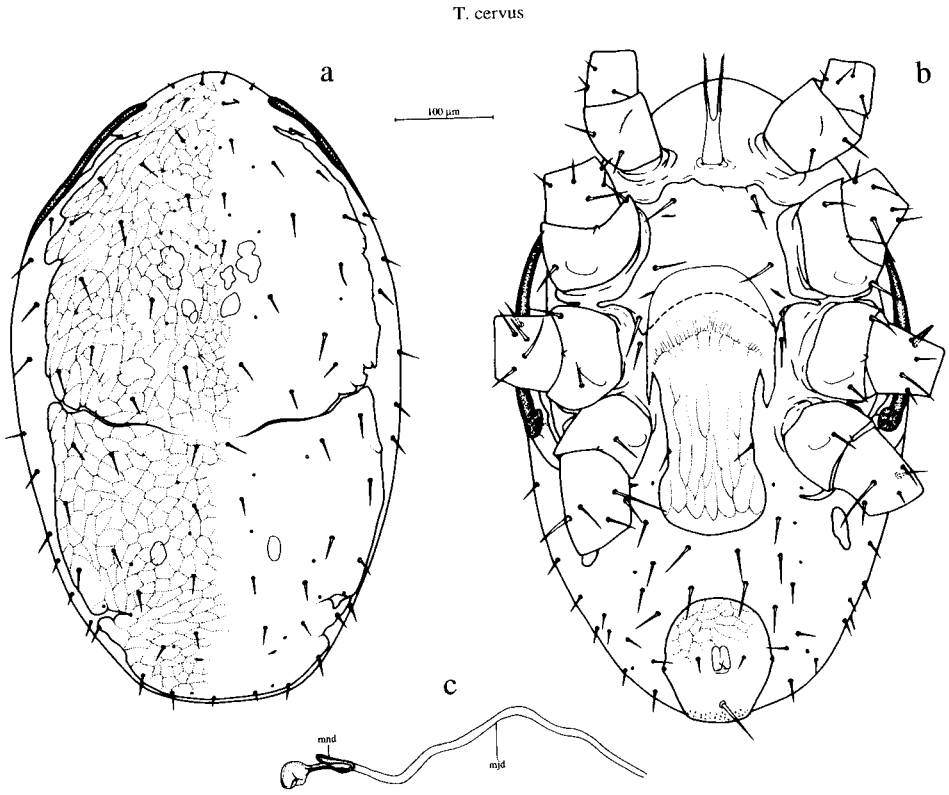

Fig. 8. *Tropicoseius cervus,* female. (a) Idiosomal dorsum (b) Idiosomal venter (c) spermatheca. mjd, major duct, mnd, minor duct.

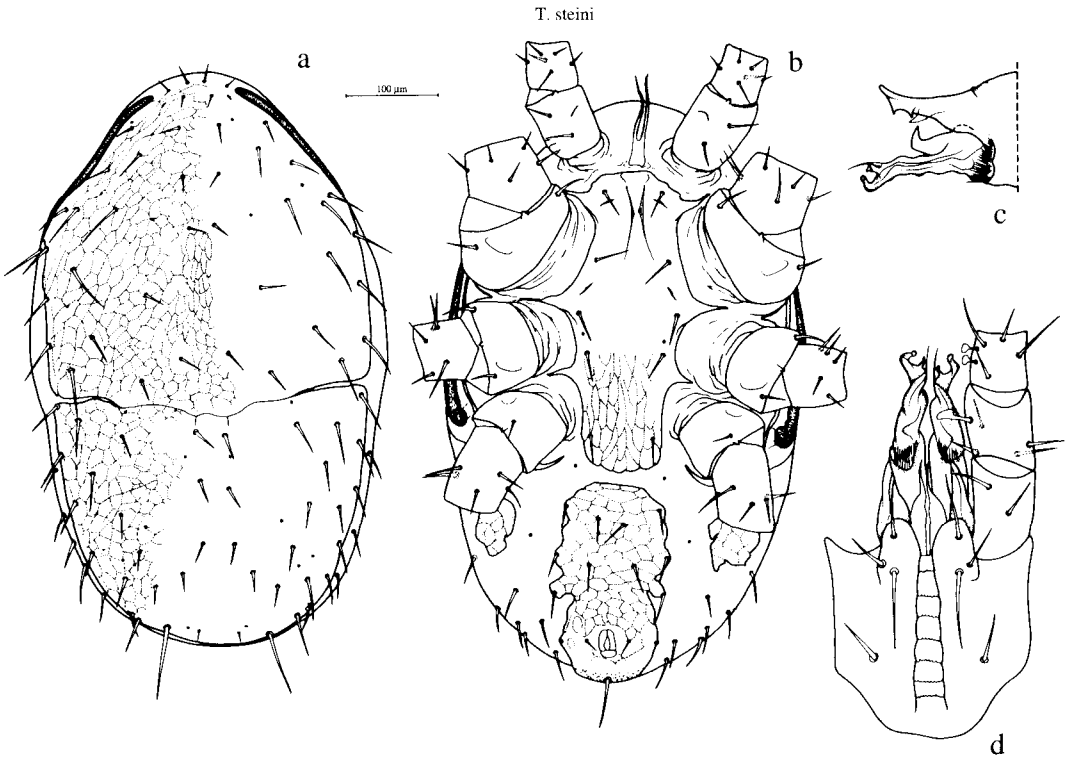

Fig. 9. *Tropicoseius steini,* male. (a) Idiosomal dorsum (b) Idiosomal venter (c) Anterior part of chelicera, lateral view (d) Venter of gnathosoma.

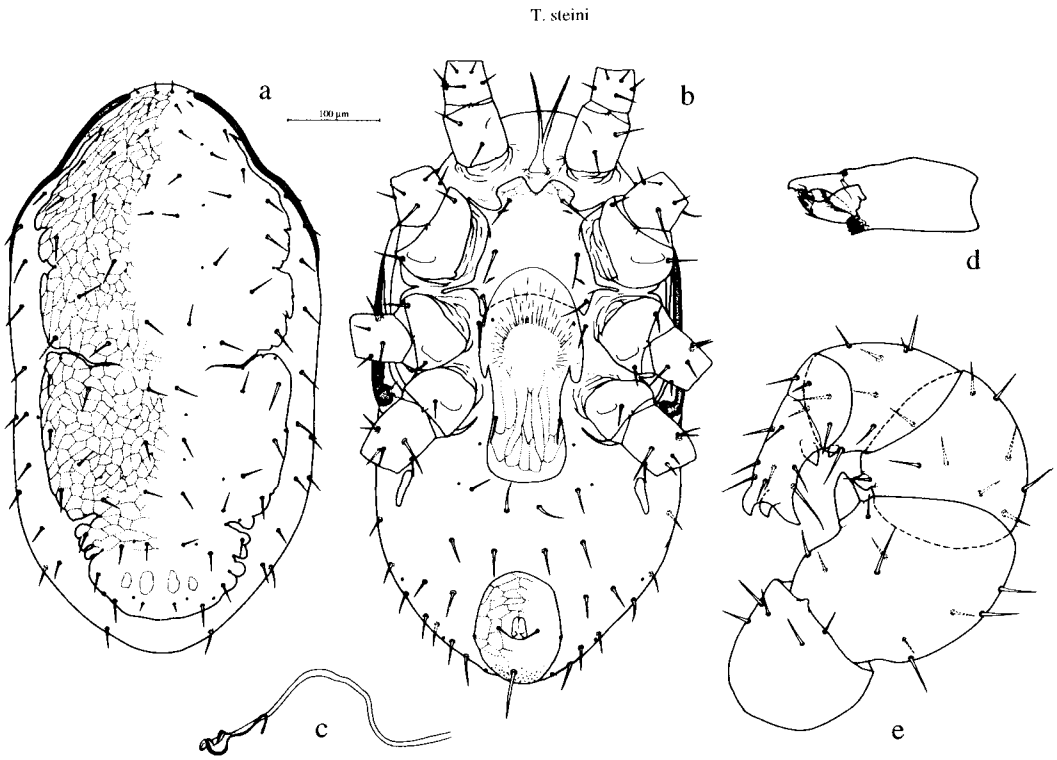

Fig. 10. *Tropicoseius steini.* (a) Female idiosomal dorsum (b) Female idiosomal venter (c) Spermatheca (d) Female chelicera, lateral view (e) Male leg II (excluding pretarsus).

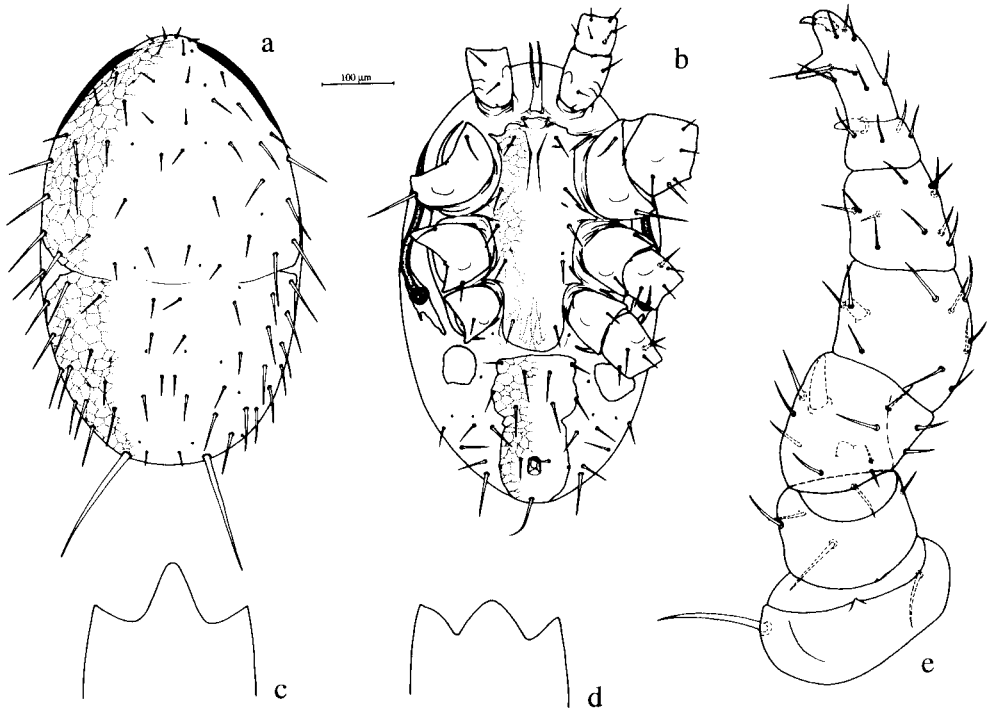

Fig. 11. *Tropicoseius kaliszewskii.* (a) Male idiosomal dorsum (b) Male idiosomal venter (c) Male tectum (d) Female tectum (e) Male leg II (excluding pretarsus).

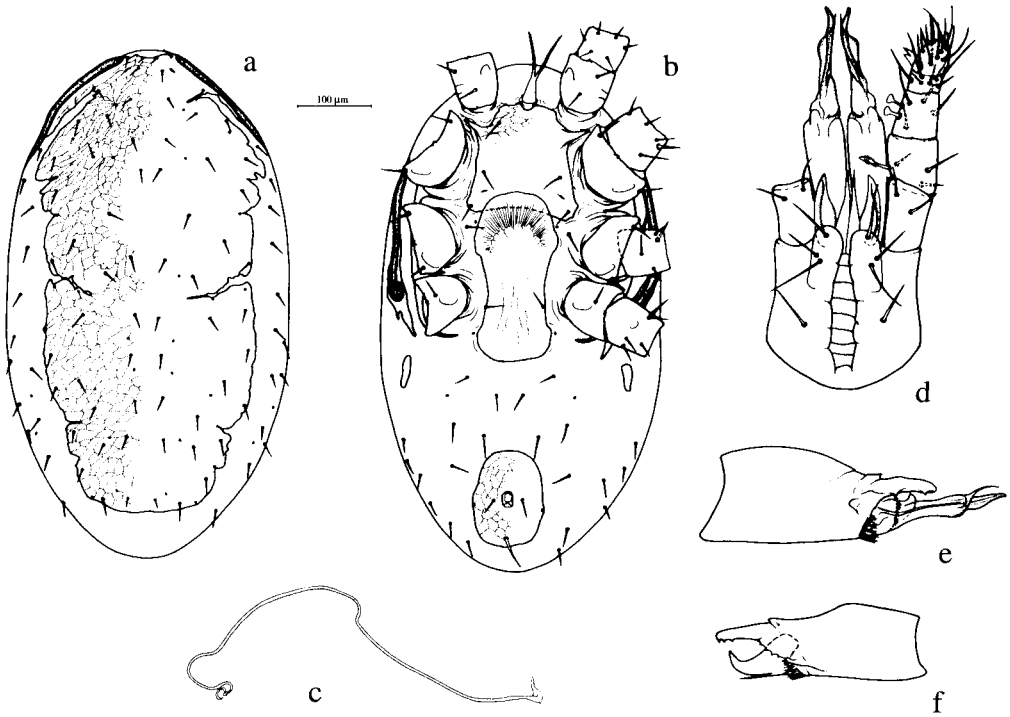

Fig. 12. *Tropicoseius kaliszewskii.* (a) Female idiosomal dorsum (b) Female idiosomal venter (c) Spermatheca (d) Venter of gnathosoma, male (e) Male chelicera, lateral view (f) Female chelicera, lateral view.

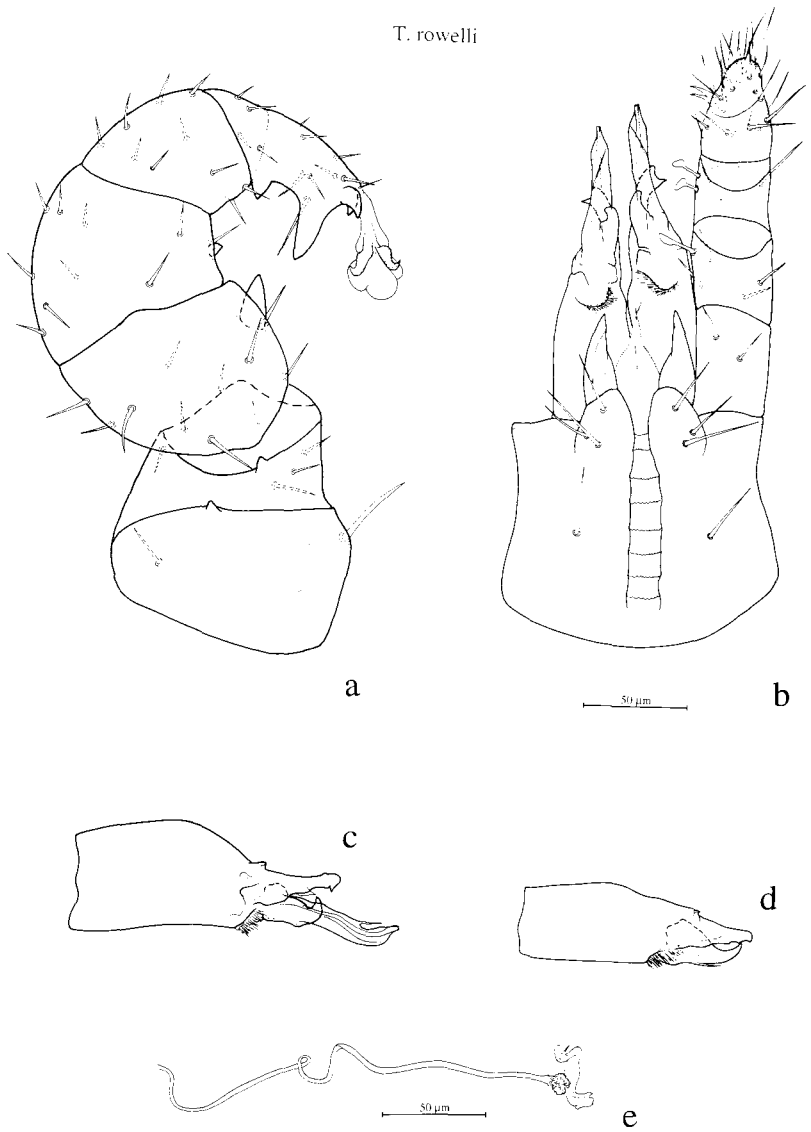

Fig. 13. *Tropicoseius rowelli.* (a) Male leg II (b) Venter of gnathosoma, male (c) Male chelicera, lateral view (d) Female chelicera, lateral view (e) Spermatheca.

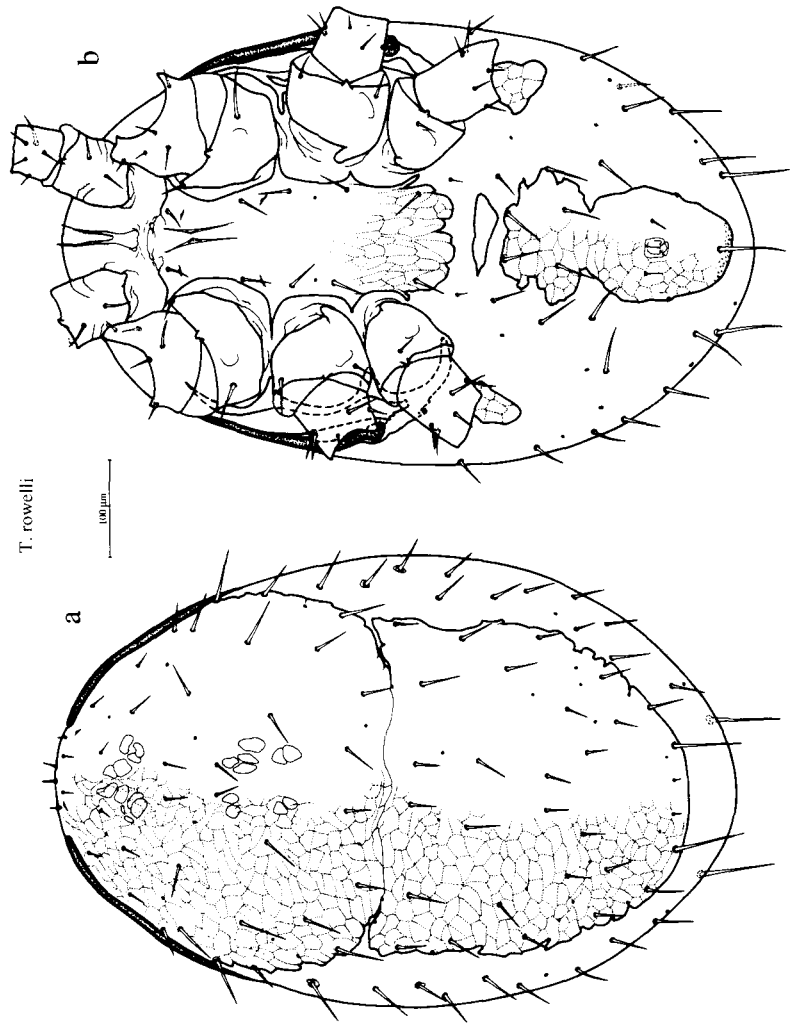

Fig. 14. *Tropicoseius rowelli*, male. (a) Idiosomal dorsum (b) Idiosomal venter.

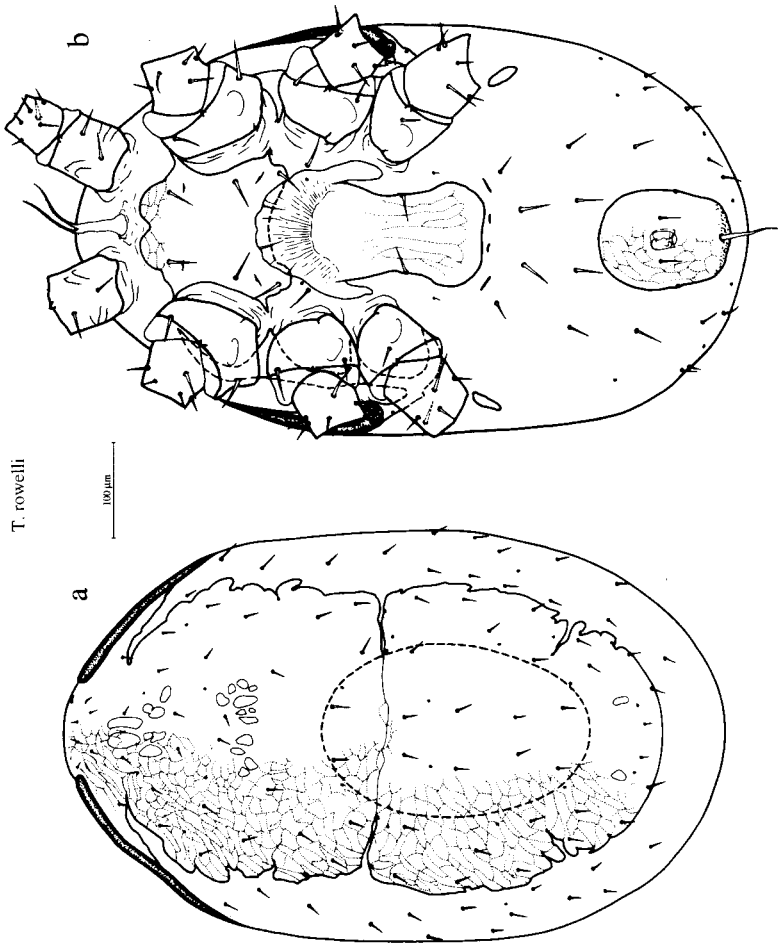

Fig. 15. *Tropicoseius rowelli*, female. (a) Idiosomal dorsum, dashed line indicates the size and position of an egg (b) Idiosomal venter.

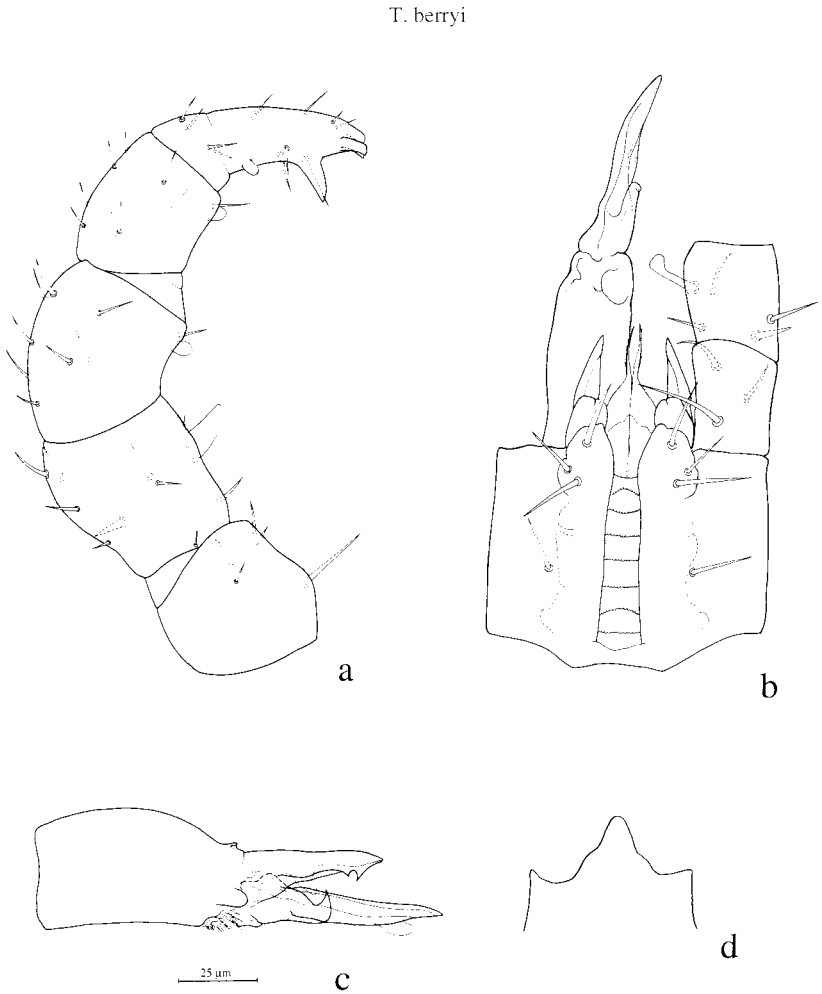

Fig. 16. *Tropicoseius berryi*, male. (a) Leg II (excluding pretarsus) (b) Venter of gnathosoma (c) Chelicera, lateral view (d) Tectum.

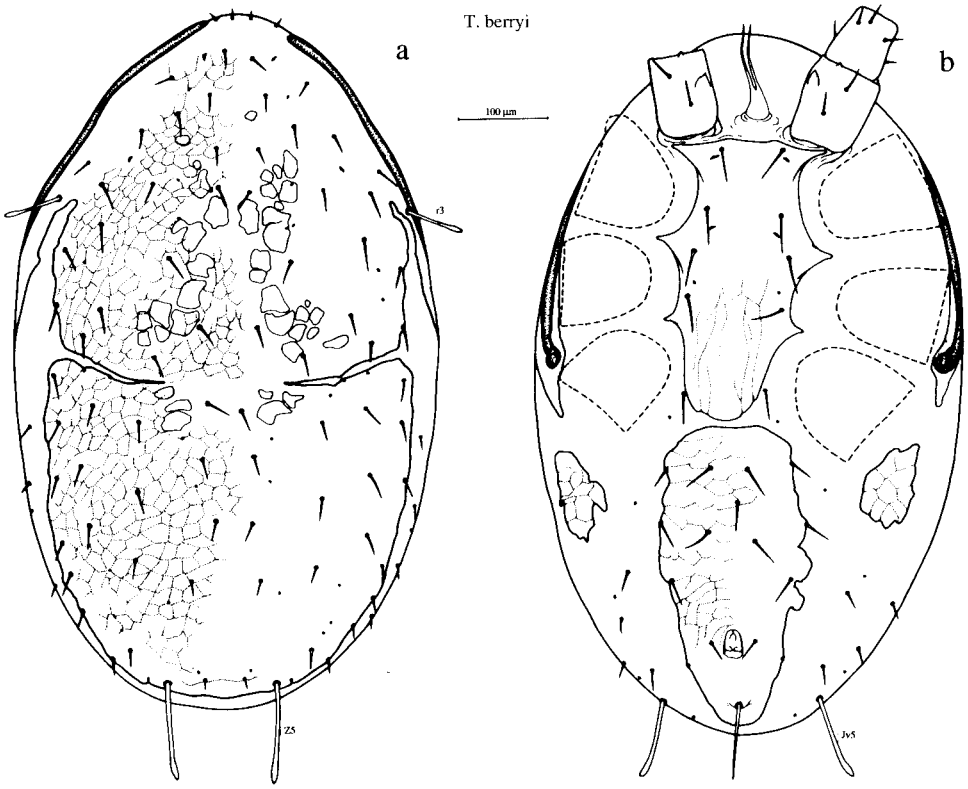

Fig. 17. *Tropicoseius berryi,* male. (a) Idiosomal dorsum (b) Idiosomal venter.

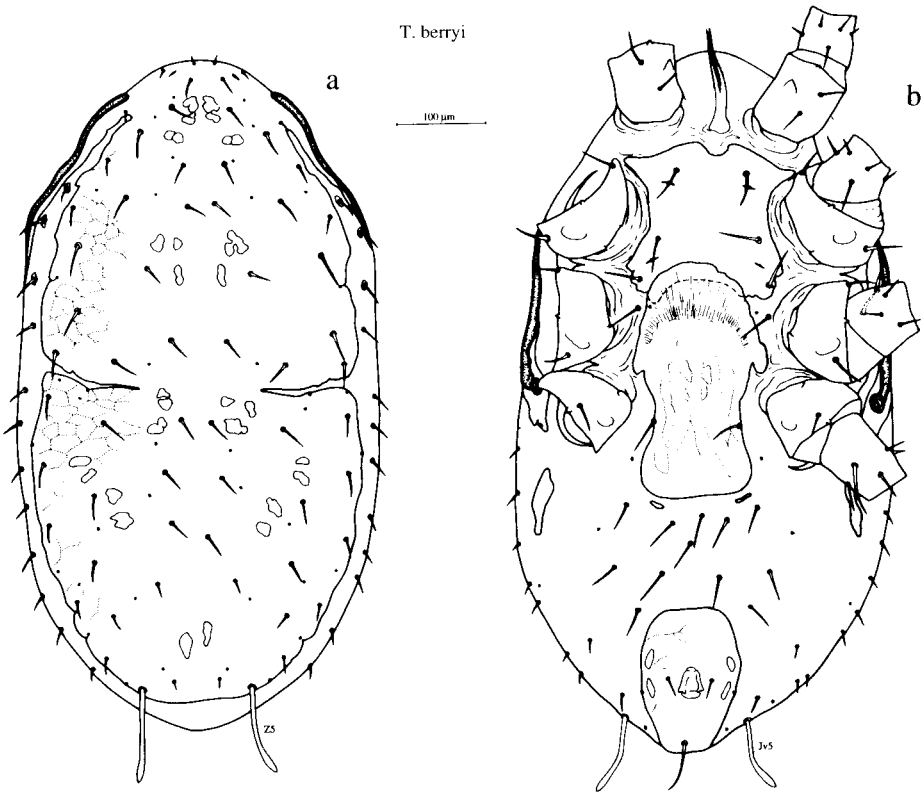

Fig. 18. *Tropicoseius berryi,* female. (a) Idiosomal dorsum (b) Idiosomal venter.

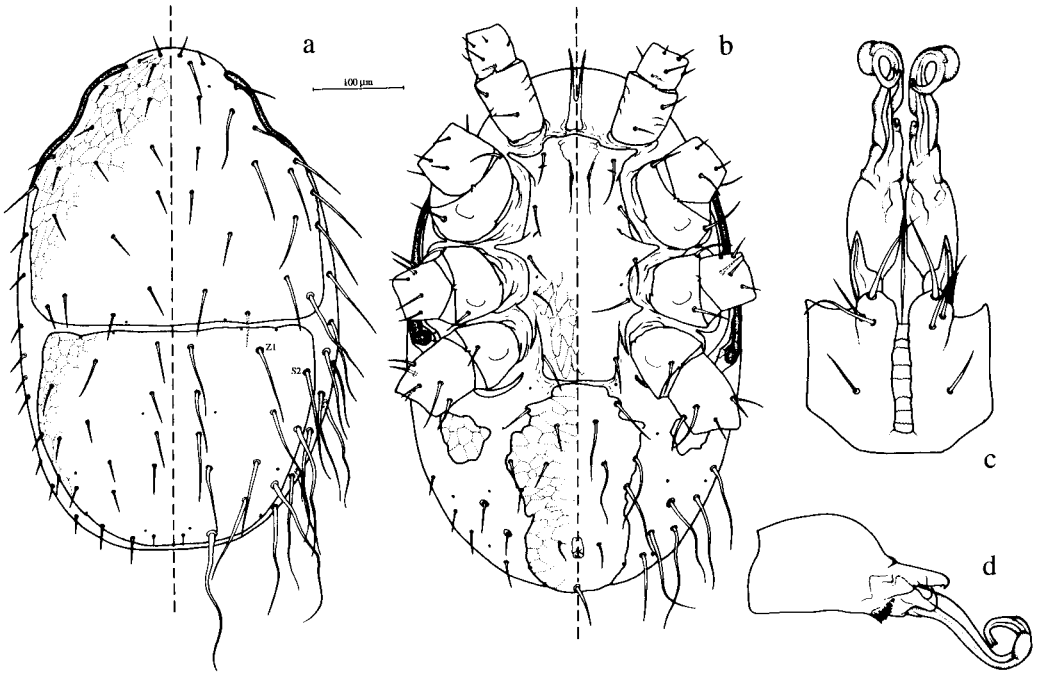

Fig. 19. *Tropicoseius erioxynon,* male. (a) Idiosomal dorsum, showing variation in the development of setae (left side, homeomorphic form, right side, heteromorphic form) (b) Idiosomal venter, showing variation in the development of setae (left side, homeomorphic form, right side, heteromorphic form) (c) Venter of gnathosoma (d) chelicera, lateral view.

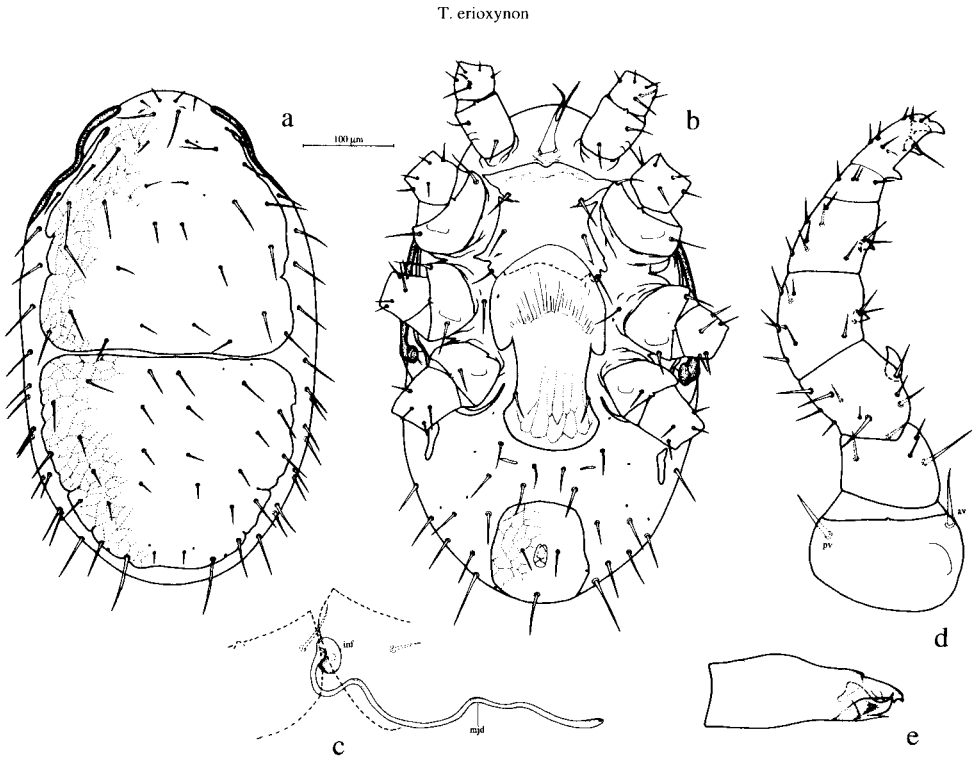

Fig. 20. *Tropicoseius erioxynon.* (a) Female idiosomal dorsum (b) Male idiosomal dorsum (c) Spermatheca (d) Male leg II (excluding pretarsus) (e) Female chelicera, lateral view. inf, infundibulum, mjd, major duct.

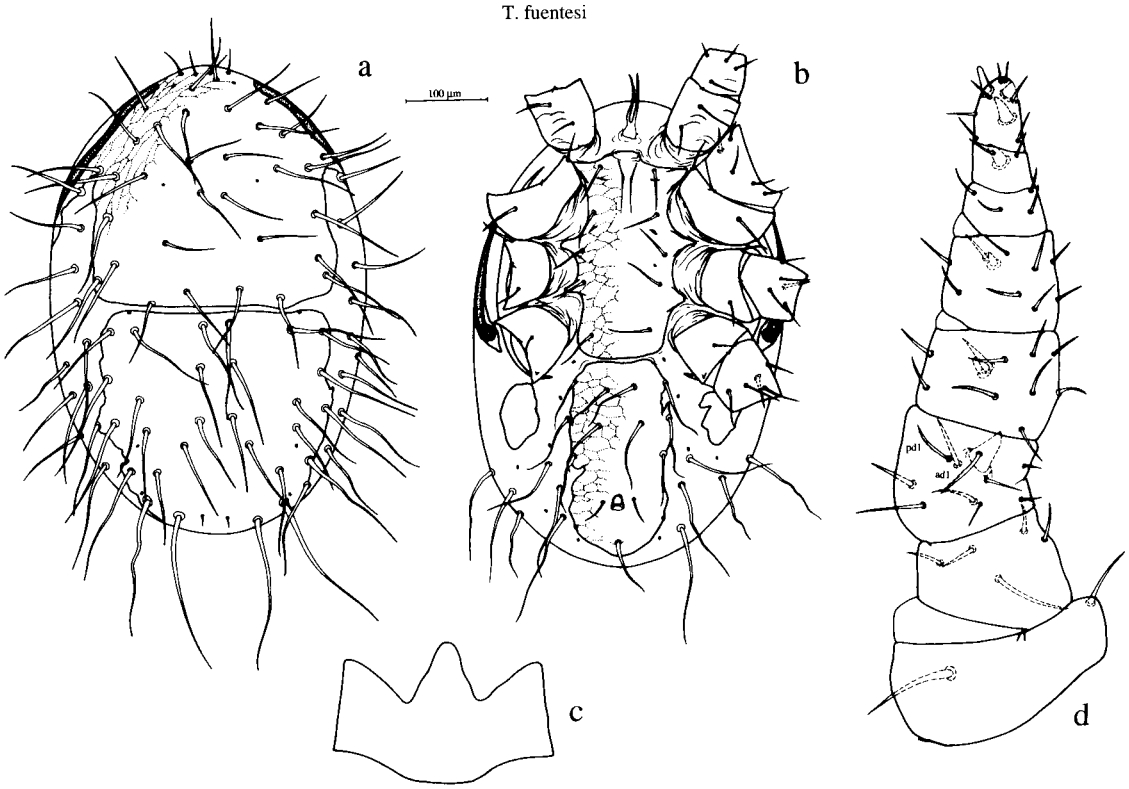

Fig. 21. *Tropicoseius fuentesi,* male. (a) Idiosomal dorsum (b) Idiosomal venter (c) tectum (d) Leg II (excluding pretarsus).

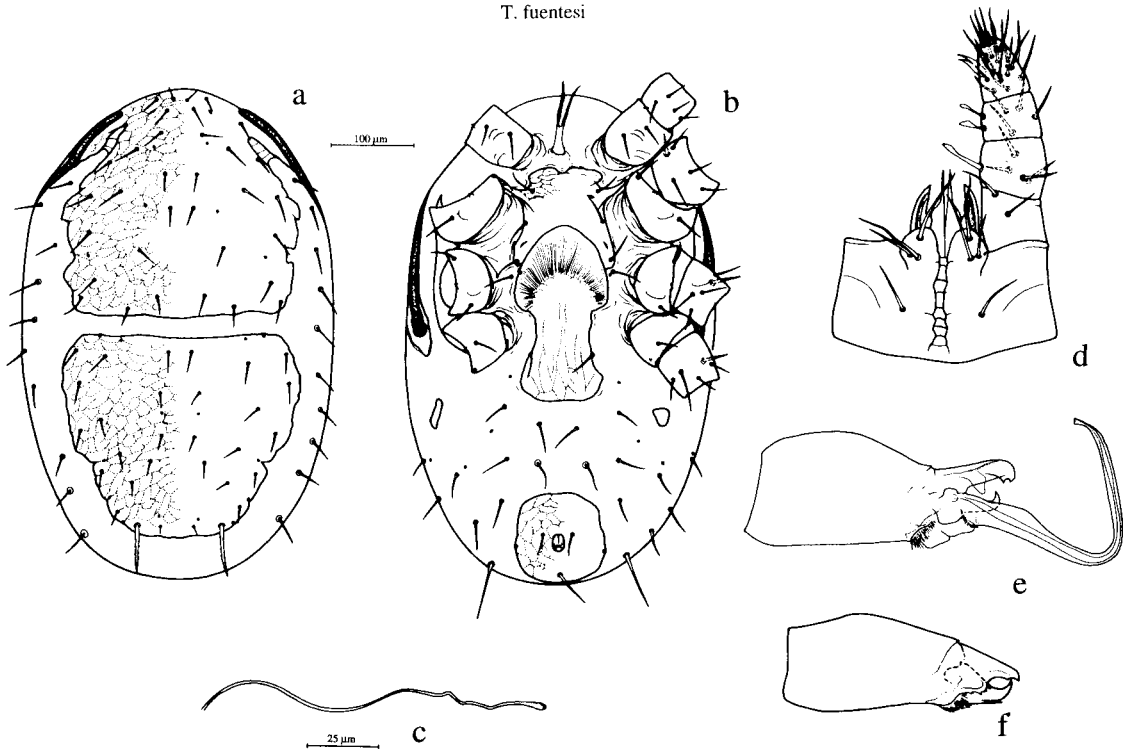

Fig. 22. *Tropicoseius fuentesi.* (a) Female idiosomal dorsum (b) Female idiosomal venter (c) Spermatheca (d) Venter of gnathosoma, male (e) Male chelicera, lateral view (f) Female chelicera, lateral view.

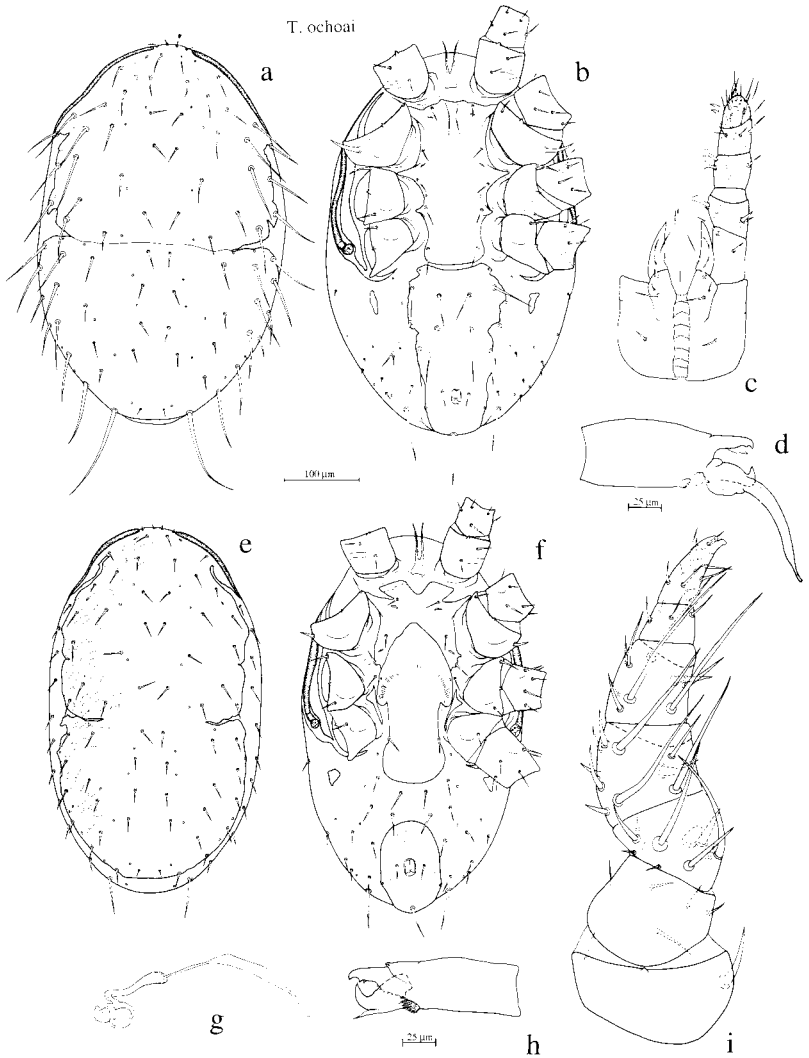

Fig. 23. *Tropicoseius ochoai.* (a) Male idiosomal dorsum (b) Male idiosomal venter (c) Venter of gnathosoma, male (d) Male chelicera, lateral view (e) Female idiosomal dorsum (f) Female idiosomal venter (g) Spermatheca (h) Female chelicera, lateral view (i) Male leg II (excluding pretarsus).

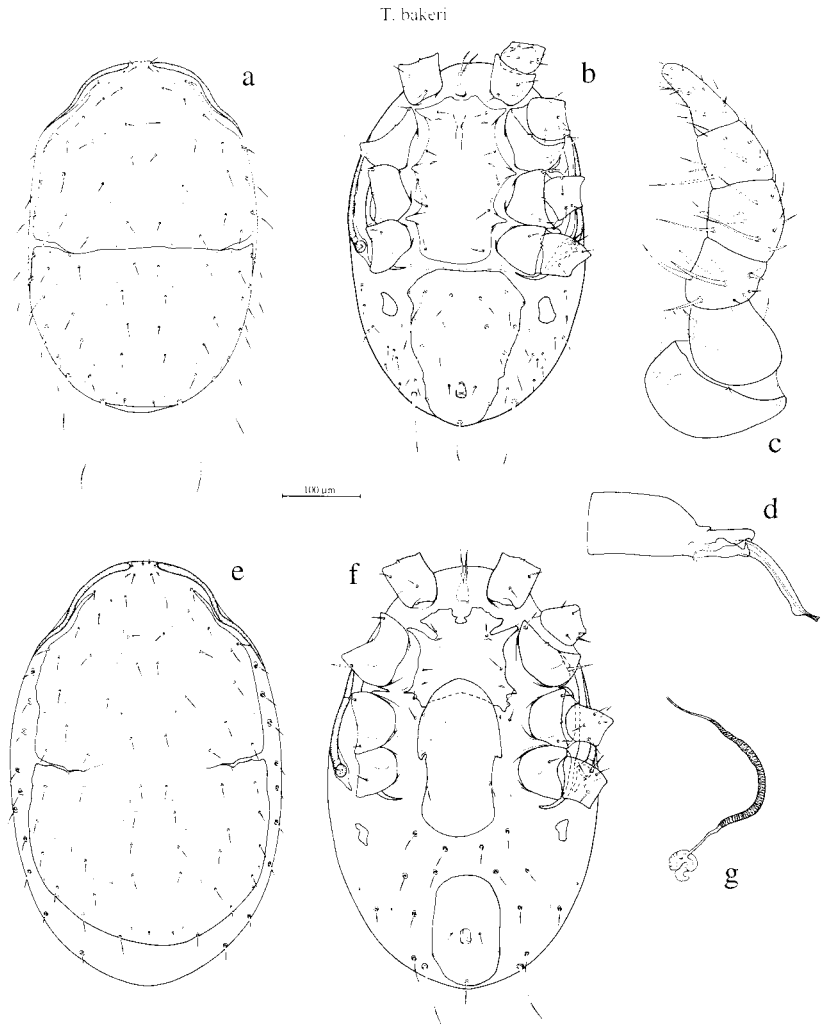

Fig. 24. *Tropicoseius bakeri.* (a) Male idiosomal dorsum (b) Male idiosomal venter (c) Male leg II (excluding pretarsus) (d) Male chelicera, lateral view (e) Female idiosomal dorsum (f) Female idiosomal venter (g) Spermatheca.

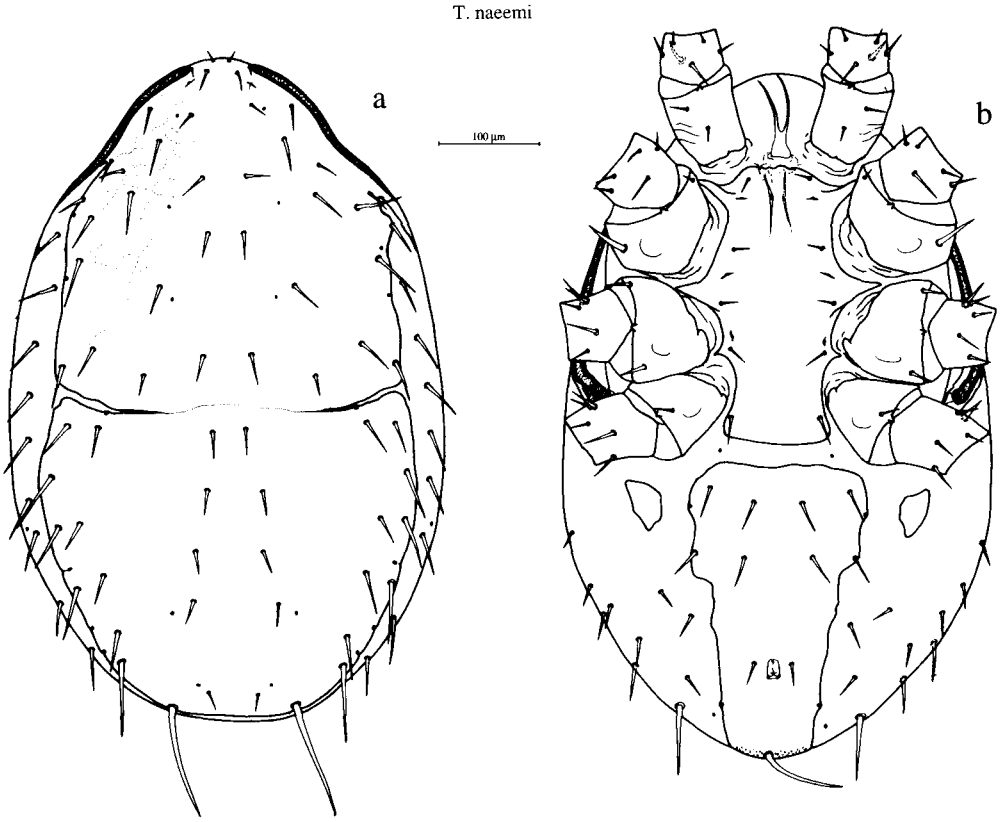

Fig. 25. *Tropicoseius naeemi,* male. (a) Idiosomal dorsum (b) Idiosomal venter.

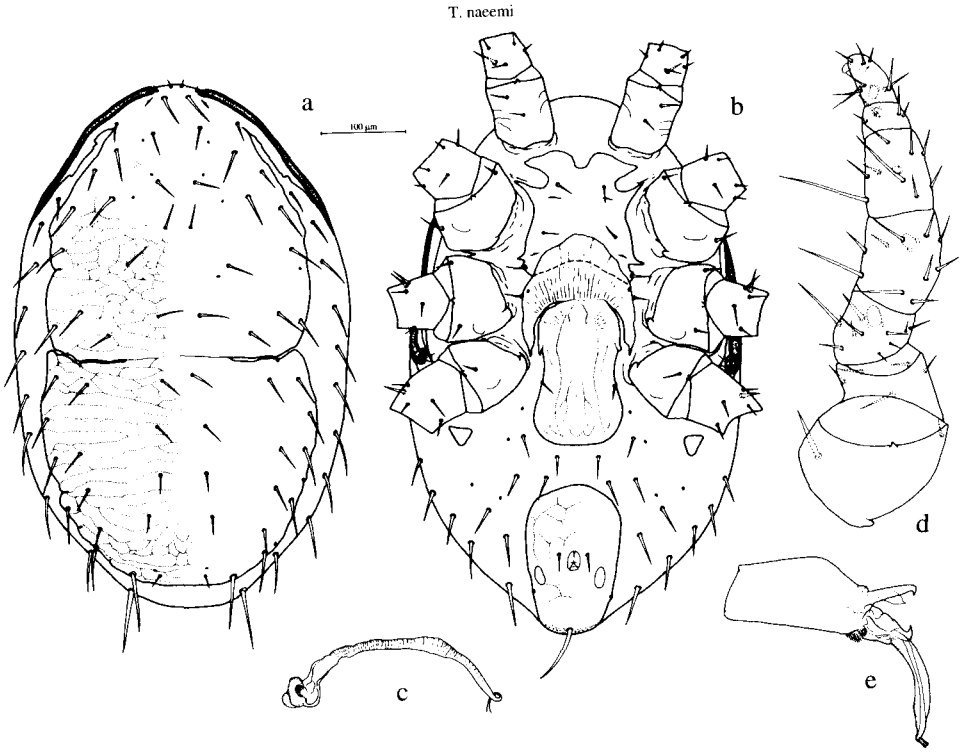

Fig. 26. *Tropicoseius naeemi.* (a) Female idiosomal dorsum (b) Female idiosomal venter (c) Spermatheca (d) Male leg II (excluding pretarsus) (e) Male chelicera, lateral view.

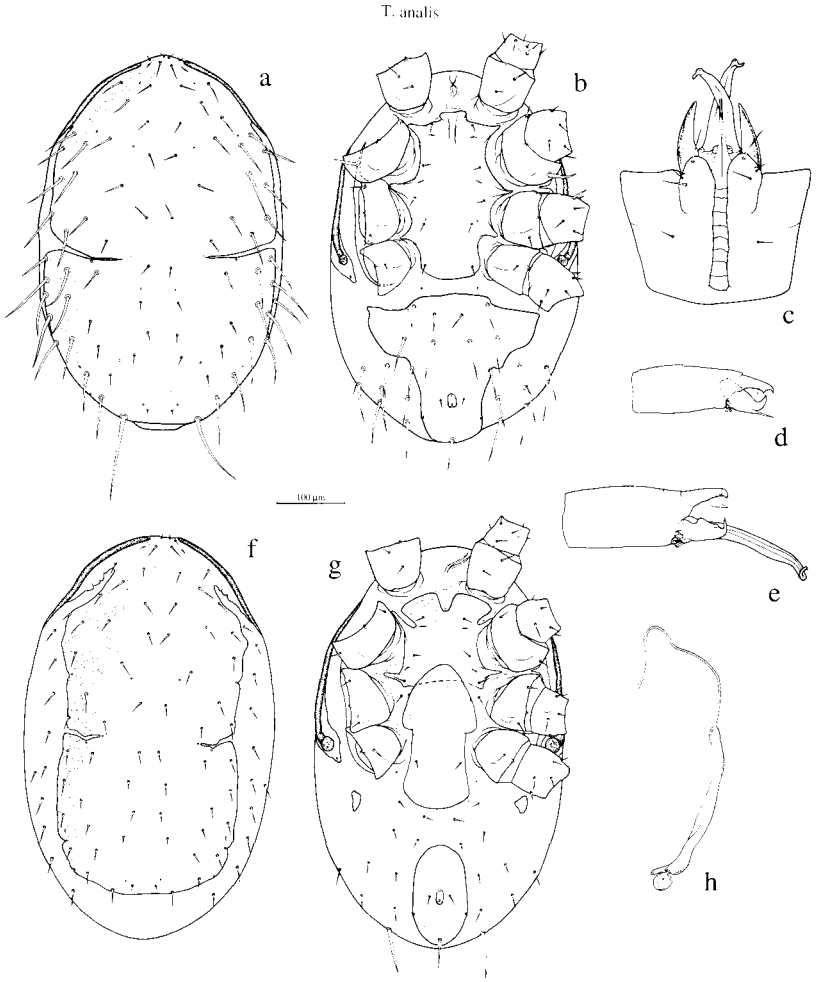

Fig. 27. *Tropicoseius analis*: (a) Male idiosomal dorsum (b) Male idiosomal venter (c) Venter of gnathosoma, male (d) Female chelicera, lateral view (e) Male chelicera, lateral view (f) Female idiosomal dorsum (g) Female idiosomal venter (h) Spermatheca.

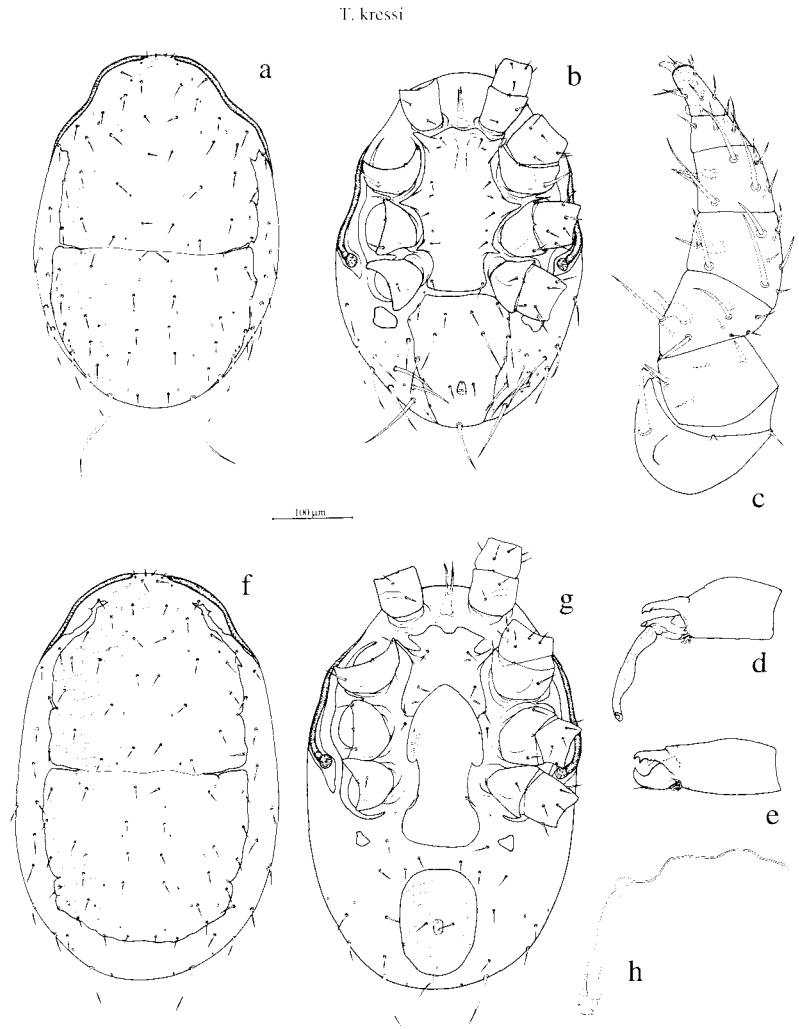

Fig. 28. *Tropicoseius kressi*. (a) Male idiosomal dorsum (b) Male idiosomal venter (c) Male leg II (excluding pretarsus) (d) Male chelicera, lateral view (e) Female chelicera, lateral view (f) Female idiosomal dorsum (g) Female idiosomal venter (h) Spermatheca.

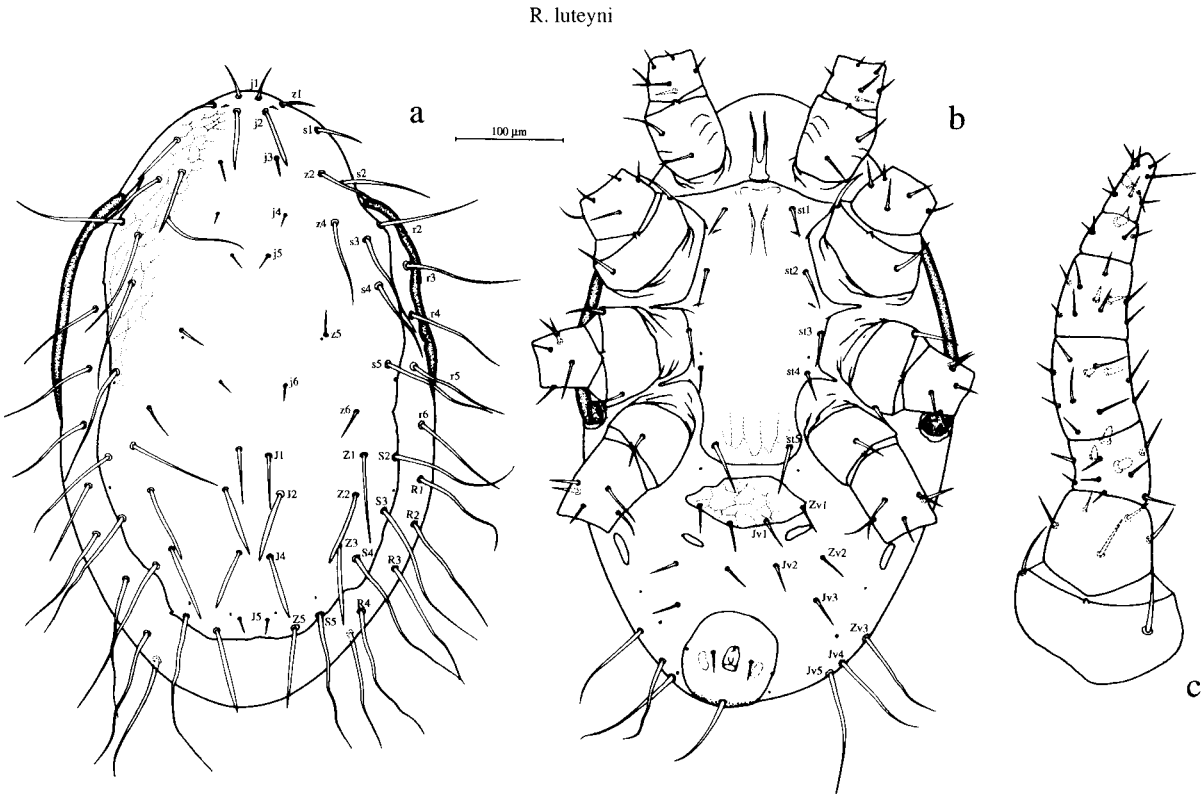

Fig. 29. *Rhinoseius luteyni,* male. (a) Idiosomal dorsum (b) Idiosomal venter (c) Leg II (excluding pretarsus).

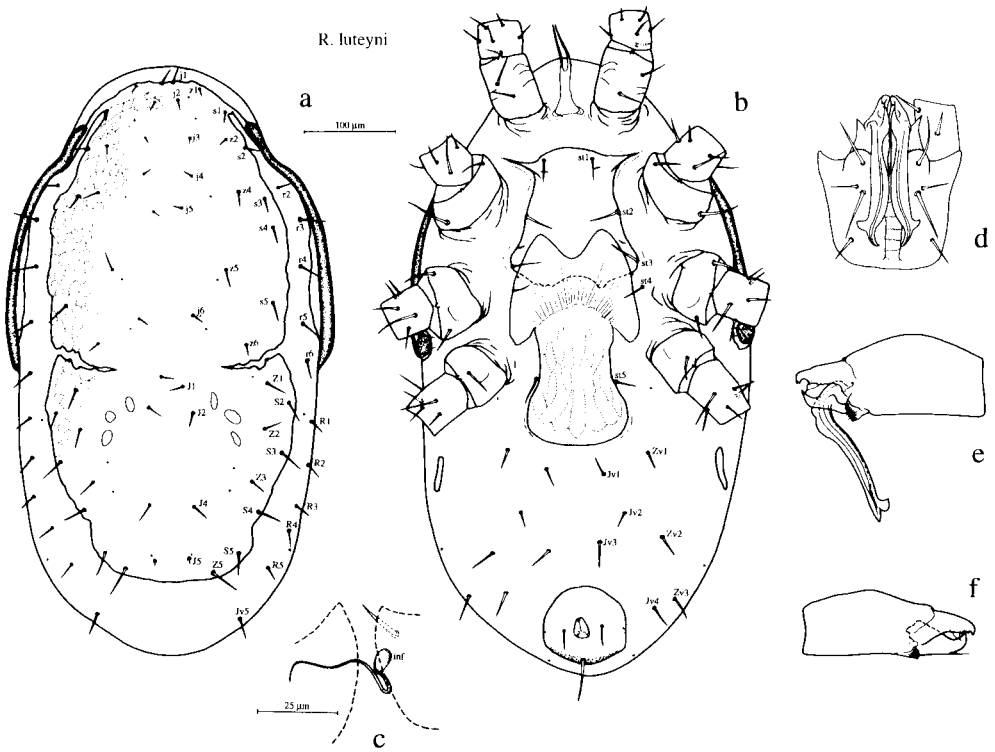

Fig. 30. *Rhinoseius luteyni.* (a) Female idiosomal dorsum (b) Female idiosomal venter (c) Spermatheca (inf, infundibulum) (d) Venter of gnathosoma, male (e) Male chelicera, lateral view (f) Female chelicera, lateral view.

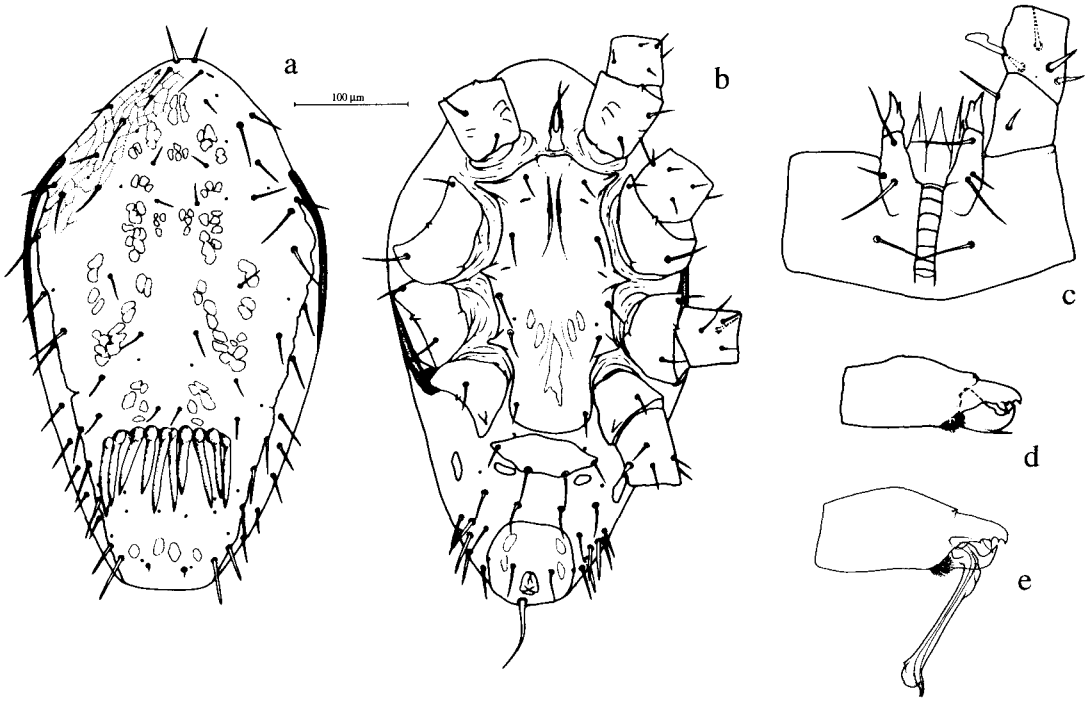

Fig. 31. *Rhinoseius nadachowskyi.* (a) Male idiosomal dorsum (b) Male idiosomal venter (c) Venter of gnathosoma, male (d) Female chelicera, lateral view (e) Male chelicera, lateral view.

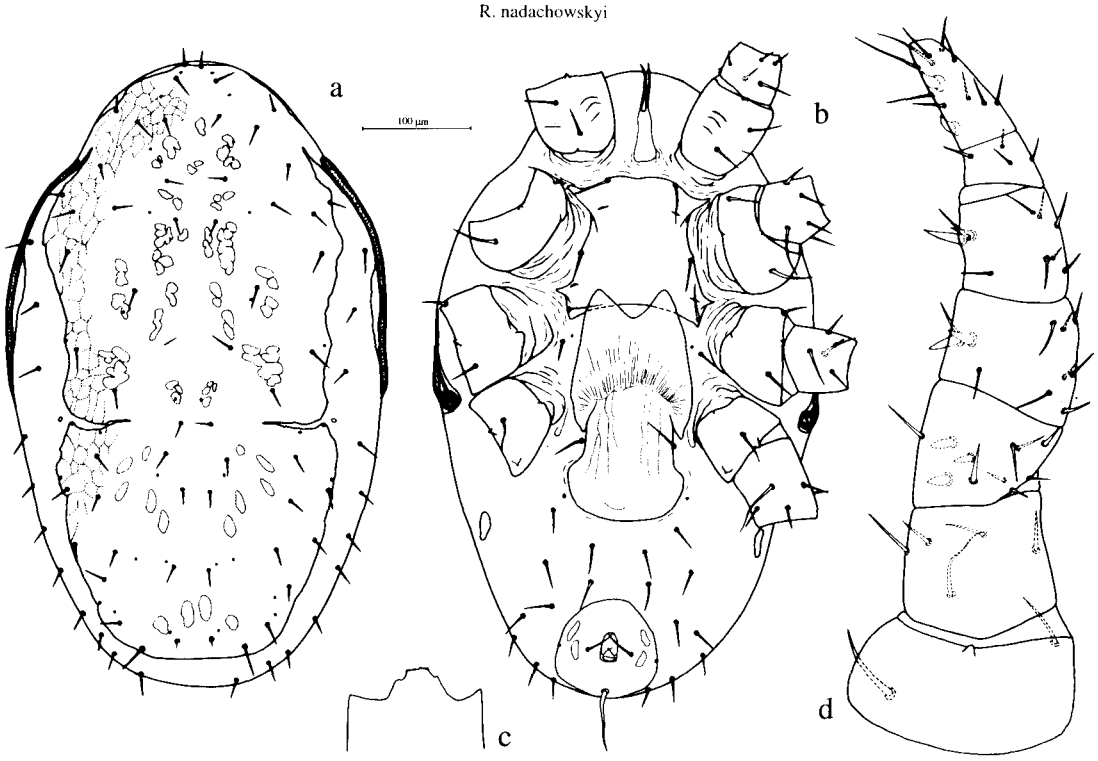

Fig. 32. *Rhinoseius nadachowskyi.* (a) Female idiosomal dorsum (b) Female idiosomal venter (c) Female tectum (d) Male leg II (excluding pretarsus).

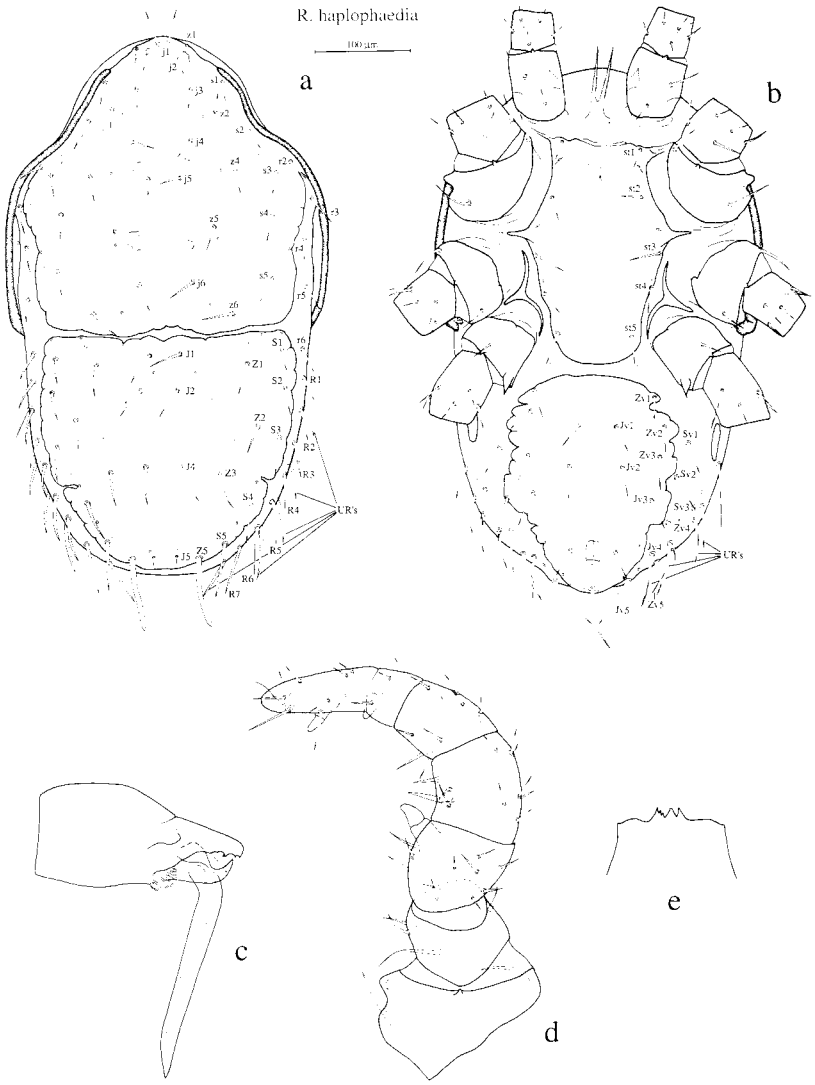

Fig. 33. *Rhinoseius haplophaedia,* male. (a) Idiosomal dorsum (b) Idiosomal venter (c) Chelicera, lateral view (d) Leg II, excluding pretarsus (e) Tectum.

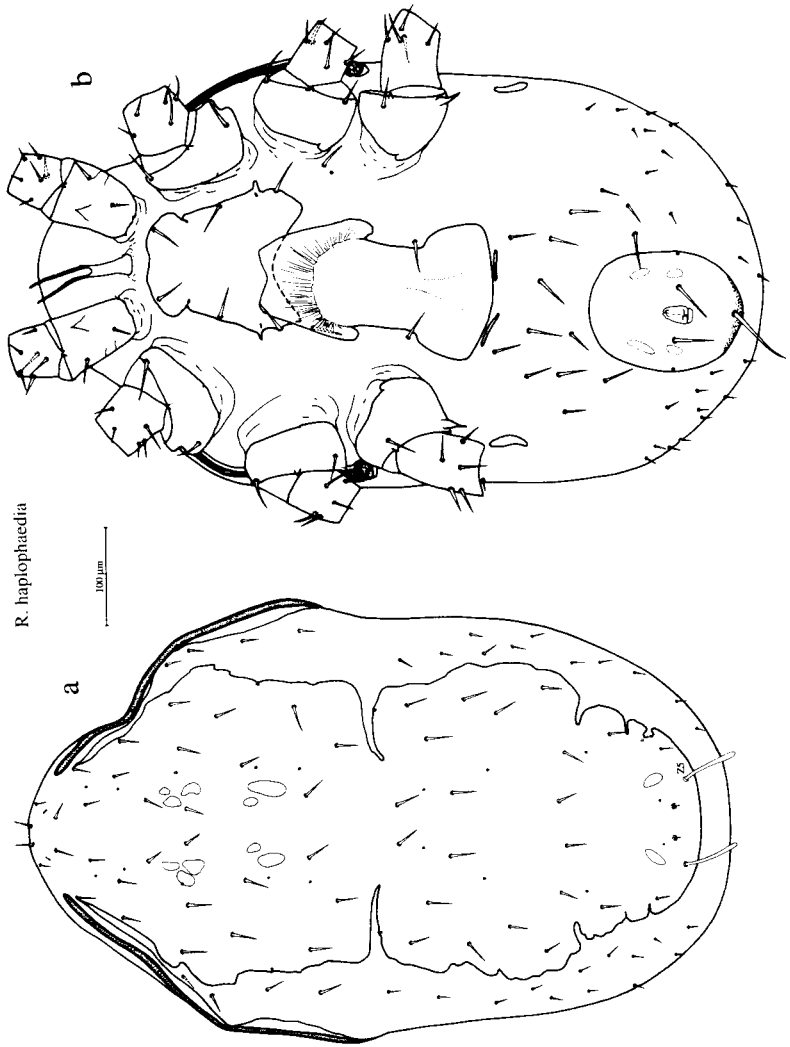

Fig. 34. *Rhinoseius haplophaedia,* female. (a) Idiosomal dorsum (b) Idiosomal venter.

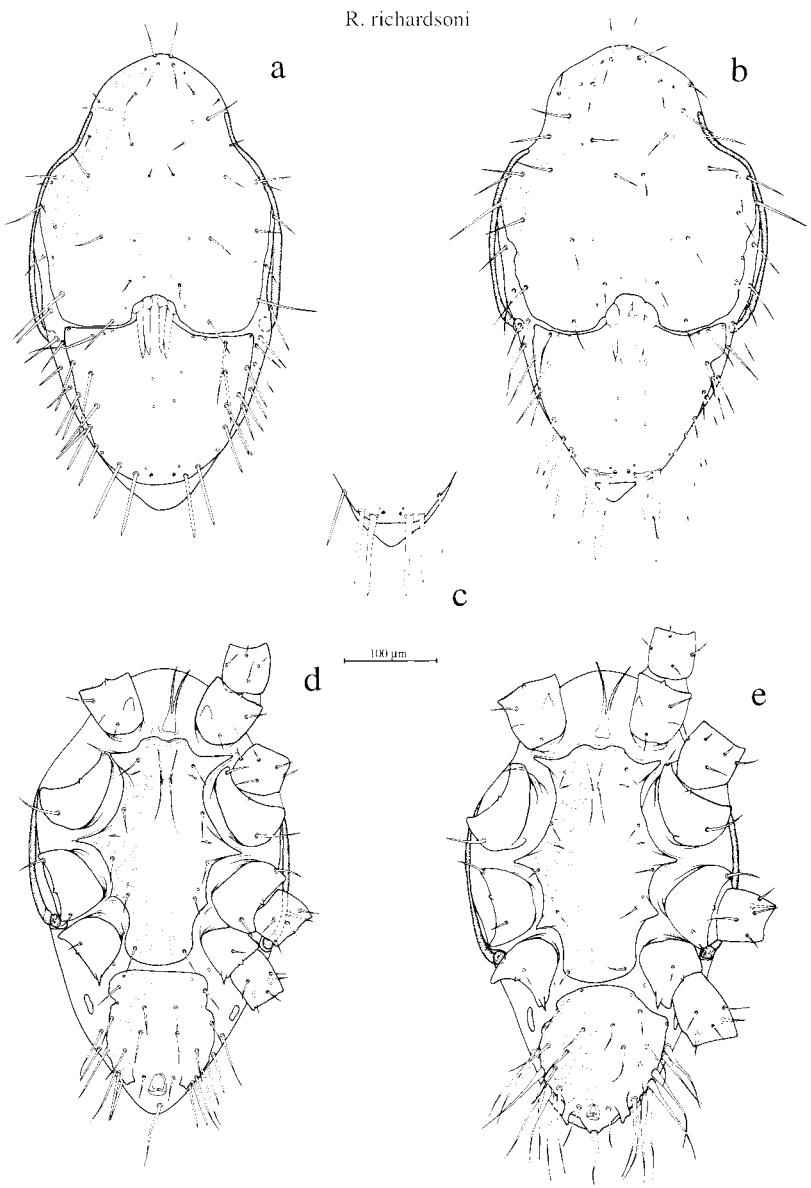

Fig. 35. *Rhinoseius richardsoni,* male. (a) Idiosomal dorsum, homeomorphic form (b) Idiosomal dorsum, heteromorphic form (c) Posterior part of opisthonotum, intermediate form (d) Idiosomal venter, homeomorphic form (b) Idiosomal venter, heteromorphic form.

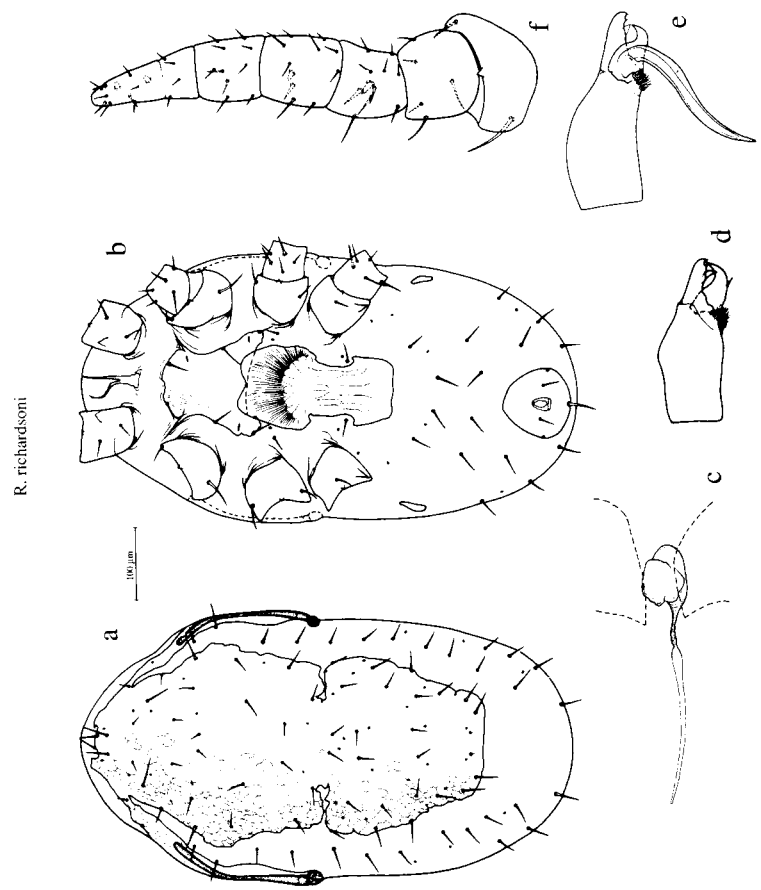

Fig. 36. *Rhinoseius richardsoni.* (a) Female idiosomal dorsum (b) Female idiosomal venter (c) Spermatheca (d) Female chelicera, lateral view (e) Male chelicera, lateral view (f) Male leg II (excluding pretarsus).

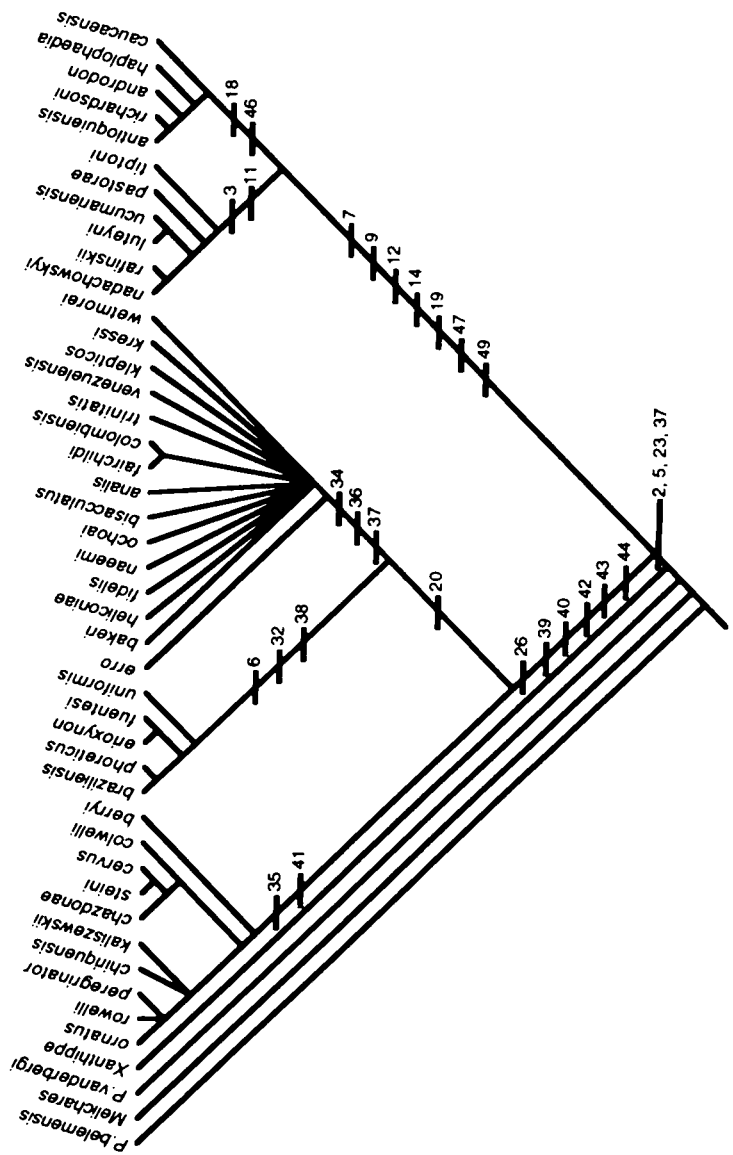

Fig. 37. Cladogram resulting from the analysis of the relationships among species of *Rhinoseius* sensu Lindquist and Evans 1965 (CI = 0.605, RI = 0.918, RC = 0.555, HI = 0.395) numbers on internodes indicate synapomorphies (only synapomorphies supporting species groups and larger clades are shown).

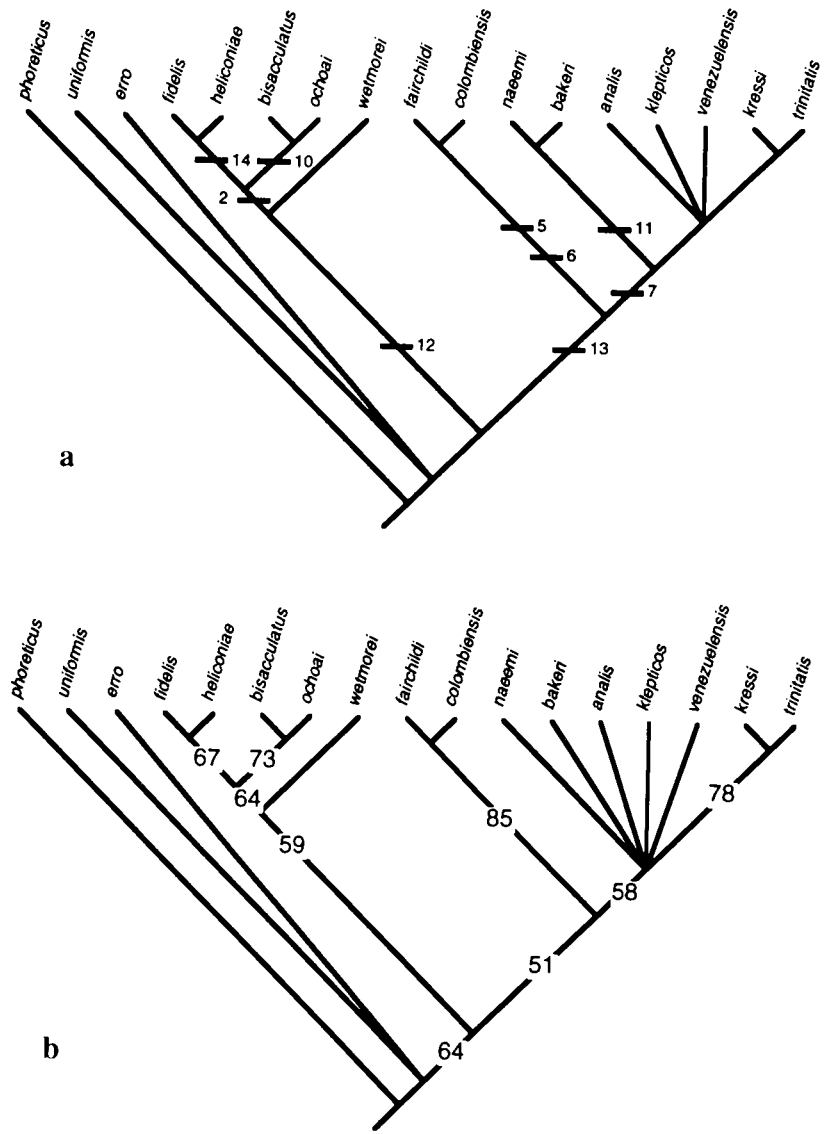

Fig. 38. (a) Cladogram resulting from the analysis of the relationships among species of the *wetmorei* group (CI = 0.824, RI = 0.917, RC = 0.755, HI = 0.176) numbers on internodes indicate synapomorphies; (b) The same tree showing bootstrap values for individual nodes (note the collapse of *baker–naeemi* clade).

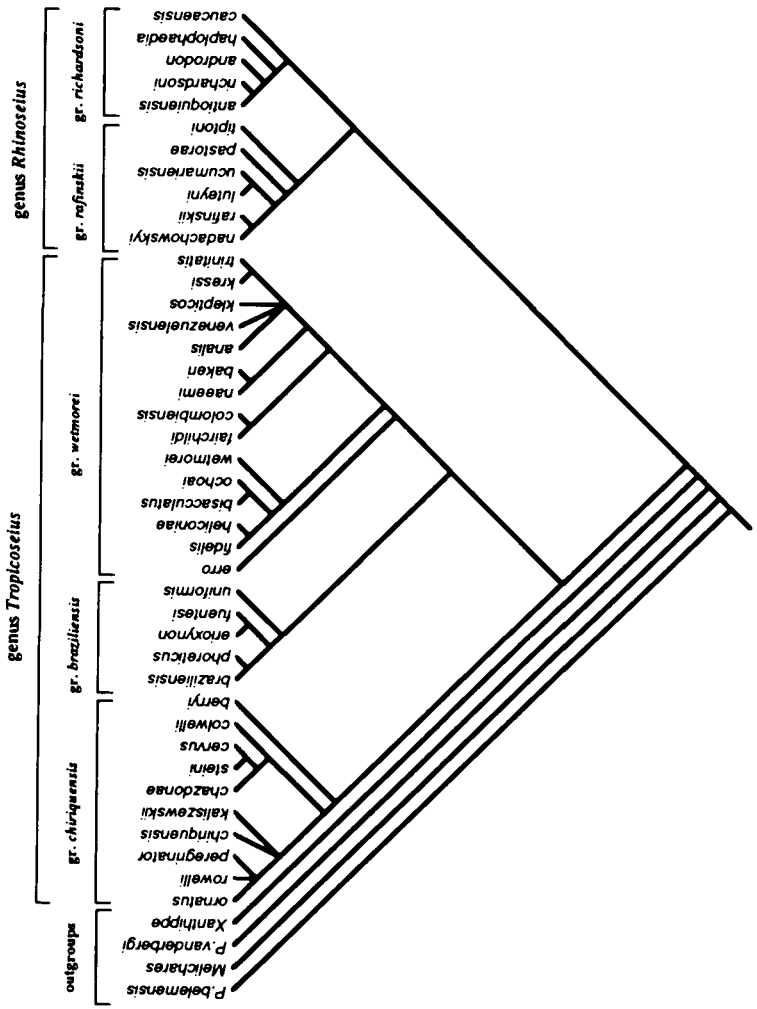

Fig. 39. A combined tree showing taxonomic implications of the cladistic analysis of species previously included in the genus *Rhinoseius* sensu Lindquist and Evans 1965.

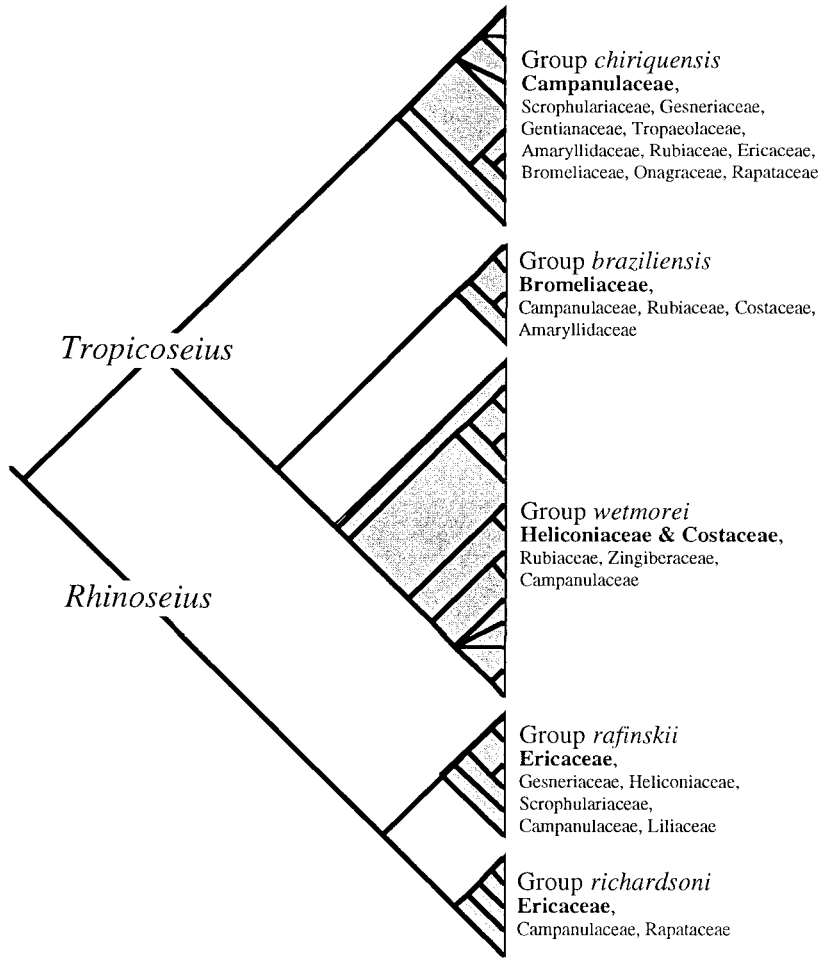

Fig. 40. Major host plant affiliations of species groups within genera *Tropicoseius* and *Rhinoseius*.