

**THE SEMIAQUATIC GENUS *TEGEOCRANELLUS*
(ACARI: ORIBATIDA: AMERONOTHROIDEA)
OF NORTH AND CENTRAL AMERICA**

VALERIE M. BEHAN-PELLETIER

Research Branch, Agriculture and Agri-Food Canada, K.W. Neatby Building, Ottawa, Ontario,
Canada K1A 0C6

Abstract

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Species of the oribatid mite genus *Tegeocranellus* from North and Central America are discussed, and immatures are described for the first time. Six new species are described and keyed: *Tegeocranellus alas* from Costa Rica, *T. barbarae* from Alabama, Mississippi, and Florida, *T. kethleyi* from Alabama and Mississippi, *T. mississippii* from Louisiana and Texas, *T. muscorum* known from Ontario to Florida, and *T. mediolamellatus* from Guatemala. Descriptions of *T. alas*, *T. barbarae*, *T. mediolamellatus*, and *T. muscorum* are based on adults and immatures, and those of the other two species on adults only. I expand the generic diagnosis to include information on the apherodermous, plicate immatures, and present a character analysis hypothesizing that the monogeneric family Tegeocranellidae is a member of the Ameronothroidea, closely related to Selenoribatidae and Fortuyniidae.

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Résumé

On trouvera ici une étude des oribates du genre *Tegeocranellus* d'Amérique du Nord et d'Amérique centrale, ainsi qu'une description inédite de stades immatures. Six nouvelles espèces sont décrites: *Tegeocranellus alas* du Costa Rica, *T. barbarae* de l'Alabama, du Mississippi et de la Floride, *T. kethleyi* de l'Alabama et du Mississippi, *T. mississippii* de la Louisiane et du Texas, *T. muscorum* répandu de l'Ontario à la Floride et *T. mediolamellatus* du Guatemala. Une clé d'identification permettra de reconnaître les espèces. Les descriptions de *T. alas*, *T. barbarae*, *T. mediolamellatus* et de *T. muscorum* sont basées sur l'examen des adultes et des stades immatures, alors que, dans le cas des deux autres espèces, seuls des adultes ont été examinés. La diagnose générique comporte des informations sur les stades immatures apherédermes, plissés, et l'analyse des caractères suppose que la famille monogénérique des Tegeocranellidae appartient aux Ameronothroidea, étroitement apparentés aux Selenoribatidae et aux Fortuyniidae.

[Traduit par la Rédaction]

INTRODUCTION

Tegeocranellus Berlese (1913) is a genus of small- to medium-sized oribatid mites known from semiaquatic habitats, with nine described species: *T. africanus* Mahunka known from Africa, *T. bolivianus* Balogh and Mahunka from Bolivia, *T. bosniae* (Frank) from Bosnia, *T. concavus* J. and P. Balogh and *T. convexus* J. and P. Balogh from Australia, *T. knysnaensis* Kok and *T. sacchareus* Kok from South Africa, *T. laevis* (Berlese) from Europe, and *T. opcus* Tseng from Taiwan. Prior to the present study, this genus was recorded in North America only from the state of New York and the province of Nova Scotia (Marshall et al. 1987), and there were no published records from Central America.

The classification of *Tegeocranellus* has a chequered history. Grandjean (1962), in his consummate paper, declined to classify the genus because he lacked data for immatures. Balogh (1961, 1972) placed *Tegeocranellus* in Tectocephidae, a placement questioned by Grandjean (1965). The first proposal of the family Tegeocranellidae was by Balogh and Balogh (1988, p. 77); the family was included in their identification key to the families of pycnonotic Brachypylina, but no superfamily placement was given. Balogh and Balogh

attributed the family designation to "P. Balogh 1987". I could find no paper by P. Balogh in 1987 containing reference to *Tegeocranellus* or Tegeocranellidae, and this was confirmed by S. Mahunka (in litt. 1995). Balogh and Balogh (1992) considered Tegeocranellidae a member of the Polypterozetoidea, though they gave no reason for this placement. The Polypterozetoidea as defined by Balogh and Balogh (1992) were appropriately keyed in the cepheoid part of their generic key, as Polypterozetidae are eupheredermous Brachypylna.

In this paper, I describe six new species of *Tegeocranellus* from North and Central America, including the first descriptions of immature stages, present a key to species for North and Central America, and briefly discuss their habitats. I expand the diagnosis of the genus given by Grandjean (1962) to include information on immatures, which are apheredermous and plicate. Based on synapomorphic adult and immature characters I hypothesize that Tegeocranellidae is a family of pycnonotic, apheredermous Brachypylna most closely related to Selenoribatidae and Fortuyniidae in the Ameronothroidea.

MATERIALS AND METHODS

Terminology used in this study is based on that developed by Grandjean (1962) for his redescription of *Tegeocranellus laevis* (Berlese). Wherever appropriate I refer to his figures for clarification of this terminology, much of which, particularly that of the lateral region of the podosoma, is generic to *Tegeocranellus*. General oribatid mite terminology used follows that of F. Grandjean (see Travé and Vachon 1975 for many references). The following conventions of measurement and description are used in this study:

Total length: measured from tip of rostrum to posterior edge of notogaster.

Notogastral width: refers to maximum notogastral width.

Notogastral length to width ratio: measured when viewed perpendicular to circumgastric scissure.

Leg setal formula: famulus is included in tarsal setal count on leg I and solenidial counts are in parentheses.

Abbreviations of collections: CNC, Canadian National Collection of Insects and Arachnids, Agriculture and Agri-Food Canada, Ottawa; FMNH, The Field Museum, Chicago; NHM, The Natural History Museum, London; HNHM, Hungarian Natural History Museum, Budapest; RAN, collection of R.A. Norton, SUNY, Syracuse.

Abbreviations of collectors: VBP, V. Behan-Pelletier; EEL, E.E. Lindquist.

Note. The order in which species are described is alphabetical.

SYSTEMATICS

TEGEOCRANELLUS

Tegeocranellus Berlese, 1913, p. 93.

Type-species: *Tegeocranus laevis* Berlese 1905, p. 237.

Diagnosis. Apheredermous, pycnonotic Brachypylna. Normal tracheal system present. Lateral border of lamella curving on itself, appearing thickened. Tutorium, discidium present, custodium and circumpedal carina absent. Pedotectum I large, principal part (*PdIp*) covering acetabulum I, superior part (*PdIs*) subrectangular to tapered. Integument dorsal to acetabula II and III smooth, with tectal edges. Humeral porose area Ah present. Rostrum without genal incision. Ten or 12 pairs of notogastral setae. Lenticulus usually present. Notogastral depressions (*fs*) present or absent. Notogaster without posterior notogastral tectum. Epimeral borders clearly evident. Epimeral setation 2-1-2-3. Sternal depression present medially on border of epimera III and IV, or absent. Ovipositor and spermapositor with 11 setae: one seta of pair ψ_2 absent. Six pairs of genital setae. Tarsi monodactyl. Seta *d* absent from genua and tibiae. Solenidion ω_2 absent from tarsus II. Opisthosoma of immatures plicate laterally and ventrally, smooth centrodorsally, slightly convex; apheredermous. Nymphs unideficient; seta h_3 absent from larva (11 gastronomic pairs present).

Description. ADULT. Prodorsum. Lamella large, long; prodorsal surface between lamellae flattened. Lateral border of lamella curving on itself (Grandjean 1962, his fig. 4E), appearing thickened. Lamellar cusps anteriorly strongly tapered and curved ventrally; shape clearly visible only when viewed from anterior aspect; lamellar cusps broad or narrow, medially touching or not (Figs. 5, 43). Lamellar seta (*le*) borne dorsally on lamellar cusps; its long canal, with enlargement along its length and narrowing posteriorly, extending from alveolus of seta *le* posteriorly. Interlamellar seta (*in*) borne on lamella posteriorly, with short canal. Canal *xx* similar in length and shape to canal associated with seta *le*, present or not evident, when present extending through lamella anterior to seta *in* (Fig. 1; Grandjean 1962, his figs. 1, 4E). Translamella absent, but surface of prodorsum slightly thickened in translamellar region (Figs. 1, 16, 62), appearing darker in transmitted light. Rostrum entire, margin sometimes slightly undulating. Rostral seta (*ro*) medially positioned, usually inserted on ridge (Figs. 5, 6, 16). Ridge paralleling margin of rostrum to level of *w*, with small tooth (α) anterolaterally (Grandjean 1962, his fig. 4A and D), may extend medially to seta *ro* (Figs. 5, 6, 16). Exobothridial seta (*ex*) reduced to alveolus. Bothridium with large, rounded, granulate protuberance posterolaterally (Figs. 17, 45). Sensillus of medium length, clavate or fusiform, smooth or barbed, directed laterally to posterolaterally. Distinct dorsosejugal groove (*dsj*) formed between the anterior margin of the notogaster and the posterior crest (*arp*) of prodorsum (Grandjean 1962, his fig. 1).

Lateral region. Tutorium long, well-developed, with ridges dorsally; cusp present (Figs. 6, 16, 35, 64). Pedotectum I large, in two parts (Fig. 9; Grandjean 1962, his fig. 4A and B): principal part (*Pdlp*) sculptured with irregular ridges or tubercles, convex anteriorly, completely covering acetabulum I; superior part (*Pdls*) positioned dorsally to *Pdlp*, subrectangular to tapered, smooth to granulate anteriorly. *Pdls* overlaps *Pdlp* with narrow tectum (*be*) (Grandjean 1962, his fig. 4B). Dorsally tectum (*b2*) of *Pdls* may cover alveolus of seta *ex*. Dorsal to acetabulum II, large, smooth region (*Zl2*) with dorsal and posterior tecta (*b2*) (Grandjean 1962, his fig. 4B) contrasts with strongly tuberculate integument ventral to bothridium and along sejugal scissure (Figs. 9, 18, 45). Cerotegument well-developed along sejugal scissure and on tuberculate integument ventral to bothridium. Small carina extending from base of bothridium to level of seta *ex* (Fig. 9). Dorsal to acetabulum III smooth, subrectangular region (*Zl3*) with narrow tecta (*b3*) present dorsally, anteriorly and anteroventrally (Figs. 9, 18; Grandjean 1962, his fig. 4B), or one or more tecta absent. Rectangular anterior tectum (*b3*) of *Zl3* ends closely adjacent to, or projects over or under, straight posterior tectum (*b2*) of *Zl2*. Aperture of coxal gland (*z*) close to posterior border of *Zl2*. Posterior to acetabulum II tectum (*bj*) protects opening of tracheal vestibule (Grandjean 1962, his fig. 4B). Humeral porose area *Ah* present, concave; difficult to see because obscured by carina extending from base of bothridium to seta *ex*. Apodemato-acetabular tracheal system normal (Norton et al. 1997).

Ventral region. Genital and anal plates closely adjacent. Genital plates large, combined plates wider than long, wider than anal plates, integument may be darker than that of anal plates; with six pairs of medially positioned genital setae. One pair aggenital, two pairs of anal, and three pairs of adanal setae. Lyrifissure *iad* long, positioned laterally or posterolaterally of anal plate, medial, or slightly anterior, or posterior to seta *ad*₂. Preanal organ subtriangular (Grandjean 1962, his fig. 3D–F). Ovipositor with well-developed setae *k* (Fig. 20; Grandjean 1962, his fig. 2C). Ovipositor and spermapositor with 11 setae: one seta of pair ψ ₂ absent. Sternal and epimeral apodemes strongly developed. Sternal depression (*st*) medially, at level of apodeme III present or absent (Figs. 2, 13, 39). Small depression medially, at level of apodeme II present or absent (Grandjean 1962, his fig. 3A). Homology of epimeral setae difficult to establish without reference to immatures: setae *1a* and *2a* developed or reduced to alveolus; seta *1b* developed; seta *1c* lost in adult; seta *3a* present, but positioned laterally on epimere; seta *3b* positioned laterally on epimere; seta *4c* present,

positioned medial to discidium; setae *4a* and *4b* closely adjacent, positioned ventral to apodeme III. Ventral to pedotectum I, tectum usually extends from anterolateral margin of epimere I posteriorly almost to seta *3b* (Fig. 2). Discidium present (Fig. 19). Carina *cm* present medial to discidium (Grandjean 1962, his fig. 3A), or absent. Carina *cob* may be present posterior of acetabulum IV, in circumpedal position, usually strongly curving anteriorly to form distinct depression (*cpd* = circumpedal depression) (Figs. 2, 66).

Notogaster. Porose organs absent. Lenticulus generally present, convex (Fig. 4); weakly developed or absent in some specimens of some species. Notogaster with or without ridges or carina (*ts*) delimiting raised lenticulus (Fig. 36). With or without pair of depressions (*fs*) on notogaster posterolateral to lenticulus, border of *fs* merging with ridge *ts*, or not (Figs. 8, 36, 62, 63). Notogaster with small humeral carina laterally, projecting anterior of margin of notogaster as humeral tubercle, bearing seta *c* (Fig. 8). Humeral carina usually with granulate integument. Ten or 12 pairs of notogastral setae: setae *c*₁, *c*₃, *d*₁ (*da*), *f*₁ (*lp*) absent, *d*₂ (*dm*) and *e*₁ (*dp*) present or absent. Setae *c*, *h*₁ and *p*₁, *p*₂, *p*₃ similar in size, small; other notogastral setae subequal in size, medium in length. Five pairs of lyrifissures in usual positions; *ia* on humeral carina difficult to see because of granulation; only lyrifissure *im* easily visible in dorsal aspect, lateral to seta *e*₂ (*lm*), other lyrifissures visible in lateral aspect. Pair of carinae (*eg*) positioned slightly anterolateral to setae *cp* (*la*), present or not (Figs. 8, 12).

Gnathosoma. Infracapitulum diarthric (Figs. 37, 65). Cheliceral dentition variable, species specific; either fixed and movable digits toothed, or fixed digit with small tooth medially, movable digit toothless (Figs. 3, 14, 41, 51, 58). Axillary saccule of the infracapitulum absent. Palp setal formula 0-2-1-3-9(1). Palptarsal solenidion arising at level of seta *lt'*, lying parallel to tarsal surface, extending anteriorly to base of eupathidium *acm* (Fig. 59).

Legs. Tarsi monodactylous. Leg setation: trochanter 1-1-2-1; femur 5-5-3-2; genu 2(1)-2(1)-1(1)-2; tibia 4(2)-4(1)-3(1)-3(1); tarsus 18(2)-15(1)-15-12 (Figs. 53-56). Seta *d* absent from genua I-III and tibiae I-IV. Seta *pl'* of tarsus I very long and acuminate, longest seta on leg I. Solenidion ω_2 absent from tarsus II. Setae (*p*) and *s* on tarsus I eupathidial; setae (*u*) on tarsi I-IV smooth. Solenidion ϕ_1 of tibia I long, not borne on apophysis. Porose areas present on femora I-IV and trochanters III, IV. Femora with ventral carina. Trochanters III and IV with triangular tectum paraxially. Tibia I with or without small dens proximoven-trally.

IMMATURE INSTARS. Apherodermous, without evident cerotegument. Hysterosoma slightly convex and smooth centrodorsally, with or without regularly spaced puncta (Fig. 23); plicate laterally and ventrally, with large folds, without defined, carinate border (Figs. 22, 26). Rostrum with row of foveae along margin (Fig. 28). Larva with 11 pairs (seta *h*₃ absent) and nymphs with 15 pairs of gastronotal setae (unideficent: *f*₁ absent). Paraproctal atrichosy in protonymph and deutonymph. Development of epimeral, genital, aggenital, anal, and adanal setae as in Table 2. Porose regions present posteromedially on prodorsum, posterior of bothridia (Figs. 24, 27), between epimera II and III, in adanal region, extending or not laterally in aggenital region, and surrounding opening of opisthosomal gland (Fig. 22); porose regions anterolateral and posterolateral of bothridia present or absent. Insertion areas of legs I-III with porose integument. Seta *d* absent from tibiae I-IV and genua I-III. Porose areas of femora I and II appear in protonymph, those of femora III and IV appear in adult; those of trochanters III and IV appear in deutonymph.

Remarks. 1. As noted above, adult epimeral chaetotaxy, especially that of epimeres III and IV, is difficult to establish without reference to immatures (see Grandjean 1962, fig. 3A). Two setae are present on larval epimere III in the positions of *3a* and *3b* (Fig. 30). No additional setae are added during ontogeny. The position of epimere III setae in the adult is that usual for *3b* and *3c*, i.e. positioned medially and laterally on the epimere (Figs. 2, 13). I hypothesize that the adult setae are homologous with those of the larva, but that their

position is shifted laterally. Similarly, positions of setae *4a*, *4b*, and *4c* in the tritonymph are normal for immature oribatid mites (Figs. 22, 48). In the adult, however, seta *4a* is shifted laterally, closely approximate to seta *4b*, and the two setae are positioned anteriorly on the epimere, ventral to apodeme III (Figs. 2, 19).

2. Development of porose areas on femora I–IV and trochanters III and IV in *Tegeocranellus* is unusual in that those of trochanters III and IV develop in the deutonymph, whereas those of femora III and IV do not develop until the adult. Where studied, femoral porose areas appear earliest in ontogeny (Grandjean 1940; Travé 1977), but as Norton et al. (1997) noted, there are few data on such ontogenetic patterns.

3. *Tegeocranellus* species have normally shaped chelicerae. However, all known instars of two species, *T. alas* sp.nov. and *T. mississippii* sp.nov., lack all but the distal tooth on the movable digit and have only one small tooth medially on the fixed digit, a character state unknown elsewhere in the Brachypylina (Kaneko 1988). However, in a population of the aquatic oribatid species *Mucronothrus nasalis* (Willmann), a member of the Desmonomata, cheliceral dentition varies among individuals, ranging from complete development to reduced dentition to edentate, without an overall change in shape of the chelicerae (Norton et al. 1996). No variation in shape of chelicera is associated with loss of teeth in *Tegeocranellus* either. The type of food ingested probably reflects the reduction in dentition, but insufficient gut contents were observed to test this hypothesis (Kaneko 1988).

RELATIONSHIPS AND CLASSIFICATION

It is unclear why Balogh and Balogh (1992) placed *Tegeocranellus* in the Polypterozeoidea, a superfamily that in general is poorly characterized. Polypterozetidae are eupheredermous, and have a highly modified infracapitulum, including modified chelicerae, rutella, and a mental tectum. Adult polypterozetids show no evidence of a lenticulus, and both prodorsum and notogaster are covered with a thick layer of cerotegument (Grandjean 1959).

As anticipated by Grandjean (1962), adults and especially immatures of *Tegeocranellus* provide data important to developing hypotheses of relationship (Table 1). Among pycnonotic Brachypylina, *Tegeocranellus*, Ameronothroidea, and Cymbaeremacoidea have many porose regions (or their sacculle homologues) on the prodorsum and hysterosoma of immatures (Grandjean 1955; Schubart 1975; Behan-Pelletier 1987, 1988; Norton et al. 1997), and I considered these synapomorphies of these taxa (Table 1). Specifically, these are an unpaired region posteromedially on the prodorsum; a pair of anterolateral and posterolateral porose areas, anterior and posterior to the bothridia respectively; a pair of latero-opisthosomal porose areas, adjacent to or surrounding the opening of the opisthosomal gland; and a pair of adanal porose areas lateral of the adanal setae.

Immatures of *Tegeocranellus* are apheredermous and have a plicate hysterosomal integument laterally and ventrally. Among pycnonotic Brachypylina, immatures of Tectocephidae, Ameronothroidea [Ameronothridae (sensu Weigmann and Schulte 1977), Selenoribatidae, Fortuyniidae], and Cymbaeremacoidea (Cymbaeremacidae, Micreremidae) also are apheredermous and plicate. A plicate hysterosomal integument in immatures is considered plesiomorphic among Brachypylina (Norton and Behan-Pelletier 1986). However, the nature of the plicate integument in *Tegeocranellus* is distinct; the hysterosoma of nymphs and larvae has large folds except for the centrodorsal region which is smooth and convex. This pattern is also expressed in the Selenoribatidae and Fortuyniidae (Grandjean 1966, 1968; van der Hammen 1963; Schuster 1963) and I consider it a synapomorphy for these families + *Tegeocranellidae* (Table 1).

Known larvae of *Tegeocranellus* are bidificent, with seta *h*₃ absent, a character state found also in Selenoribatidae and Fortuyniidae (Ameronothroidea). Seta *h*₃ is convergently lost in the Tenuialidae (Gustavioidea) and Amerobelbidae (Amerobelboidea) (Grandjean

TABLE 1. Summary of character state distribution in *Tegeocranellus* and related taxa

| Character state | Tegeo- cranellidae | Ameronothroidea | | | Cymbaeremacoidea | |
|--|--|--|--|--|--|--|
| | | Amerono- thridae | Selenori- batidae | Fortuy- niidae | Micrere- midae | Cymbae- remaeidae |
| Adults | | | | | | |
| Lamellar canal <i>xx</i> | + | — | — | — | — | — |
| Epimeral setation I–IV | 2-1-2-3 | 3-1-2-2 or 3-1-2-3 | 1-0-1-1 | 3-1-3-2 | 3-1-2-2 | 3-1-2-2 |
| Lenticulus | + | — | — | + | — | — |
| Notogastral setae | 10/12 | 14/15 | 13/15 | 14 | 14 | 10/13 |
| Aggenital setae | + | + | — | + | — | + |
| Dorso/pleurophragmata | + | — | — | + | — | + |
| Seta <i>d</i> of tibia I | — | Adult/— | — | — | — | Nymph/ adult |
| Solenidion ω_2 on tarsus II | — | +/— | — | + | — | +/— |
| Pedotectum I | + | +/— | — | + | + | + |
| Pedotectum II | — | +/— | — | + | + | + |
| Tutorium | + | — | — | — | — | +/— |
| Regions <i>ZI2</i> , <i>ZI3</i> | + | — | — | — | — | — |
| Insertion of tendon β | Near genital aperture | Removed from genital aperture | Near genital aperture | Near genital aperture | Removed from genital aperture | Removed from genital aperture |
| Medial depression at level of apodeme II | +/— | — | +/— | — | — | — |
| Sternal depression | +/— | — | +/— | — | — | — |
| Palptarsal solenidion | Not on tubercle, not associated with <i>acm</i> | Not on tubercle, not associated with <i>acm</i> | Not on tubercle, not associated with <i>acm</i> | Not on tubercle, not associated with <i>acm</i> | On tubercle, associated with <i>acm</i> | On tubercle, associated with <i>acm</i> |
| Genital setal ontogeny PN–AD | 1-3-5-6 | 1-3-5-6 | 1-2-3-3 | 1-2-4-5 | 1-3-5-6/ 1-2-4-4 | 1-2-3-4 |
| Partial fusion of tibia/tarsus | — | — | + | + | — | — |
| Number of seta ψ_2 of ovipositor | 1 | 2 | 1 | ? | 2 | 2 |
| Lyrifissure <i>iad</i> | Beside or posterior to <i>ad</i> ₂ | Anterior to <i>ad</i> ₃ | Anterior to <i>ad</i> ₃ | Beside or posterior to <i>ad</i> ₂ | Anterior to <i>ad</i> ₃ | Anterior to <i>ad</i> ₃ |
| Immatures | | | | | | |
| Hysterosomal plica | Large | Small | Large | Large | Small | Small |
| Centrodorsal region without plica, arched | + | — | + | + | — | — |
| Prodorsal porose areas | + | +/— | ? | ? | — | +/— |
| Adanal porose areas | + | +/— | ? | ? | + | +/— |
| Latero-hysterosomal porose areas | + | + | ? | ? | + | +/— |
| Gastronotal setal deficiencies: larva | <i>h</i> ₃ | None | <i>h</i> ₃ | <i>h</i> ₃ vestigial | None | None |

1961, 1965, 1966, 1968). Setae *dm* and *dp* of larval *Thalassozetes* (Selenoribatidae) are thicker and longer than other hysterosomal setae (Schuster 1963), a character state shared with known larvae of *Tegeocranellus* (Figs. 10, 29, 69).

Adults of species of *Tegeocranellus* have two apomorphies apparently unique to the genus: the presence of canal *xx* in the lamellae, and the development of regions *ZI2* and *ZI3*

with associated tecta on the lateral surface of the podosoma. Grandjean (1962) noted that canal *xx* is almost identical to that associated with seta *le*, and he speculated that canal *xx* may be a vestige of the second exobothridial seta. However, there is no evidence of a second exobothridial seta in immatures.

Depressions are found anteriorly on the notogaster in *Selenoribates* as in some species of *Tegeocranellus*, but those of *Selenoribates* are large (Grandjean 1966). Depressions *fs* on the notogaster of many species of *Tegeocranellus* also are similar to those of *Charassobates*, as noted by Grandjean (1962), and a relationship between these genera could be evoked as *Charassobates* also lacks pedotectum II and solenidion ω_2 on tarsus II. However, *Charassobates* are eupheredermous and lack prodorsal and hysterosomal porose areas in immatures (Behan-Pelletier 1988).

The unusual development of pedotectum I and tecta associated with regions *ZI2* and *ZI3* on the lateral surface of the podosoma in *Tegeocranellus* are unique to the genus. As species of *Tegeocranellus* are semiaquatic, primarily found in marshy habitats, Grandjean (1962) hypothesized that *ZI2* and *ZI3* and associated tecta maintain a plastron of air around the sejugal region and acetabulum III, and provide air for trachea *sj* and trachea III; this hypothesis was reiterated by Travé (1986). These structures are similar to the taenidia, covered by tecta, dorsal and anterior of acetabulum III and associated with openings of trachea III and the sejugal trachea in *Fortuynia* (van der Hammen 1963, fig. 3A), and further described under the term "van der Hammen's organ" by Pugh et al. (1990). Development of the cerotegument ventral to the bothridium in *Tegeocranellus* is similar to that illustrated by Pugh et al. (1990, fig. 2D) for *Fortuynia maculata* Luxton. However, it is difficult to homologize structures of *Tegeocranellus* with the taenidial system (van der Hammen's organ) of *Fortuynia*, and it may be that an analogue has evolved independently in the Tegeocranellidae to withstand periodic inundation. Development of tuberculate cerotegument ventral to the bothridium also has been described and illustrated by Messner et al. (1992) for *Dolicheremaeus amazonicus* Balogh and Mahunka, and a species of *Eremobelba*.

Tegeocranellidae and Selenoribatidae share the loss of solenidion ω_2 from tarsus II. This loss also occurs in some species of Ameronothridae, in Micreremidae (Table 1), and in some poronotic Brachypylina (Behan-Pelletier 1994); the latter is clearly a convergent loss.

Loss of one seta from setal pair ψ_2 of the ovipositor is a synapomorphy of Selenoribatidae and Tegeocranellidae (Table 1). Setae *k* are large in *Tegeocranellus*; those of *T. laevis* (Berlese), described by Grandjean (1962), are particularly so. Large setae *k* are also found in *Selenoribates*, though they are small in the confamilial genus *Thalassozetes* (Grandjean 1966).

In Brachypylina insertion of tendon β on the ventral plate is usually removed from the genital region, and associated with the edge of epimere IV (e.g. Grandjean 1960, fig. 2). This tendon is inserted close to the anterolateral margin of the genital opening in Tegeocranellidae, as in Selenoribatidae and Fortuyniidae (Grandjean 1968) and the sigilla is as large as that illustrated for *Schusteria littorea* by Grandjean (1968, fig. 2A). I consider this position of the sigilla a synapomorphy for Selenoribatidae, Fortuyniidae, and Tegeocranellidae.

Normal dorsophragmata and pleurophragmata are found on adult Tegeocranellidae, as in Fortuyniidae; Ameronothridae and Selenoribatidae lack dorsophragmata (Grandjean 1968).

The reduction of epimeral setation to 2-1-2-3 in adult *Tegeocranellus* is unique among Ameronothroidea. Epimeral seta *1c*, present in known immatures of all species of *Tegeocranellus*, is lost in the adult (Figs. 2, 22). Absence of seta *1c* from the adult is rare in the Brachypylina, being recorded for Selenoribatidae (Grandjean 1966), Gymnodamaeidae (*Arthrodamaeus*, *Jacotella*) (Paschoal and Johnston 1982), Otocephidae (*Fissicepheus* and *Psammocephus*) (Balogh and Balogh 1992), and Carabodidae (*Klapperiches*, *Pentabodes*) (R.M. Reeves, pers. comm. 1996). It is unclear at which stage seta *1c* is lost in the

gymnodamaeid, otocephid, and carabodid genera noted. In Selenoribatidae, it is absent from nymphs, but whether it is present or absent in the larva is unresolved (Grandjean 1966, 1968). For example, it is present in the larva of the macropyline *Phthiracarus anonymus* Grandjean, but absent from nymphs and adult (Grandjean 1934).

The position of lyrifissure *iad* in relation to the anal region and adanal setae is quite variable among pycnonotic Brachypylina (Balogh and Balogh 1992). In most aphereder-mous, plicate, pycnonotic Brachypylina, e.g. Tectocephidae, Ameronothridae, Podacaridae, Selenoribatidae, and Cymbaeremaeoidea, it is anterior to seta ad_3 . In Tegeocranellidae and Fortuyniidae it is medial to, posterior to, or slightly anterior to seta ad_2 (Figs. 2, 13, 32; Luxton 1992; van der Hammen 1963, fig. 1*b*), a position considered a synapomorphy for these families.

Among the Brachypylina only Tegeocranellidae, Cymbaeremaeoidea, and Ameronothroidea share the apomorphy of adanal porose areas in immatures. No synapomorphies relate Tegeocranellidae exclusively with the Cymbaeremaeoidea. However, seven synapomorphies support relationship between Tegeocranellidae and Selenoribatidae + Fortuyniidae within the Ameronothroidea (Table 1): (i) hysterosoma of immatures with large plica, smooth centrodorsally (shared with Selenoribatidae and Fortuyniidae); (ii) hysterosomal seta h_3 absent or vestigial in larva (shared with Selenoribatidae and Fortuyniidae); (iii) loss of one seta ψ_2 from ovipositor (shared with Selenoribatidae); (iv) insertion of tendon β on the margin of the genital plate (shared with Selenoribatidae); (v) depressions on the anterior of the notogaster (shared with Selenoribatidae); (vi) sternal depressions (shared with Selenoribatidae); and (vii) position of lyrifissure *iad* posterior to ad_3 (shared with Fortuyniidae).

A phylogenetic analysis of the relationship of families in the Ameronothroidea is beyond the scope of this paper. However, it is clear from this character analysis that Tegeocranellidae is a member of the Ameronothroidea, most closely related to Selenoribatidae and Fortuyniidae.

Most members of this superfamily are found in marine littoral or brackish habitats and are able to withstand periods of inundation: Ameronothridae include species found in intertidal and supralittoral as well as terrestrial habitats, and Selenoribatidae and Fortuyniidae occur exclusively in littoral and supralittoral habitats (Grandjean 1966, 1968; Pugh et al. 1990; Schuster 1966, 1977, 1979; Schulte and Weigmann 1977; Schulte et al. 1975). In contrast, Tegeocranellidae live exclusively in terrestrial habitats subject to periodic inundation. As Schuster (1966) commented, both autecological research and ecophysiological research are needed along with a phylogenetic analysis to resolve relationships in this diverse superfamily.

On the basis of the character states of both adult and immatures discussed above, I propose the following new diagnosis for the Tegeocranellidae.

Tegeocranellidae Balogh and Balogh 1988

Pycnonotic Brachypylina with integument of immatures plicate laterally and ventrally, smooth centrodorsally. Larva bifidicent, seta h_3 absent; nymphs unidificient. Paraproctal atrichosy in protonymph and deutonymph. Seta d absent from tibiae and genua of immatures and adults. Adult prodorsum without genal incision, pedotectum II, or custodium; with lamellae, lamellar cusps, tutorium, pedotectum I (divided into two parts), discidium, and porose area Ah. Series of tecta dorsal to acetabulum II, III and bordering ventrolateral sejugal region. Epimeral setation 2-1-2-3, seta Ic present in immatures, lost in adult. Genital and anal plates large, closely adjacent. Lyrifissure *iad* posterior to seta ad_3 . One seta of setal pair ψ_2 absent from ovipositor. Tendon β inserted on ventral plate close to margin of genital plate. Palpal eupathidium *acm* free. Axillary saccule of the infracapitulum absent. Notogaster with small humeral projection; without pteromorphs. Notogastral setation 10 or 12 pairs: c_1 , c_3 , f_1 , d_1 (*da*) absent, d_2 (*dm*), e_1 (*dp*) present or absent.

Type-genus: *Tegeocranellus*.

DESCRIPTION OF NEW SPECIES

Tegeocranellus alas sp.nov.

(Figs. 1–11; Map 1A)

Diagnosis. Adult total length 292–330 μm ; with ridge extending laterally from seta *ro*; seta *le* positioned about 20 μm dorsoposteriorly of lamellar tip; lamellar cusps narrow, well-separated; sensillus barbed, narrowly clavate; notogaster with *fs*, without ridges *ts*; 12 pairs of notogastral setae; sternal depression and circumpedal depression present; fixed digit of chelicera with single, minute tooth medially, movable digit toothless; ovipositor seta *k* 10–14 μm long. Tritonymph prodorsum with seven porose regions; opisthosoma with one pair of porose areas laterally. Larva with pattern of shallow grooves and porose plates centrodorsally.

ADULT. Measurements. Mean total length: females ($n = 8$) 316 μm (range 305–330); males ($n = 10$) 303 μm (range 292–312). Mean notogastral width: females 204 μm (range 200–214); males 197 μm (range 188–200).

Integument. Microtuberculate over whole body and legs. In addition, integument of humeral region of notogaster granulate. Cerotegument granulate.

Prodorsum. Narrow carina extending laterally from seta *ro* (Figs. 5, 6). Seta *ro* about 12 μm long, barbed, tapered. Lamella 94–140 μm long, about 24 μm wide at base of lamellar cusp. Lamellar cusps narrow and well-separated, 40–54 μm long, tapered, abruptly narrowing at level of lamellar seta; tip of cusp directed medially, bearing seta *le* about 20 μm dorsoposteriorly from tip. Canal *xx* present. Lamellar cusp with or without small lateral dens at level of seta *le* (Fig. 5). Seta *le* about 8 μm long, barbed, tapered. Distance between lamellae at base of cusps about 34 μm . Seta *in* about 10 μm long, barbed, tapered. Mutual distance of setal pairs *ro*–*ro*, *le*–*le*, and *in*–*in*, approximately 24, 42, and 80 μm , respectively. Sensillus about 58–62 μm long, clavate, expanded tip thickly barbed unilaterally, barbs progressively smaller proximally (Fig. 7).

Lateral region. Tutorium about 78 μm long, with ridges dorsally; tutorial cusp about 14 μm long, triangular (Fig. 9). *Pdls* narrow, width about 5–8 μm , about 24 μm long, blunt to pointed anteriorly (Fig. 9).

Notogaster. Slightly longer than wide; ratio 1.1:1. Humeral carina on anterior margin of notogaster rounded, with granulate integument (Figs. 1, 8). Integument delimiting lenticulus thickened, but ridges (*ts*) absent (Figs. 4, 8). With pair of cavities (*fs*) on notogaster posterolateral to lenticulus, cavities about 8 μm in diameter; tubercle extending over depression laterally (Figs. 1, 8). Carina (*eg*) weakly developed, without granulate integument (Fig. 8). Twelve pairs of notogastral setae: *c* and row *p* 3–4 μm , barbed, tapered, *h*₁ barbed, tapered, about 10 μm long; other notogastral setae subequal in size, medium in length, minutely barbed, tapered, about 24–29 μm .

Ventral region. Epimere I with tectum extending from anterolateral margin posteriorly almost to seta *3b*. Epimeral setae smooth, *1a* reduced to alveolus; *1b* thin, filiform, about 22 μm long; *2a* thin, about 10 μm long, or reduced to alveolus; *3a* filiform, about 22 μm long; *3b* about 14 μm long; *4a* and *4b* filiform, about 38 μm long; *4c* about 24 μm long. Carina *cm* present. Tubercle present posterolateral to setae *4a* and *4b* (Fig. 2). Carina *cob* present, curving anteriorly and forming depression *cpd* at level of anterior margin of genital plates (Fig. 2). Sternal depression (*st*) present, subtriangular, about 10 μm at widest part (Fig. 2). Depression medially at level of apodeme II minute. Genital, aggenital, anal, and adanal setae acuminate, about 10 μm . Lyrifissure *iad* 14 μm long, oriented parallel to lateral edge of anal plate, slightly anterior to seta *ad*₂. Genital plates (♀ and ♂) about 51 μm long by 66 μm wide; anal plates (♀ and ♂) about 45 μm long by 42 μm wide. Ratio of length of genital to anal plates about 1.13:1; ratio of width of genital to anal plates about 1.6:1.

Gnathosoma. Setae *a*, *m*, and *h* smooth, acuminate, about 16 μm long. Fixed digit of chelicera with minute tooth medially; movable digit toothless (Fig. 3).

Ovipositor. Seta *k* thick, spinous, 10–14 μm long.

Legs. Setation as for genus.

IMMATURES. Measurements. Mean length: larva ($n = 1$), 172 μm ; tritonymph ($n = 1$), 285 μm .

TRITONYMPH (Fig. 11). **Prodorsum.** Rostrum with single row of foveae along margin; thin ridges extending posteriorly from foveae. Integument of prodorsum microtuberculate, except for faintly micropunctate central region medial to seta *le*, anterior and posterior to seta *ro*, and anterior to seta *in*. Prodorsum with seven porose areas: single porose area posteromedially, pair posterior to bothridia, pair posterolateral to bothridia, and pair anterolateral to bothridia (Fig. 11). Posteromedial porose area fused or not with pair posterior to bothridia. Porose areas posterior to bothridia fused or not to pair posterolateral to bothridia. Setae *ro* and *le* barbed, tapered, about 6 μm long. Setae *in* and *ex* about 3 μm long, *in* on tubercle. Mutual distance of setal pairs *ro*–*ro*, *le*–*le*, and *in*–*in*: 17, 37, and 39 μm , respectively. Sensillus narrowly fusiform, about 66 μm long.

Gastronotic region. Dorsum medial to δ distinctly punctate (Fig. 11). Integument lateral to δ , primarily microtuberculate. Pattern of paired, shallow, surface grooves absent. All gastronotic setae, barbed, blunt, 3–6 μm .

Ventral region. Integument of mentum micropunctate. Integument on epimeral plate I micropunctate medially, microtuberculate laterally around seta *1c*. Epimeral plates II–IV with only small area of micropunctate integument medially. Oval porose area present surrounding opening of opisthosomal gland. Adanal porose areas present, extending to posterior of anal/adanal region; extending at right angles anterolaterally, posterolateral of genital region. Epimeral, genital, aggenital, anal, and adanal setae as for tritonymph of *T. muscorum* (Table 2). Epimeral setae filiform: *1a*, *1c*, *2a*, *3a*, *4a*, *4b*, *4c* about 4–6 μm , *1b* about 26 μm , *3b* about 10 μm . Genital, aggenital, anal, and adanal setae about 6 μm long, acuminate.

Legs. Development of setae and solenidia as for tritonymph of *T. muscorum* (Table 3). Porose areas not developed on femora III and IV.

LARVA (Fig. 10). Integument of prodorsum distinctly micropunctate medially; integument of rest of body microtuberculate except for centrodorsal gastronotic region, anal region, medial region of epimera, and legs. Integument of gastronotic region centrodorsally with pattern of shallow grooves and distinct porose plates (Fig. 10). Five porose regions on prodorsum: paired anterolateral, paired post-bothridial, and single posteromedial porose region. Sensillus narrowly fusiform, about 28 μm long. Gastronotal setae heavily barbed, barely tapered; setae of rows *c* and *p* thin, about 5 μm long; *d*₁ (*da*), *d*₂ (*dm*), *e*₁ (*dp*) thick, about 8, 14, 11 μm long, respectively; *cp* (*la*), *e*₂ (*lm*), *f*₂ (*lp*) thick, about 5, 6, 5 μm , respectively. Adanal porose area and porose area surrounding opening of opisthosomal gland present. Trochanter III and femora I–III without porose areas.

Material Examined. *Holotype*: adult female, COSTA RICA, Heredia, Estación Biológica La Selva, 50–150 m, 10°26'N, 84°01'W, Camino Experimental Sur, Experimental Swamp, 11 November 1992 (EEL and VBP) from moss on trunks partially in water, Berlese extraction; deposited in INBio (Instituto Nacional de Biodiversidad), Santo Domingo, Costa Rica. *Paratypes*: 10 with same data as holotype; 15 with same data as holotype, except 17 May 1995 (VBP) from detritus about 1 m from edge of water, Berlese extraction. Paratypes deposited in the CNC (Type No. 22214), INBio, FMNH, NHM, HNHM, and RAN.

Remarks. 1. Morphologically adults of *T. alas* are almost identical to those of *T. mississippii* sp.nov. (described below); they differ by few character states (see key to species and Table 4).

TABLE 2. Number of ventral setae during ontogeny of *Tegeocranellus muscorum* sp.nov.

| | Larva | Protonymph | Deutonymph | Tritonymph | Adult |
|---------------|-------|------------|------------|------------|---------|
| Epimeral I–IV | 3-1-2 | 3-1-2-1 | 3-1-2-1 | 3-1-2-3 | 2-1-2-3 |
| Genital | 0 | 1 | 3 | 5 | 6 |
| Aggenital | 0 | 0 | 1 | 1 | 1 |
| Anal | 0 | 0 | 0 | 2 | 2 |
| Adanal | 0 | 0 | 3 | 3 | 3 |

Further collecting from semiaquatic habitats between Texas and Costa Rica may yield more specimens, and prove these species conspecific.

2. The experimental swamp at La Selva was the focus of intensive collecting for mites during February 1995, yet no specimens of *T. alas* were recovered; the swamp lacked standing water during this period (D. Brenes and R. Vargas, pers. comm. 1995).

Etiymology. This species is named for the ALAS Project (Arthropods of La Selva) and the collaborating parataxonomists. This project provided the opportunity to collect oribatid mites in the lowland tropical rainforest ecosystem of Costa Rica.

TABLE 3. Development of leg setae and solenidia in *Tegeocranellus muscorum* sp.nov. (Setae are noted opposite the instar in which they first appear; parentheses indicate setal pairs)

| | Trochanter | Femur | Genu | Tibia | Tarsus |
|------------|------------|---------------|-------------|---------------|---|
| Leg I | | | | | |
| Larva | — | <i>d bv''</i> | $\sigma l'$ | $\phi_1 (l)$ | <i>e \omega_1(ft)(tc)(p)(u)(a)s(pv)(pl)</i> |
| Protonymph | — | — | <i>l''</i> | <i>v'</i> | ω_2 |
| Deutonymph | — | <i>(l)</i> | — | ϕ_2 | — |
| Tritonymph | <i>v'</i> | — | — | <i>v''</i> | <i>(it)</i> |
| Adult | — | <i>v'</i> | — | — | — |
| Leg II | | | | | |
| Larva | — | <i>d bv''</i> | $\sigma(l)$ | $\phi l' v'$ | $\omega_1(ft)(tc)(p)(u)s(a)(pv)$ |
| Protonymph | — | — | — | — | — |
| Deutonymph | — | <i>(l)</i> | — | <i>l''</i> | — |
| Tritonymph | <i>v'</i> | — | — | <i>v''</i> | <i>(it)</i> |
| Adult | — | <i>v'</i> | — | — | — |
| Leg III | | | | | |
| Larva | — | <i>d ev'</i> | $\delta l'$ | $\phi v'$ | <i>(ft)(tc)(p)(u)s(a)(pv)</i> |
| Protonymph | — | — | — | — | — |
| Deutonymph | <i>v'</i> | — | — | — | — |
| Tritonymph | — | <i>l'</i> | — | <i>l' v''</i> | <i>(it)</i> |
| Adult | <i>l'</i> | — | — | — | — |
| Leg IV | | | | | |
| Protonymph | — | — | — | — | <i>ft''(p)(u)(pv)</i> |
| Deutonymph | — | <i>d ev'</i> | <i>d l'</i> | $\phi v'$ | <i>(tc)s(a)</i> |
| Tritonymph | <i>v'</i> | — | — | <i>l' v''</i> | — |
| Adult | — | — | — | — | — |

Tegeocranellus barbarae sp. nov.

(Figs. 12–30; Map 1B)

Diagnosis. Adult total length 454–531 μm ; without ridge extending laterally from seta *ro*; seta *le* positioned about 16 μm dorsoposteriorly of lamellar tip; lamellar cusps narrow, well-separated; canal *xx* not evident; sensillus smooth, clavate; notogaster without *fs*, without ridges *ts*; 12 pairs of notogastral setae; sternal depression absent, circumpedal depression weakly developed; fixed and movable digits of chelicera toothed; ovipositor seta *k* about 12 μm long. Tritonymph prodorsum with seven porose regions; opisthosoma with four pairs of porose areas laterally. Larva with pattern of shallow grooves centrodorsally, centrodorsal porose plates absent.

ADULT. Measurements. Mean total length: females ($n = 10$) 516 μm (range 492–531); males ($n = 10$) 493 μm (range 454–518). Mean notogastral width: females 395 μm (range 389–402); males 381 μm (range 365–395).

Integument. Microtuberculate over whole body and legs. In addition, integument of humeral region of notogaster faintly granulate. Cerotegument granulate.

Prodorsum. Narrow carina extending laterally from seta *ro* absent (Fig. 16). Seta *ro* 38–50 μm long, with minute barbs, acuminate. Lamella 140–160 μm long, about 20 μm wide at base of lamellar cusp. Lamellar cusps narrow, well-separated, about 52–60 μm long, tapered, bearing seta *le* about 16 μm dorsoposteriorly from tip. Seta *le* about 28 μm long, with many small barbs, tapered. Distance between lamellae at base of cusps about 66 μm . Canal *xx* not evident. Seta *in* 4–10 μm long, barbed, tapered. Mutual distance of setal pairs *ro-ro*, *le-le*, and *in-in*, approximately 40–44, 6, and 128–140 μm , respectively. Sensillus 48–60 μm long, clavate, smooth, or with few barbs distally (Fig. 17).

Lateral region. Tutorium about 106–114 μm long, narrow, surface with ridges. Tutorial cusp about 12–16 μm , short, bluntly triangular. *Pdls* oblong, about 24 μm anteroposteriorly, about 12 μm dorsoventrally (Fig. 18). *Pdls* distinguished from rest of pedotectum I by presence of ridge, or ridge absent; tectum *be* absent. *Zl2* with tectum *b2* present dorsally and anteriorly, absent ventroposteriorly. *Zl3* with ridge defining outline, without tecta except posterodorsally.

Notogaster. Slightly longer than wide; ratio 1.05:1. Humeral tubercles rounded to subtriangular. Lenticulus weakly developed, absent from some specimens in some populations. Notogaster without lines (*ts*) delimiting weakly raised lenticulus. Without pair of cavities (*fs*) on notogaster posterolateral to lenticulus. Carina *eg* weakly developed, without granulate integument. Twelve pairs of notogastral setae: *c*, *h*₁, and row *p* 3–4 μm , subequal in size and shape to seta *in*; other notogastral setae subequal in size and shape to seta *le*, medium in length, minutely barbed, tapered, about 24–30 μm .

Ventral region. Epimere I with tectum extending from anterolateral margin posteriorly almost to seta *3b* (Fig. 19). Epimeral setae smooth, *1a* about 4 μm long or reduced to alveolus; *1b* thin, filiform, about 24 μm long; *2a* thin, about 10 μm long; *3a* filiform, about 40 μm long; *3b* about 14 μm long; setae *4a* and *4b* filiform, about 46 μm long; *4c* about 24 μm long. Sternal depression usually absent, present as minute cavity on some specimens; depression medially at level of apodeme II absent (Fig. 19). Carina *cm* absent, but depression in surface extends laterally from level of apodeme II to lateral of anal plate. Carina *cob* present merging with carina extending posteriorly from discidium. Genital, aggenital, anal, and adanal setae acuminate, about 20–28 μm . Lyrifissure *iad* 16 μm long, oriented parallel to posterolateral edge of anal plate, medial to seta *ad*₂. Genital plates (♀ and ♂) about 102 μm long by 139 μm wide; anal plates (♀ and ♂) about 113 μm long by 121 μm wide. Ratio of length of genital to anal plates, 0.90:1; ratio of width genital to anal plates, 1.15:1.

Gnathosoma. Setae *a*, *m*, and *h* smooth, acuminate; *a* and *m* about 34 μm long, *h* about 24 μm long. Chelicera with well-developed teeth (Fig. 14).

Ovipositor. Seta *k* narrow, tapered, about 12 μm long.

Legs. Setation as for genus.

IMMATURES. Measurements. Mean length: larva ($n = 1$), 246 μm ; deutonymph ($n = 3$), 374 μm (range 363–389); tritonymph ($n = 11$), 485 μm (range 460–512).

Integument. Cerotegument not evident.

TRITONYMPH. Prodorsum. Rostrum with single row of foveae edging margin; thin ridges extending posteriorly from foveae (Fig. 28). Integument of prodorsum microtuberculate, except faintly micropunctate in central region medial to seta *le*, anterior and posterior to seta *ro*, and anterior to seta *in* (Fig. 24). Prodorsum with seven porose areas: single porose area posteromedially, pair posterior to bothridia, pair posterolateral to bothridia, and pair anterolateral to bothridia. Posteromedial porose area fused or not with pair posterior to bothridia. Porose areas posterior to bothridia fused or not to pair posterolateral to bothridia (Fig. 21). Seta *ro* smooth, acuminate, about 30 μm long. Seta *le* tapered, 8 μm long. Setae *in* and *ex* about 3 μm long, *in* on tubercle (Fig. 27). Mutual distance of setal pairs *ro-ro*, *le-le*, and *in-in*: 20, 58, and 64 μm , respectively. Sensillus fusiform, smooth, about 60 μm long.

Gastronotic region. Dorsum medial to circumgastric scissure faintly micropunctate; integument lateral to δ primarily microtuberculate anteriorly, faintly micropunctate posteriorly. Distinct puncta centrodorsally, giving reticulate appearance to integument (Fig. 25). Pattern of paired, shallow, surface grooves on anterior of gastronotic region, merging with δ anterolaterally (Fig. 21). All gastronotic setae, barbed, blunt, 3–6 μm .

Ventral region. Integument of mentum micropunctate; porose area on mentum posteriorly. Integument of epimeral plate I micropunctate medially, microtuberculate laterally around seta *1c*. Epimeral plates II–IV with only small area of micropunctate integument medially. Integument of genital region microtuberculate, that of anal/adanal region micropunctate. Four pairs of porose areas laterally: oval porose area surrounding opening of opisthosomal gland, narrow, long porose area extending from opisthosomal gland anteriorly to level of seta *d₁* (*da*), small, circular porose area posterior to opisthosomal porose area, and small, circular porose area anterolateral of seta *c₃*. Adanal porose areas present, extending to posterior of anal/adanal region; projecting at right angles anterolaterally, posterolateral of genital region. Development of epimeral, genital, anal, and adanal setae as for *T. muscorum* (Table 2), except seta *4b* developed in deutonymph. Epimeral setae filiform: *1a*, *1c*, *2a*, *3a*, *4a*, *4b*, *4c* about 10–14 μm , *1b* about 40 μm , *3b* about 46 μm . Genital, aggenital, anal, and adanal setae 10–14 μm long, acuminate to filiform.

Legs. Development of setae and solenidia as for *T. muscorum* (Table 3), except seta *l'* of genu I, and *v'* of tibia I appear in larva. Porose areas not developed on femora III and IV.

LARVA. Integument microtuberculate except for anal region, medial region of epimera, and legs. Microtuberculate integument both medial of and lateral of δ ; integument centrodorsally with pattern of shallow grooves and distinct puncta in pattern as shown in Figure 29. Anterolateral porose areas on prodorsum not developed. Setae *in* not borne on tubercles, subequal in size to *ex*. Gastronotal setae as for tritonymph, except seta *dm* barbed, tapered, about 32 μm long; *dp* plumose to tapered, about 23 μm long; *h₂* barbed, plumose to tapered, about 14 μm long; *h₁* smooth, acuminate, about 32 μm long. Adanal porose area, porose area surrounding opening of opisthosomal gland (Fig. 30), and porose area anterolateral to seta *c₃* present. Porose areas of trochanter III, and femora I–III not developed in larva.

DEUTONYMPH. Development of microtubercles and micropunctuation on integument as for tritonymph. Development of foveae on rostrum and puncta on gastronotic region as for tritonymph. Prodorsal and opisthosomal setae and porose areas as for tritonymph, except proportionally smaller. Porose areas on femora III and IV not developed.

Material Examined. *Holotype*: adult male, USA: ALABAMA, Conecuh Co., Conecuh National Forest, Open Pond Recreational Area, 31°05.41'N, 86°32.7'W, 10 March 1994

(VBP) from decaying sedges and grasses at edge of small pond; deposited in the CNC (Type No. 22215). *Paratypes*: 20 with same data as holotype; 15 with same data as holotype, except from detritus at edge of pond; MISSISSIPPI, Harrison Co., DeSoto National Forest, Tuxachanie Trail, 26 February 1993 (VBP) 100 from *Sphagnum* sp. at edge of small pond; GEORGIA, Okefenokee Swamp, Chesser prairie, (no date) 1 from algae (RAN); FLORIDA, Highlands Co., Archibold Biological Station, 21 January 1975 (W. Suter) 1 from sphagnum from pond, FMHD 75-35 (RAN). Paratypes deposited in the FMNH, NHM, HNHM, collection of RAN, and the CNC.

Remarks. Gut contents of immatures and adults included fungal hyphae and detritus.

Etymology. This species is named in honour of my colleague and friend Barbara Eamer.

Tegeocranellus kethleyi sp.nov.

(Figs. 31–39; Map 1C)

Diagnosis. Adult total length 363–376 μm ; with ridge extending laterally from seta *ro*; seta *le* positioned about 2–6 μm dorsoposteriorly of lamellar tip; lamellar cusps narrow, well-separated; sensillus barbed, fusiform; notogaster with *fs*, with ridges *ts*; 10 pairs of notogastral setae; sternal depression present; circumpedal depression well-developed; fixed and movable digits of chelicera toothed; ovipositor seta *k* 10–15 μm long.

ADULT. Measurements. Mean total length: females ($n = 4$) 366 μm (range 363–376). Mean notogastral width: females 242 μm (range 240–246).

Integument. Microtuberculate over whole body and legs, except integument between setae *ro* and ventral to lateral rostral carina with larger tubercles. Humeral region of notogaster with granulate integument.

Prodorsum. Narrow carina extending laterally from seta *ro* present (indicated by arrow in Fig. 37). Seta *ro* minutely barbed, isodiametric along most of length, tapered, about 16–22 μm long. Lamella about 102–124 μm long, about 36 μm wide at base of lamellar cusp. Lamellar cusps narrow, well-separated, about 32–46 μm long, tapered to point, bearing seta *le* positioned about 2–6 μm dorsoposteriorly from tip. Seta *le* 20–22 μm long, barbed, mostly isodiametric, distally tapered. Canal *xx* present, weakly developed, not indicated on Figure 31. Distance between lamellae at base of cusps about 42 μm . Seta *in* about 8 μm long, barbed (Figs. 31, 36). Mutual distance of setal pairs *ro*–*ro*, *le*–*le*, and *in*–*in*, approximately 26, 34, and 98 μm , respectively. Sensillus about 66–70 μm long, fusiform, head with large barbs, barbs progressively smaller along stalk.

Lateral region. Tutorium about 90 μm long, narrow, surface with ridges. Tutorial cusp about 18 μm long, narrowly triangular (Fig. 35). *PdIs* variable in shape (Fig. 33), about 22 μm anterioposteriorly, about 6 μm dorsoventrally. *PdIs* distinguished from rest of pedotectum I by presence of ridge, or ridge absent (Fig. 33). *Zl2* with tectum *b2* present dorsally and anteriorly, absent ventroposteriorly. *Zl3* with ridge defining outline, without tectum.

Notogaster. Slightly longer than wide; ratio 1.1:1. Humeral tubercles on anterior margin of notogaster rounded. Notogaster with ridges (*ts*) delimiting raised lenticulus (Fig. 36). With pair of cavities (*fs*) on notogaster posterolateral to lenticulus; with tubercles overhanging cavities *fs* laterally. Carina *eg* rounded anteriorly, without granulate integument. Ten pairs of notogastral setae: *c*, *h₁*, and row *p* barbed, plumose, about 4, 8, and 8 μm long, respectively; other notogastral setae subequal in size, 30–38 μm long, minutely barbed, isodiametric along most of length, distally tapered.

Ventral region. Epimere I with tectum extending from anterolateral margin posteriorly almost to acetabulum III. Sternal depression (*st*) medially, at level of apodeme III present, subtriangular, about 8 μm wide posteriorly (Fig. 39). Small depression medially, at level of apodeme II present or absent. Epimeral setae smooth, *1a*, *2a* about 2 μm long or reduced to alveolus; *1b* thin, filiform, about 14 μm long; *3a* filiform, about 22–24 μm long; *3b* about

6 μm long; *4a* and *4b* about 22 μm long, filiform, *4c* acuminate, about 14 μm long. Carina *cm* extending laterally from posterior of level of acetabulum II to posterior of acetabulum IV. Depressions present laterally on epimere III and IV (Fig. 38). Carina *cob* present, curving anteriorly to form depression *cpd* (just showing at bottom left of Fig. 38). Genital, aggenital, anal, and adanal setae thin, acuminate, about 7–10 μm long. Lyrifissure *iad* about 18 μm long, positioned parallel to lateral edge of anal plate, just posterior to seta *ad*₂. Genital plates (♀) about 58 μm long by 76 μm wide; anal plates (♀) about 74 μm long by 72 μm wide. Ratio length genital to anal plates, 0.78:1; ratio width genital to anal plates, 1.05:1.

Gnathosoma. Setae *a*, *m*, and *h* smooth, acuminate, about 22–26, 26–30, and 18–20 μm long, respectively. Fixed and movable digits of chelicera toothed.

Ovipositor. Seta *k* narrow, tapered, about 10–15 μm long.

Legs. Setation as for genus.

IMMATURES. Unknown.

Material Examined. *Holotype*: adult female, USA: MISSISSIPPI, Jackson Co., Pascagoula Wildlife Management Area, Cumbest Bluff, W Pascagoula River, 30°37'N, 88°39'W, 15 March 1994 (VBP) from clump of moss and grass in seepage area; deposited in the CNC (Type No. 22216). *Paratypes*: 2 with same data as holotype; ALABAMA, Baldwin Co., Gulf Shores State Park, 30°16'N, 87°40.5'W, 7 March 1994 (VBP) 4 from waterlilies and miscellaneous vegetation in small stream. Paratypes deposited in the FMNH and the CNC.

Gut Contents. A specimen from Alabama contained fungal hyphae, algae, and detritus in gut.

Etymology. This species is named in honour of John Kethley, of the Field Museum, Chicago, a colleague and friend who has contributed extensively to the study of mites.

Tegeocranellus mediolamellatus sp.nov.

(Figs. 40–48; Map 1A)

Diagnosis. Adult total length 428–441 μm ; with ridge extending laterally from seta *ro*; seta *le* positioned about 24 μm dorsoposteriorly of lamellar tip; lamellar cusps wide, medial margins touching; sensillus barbed, narrowly fusiform; notogaster without *fs*, without ridges *ts*; 10 pairs of notogastral setae; sternal depression minute; circumpedal depression present; cheliceral digits toothed. Tritonymph prodorsum with five porose regions; opisthosoma with one pair of porose areas laterally.

ADULT. Measurements. Mean total length: female ($n = 1$) 434 μm ; males ($n = 6$) 434 μm (range 428–441). Mean notogastral width: female 292 μm ; males 285 μm (range 279–292).

Integument. Microtuberculate over whole body and legs; except micropunctate on anal plates. In addition, granulate integument on humeral region of notogaster. Cerotegument granulate.

Prodorsum. Narrow carina extending laterally from seta *ro* present (Fig. 44). Seta *ro* about 23 μm long, with minute barbs, tapered. Lamella with longitudinal ridges, 140–162 μm long, about 62 μm wide at base of lamellar cusp. Lamellar cusps about 64 μm long, very broad, medial margins touching along length, bearing seta *le* close to medial margin, about 24 μm dorsoposteriorly from tip (Fig. 44). Seta *le* about 13 μm long, with many small barbs, tapered. Distance between lamellae at base of cusps 0–5 μm . Canal *xx* present, difficult to see because of ridges on lamella. Seta *in* about 13 μm long, barbed, tapered to plumose. Mutual distance of setal pairs *ro-ro*, *le-le*, and *in-in* about 16, 6–8, and 90–102 μm , respectively. Sensillus 72–76 μm long, narrowly fusiform, barbed (Fig. 46).

Lateral region. Tutorium about 105 μm long, narrow, surface with ridges. Tutorial cusp about 31–35 μm long, narrowly triangular. *Pdls* subrectangular, anterior margin toothed or rounded, about 37 μm long, about 10 μm wide dorsoventrally. *Pdls* distinguished from rest of pedotectum I by tectum *be*. *Zl2* with tectum *b2* present. *Zl3* with tectum *b3*.

Notogaster. Slightly longer than wide; ratio 1.07:1. Humeral tubercles broadly rounded, with tuberculate to ridged integument. Lenticulus very faintly developed, absent in some specimens. Notogastral ridges (*ts*) absent. Notogastral cavities (*fs*) absent (Figs. 40, 43). Carina *eg* well-developed, with anterior tubercle, without granulate integument. Ten pairs of notogastral setae: *c*, *h*₃, and row *p* plumose, tapered, about 11, 6–11, and 6–11 µm, respectively; other notogastral setae subequal in size, medium in length, minutely barbed, tapered, about 29 µm.

Ventral region. Epimere I with tectum extending from anterolateral margin posteriorly almost to acetabulum III. Sternal depression (*st*) at level of apodeme III reduced to small indentation (Fig. 42). Small medial depression medially at level of apodeme II present, ridge extending from this depression almost to anterior margin of epimere I. Epimeral setae smooth, *2a* normal, or reduced to alveolus; *1a* 1–4 µm long, *1b* thin, filiform, about 19 µm long; *3a* filiform, about 31 µm long, *3b* about 10 µm long; *4a* and *4b* about 28 µm long, and seta *4c* acuminate, about 12–18 µm long. Carina *cm* extending laterally from posterior of level of acetabulum II to posterior of acetabulum IV (Fig. 42). Carina *cob* present, curving anteriorly to form depression *cpd*. Genital, aggenital, anal, and adanal setae thin, acuminate, genital setae about 16 µm, other setae 6–10 µm long. Lyrifissure *iad* about 19–21 µm long, oriented parallel to lateral edge of anal plate, anterior to seta *ad*₂. Genital plates shorter than anal plates; genital plates (♂) about 67 µm long by 86 µm wide; anal plates (♂) about 92 µm long by 78 µm wide. Ratio length genital to anal plates, 0.73:1; ratio width genital to anal plates, 1.10:1.

Gnathosoma. Setae *a*, *m*, and *h* smooth, acuminate; about 19, 24, and 21 µm long, respectively. Chelicera with well-developed teeth.

Ovipositor. No data available, because ovipositor of single female lost during specimen preparation.

Legs. Setation as for genus.

IMMATURES. Measurements. Mean length: protonymph (*n* = 1), 259 µm; deutonymph (*n* = 8), 322 µm (range 311–337); tritonymph (*n* = 4), 398 µm (range 382–408).

Integument. Cerotegument not evident. Integument of legs micropunctate.

TRITONYMPH. Prodorsum. Rostrum with single row of foveae along margin; thin ridges extending posteriorly from foveae. Integument of prodorsum microtuberculate. Prodorsum with five porose areas: single porose area posteromedially, pair posterior to bothridia, and pair posterolateral to bothridia (Fig. 47). Posterolateral porose area fused or not with pair posterior to bothridia. Seta *ro* smooth, acuminate, about 10 µm long. Seta *le* tapered, barbed, about 8 µm long. Setae *in* and *ex* about 3 µm long, *in* on tubercle. Mutual distance of setal pairs *ro*–*ro*, *le*–*le*, and *in*–*in*: 11, 31, and 50 µm, respectively. Sensillus narrowly fusiform, smooth to finely barbed, about 81 µm long.

Gastronotic region. Integument centrodorsally with distinct puncta (Fig. 47); microtuberculate lateral and ventral of circumgastric scissure. Pattern of paired, shallow, surface grooves on anterior of gastronotic region, merging with circumgastric scissure anterolaterally (Fig. 47). All gastronotic setae, barbed, blunt to tapered, 6–10 µm long.

Ventral region. Integument of mentum micropunctate. Integument on epimeral plate I smooth medially, microtuberculate laterally around seta *1c*. Integument of genital region microtuberculate, that of anal region micropunctate. One pair of porose areas laterally: oval porose area surrounding opening of opisthosomal gland. Adanal porose areas present extending laterally posteriorly to aggenital setae (Fig. 48). Development of epimeral, genital, anal, and adanal setae as in *T. muscorum* (Table 2). Epimeral setae acuminate: *1a*, *2a*, *3a*, *4a*, *4b*, *4c* about 8 µm; *1b* about 22 µm, *3b* about 16 µm. Genital, aggenital, anal, and adanal setae about 8 µm long, acuminate.

Legs. Development of setae and solenidia as for *T. muscorum* (Table 3).

PROTONYMPH. Development of microtubercles and micropunctuation on integument as for tritonymph. Development of foveae on rostrum and puncta on gastronotic region as for tritonymph. Prodorsal and hysterosomal setae and porose areas as for tritonymph, except proportionally smaller. Gastronotal setae 4–6 μm long, other than *dm* (d_2), *dp* (e_1), 8–10 μm long, thicker and more heavily barbed.

DEUTONYMPH. Development of microtubercles and micropunctuation on integument as for tritonymph. Development of foveae on rostrum and puncta on gastronotic region as for tritonymph. Prodorsal and hysterosomal setae and porose areas as for tritonymph, except proportionally smaller.

Material Examined. *Holotype*: adult male, GUATEMALA, Dep. Zacapa, Sierra de Las Minas, 10 km N San Lorenzo, 7–9 November 1986 (EEL) from wet moss by/in creek, cloud forest; deposited in the CNC (Type No. 22217). *Paratypes*: 5 with same data as holotype. Paratypes deposited in the FMNH, RAN, and CNC.

Etymology. The specific epithet refers to the large lamellae of this species which abut medially.

Tegeocranellus mississippii sp.nov.

(Figs. 49–56; Map 1C)

Diagnosis. Adult total length 275–311 μm ; with ridge extending laterally from seta *ro*; seta *le* positioned about 16–24 μm dorsoposteriorly of lamellar tip; lamellar cusps narrow, medial margins well-separated; sensillus barbed, clavate; notogaster with *fs*, without ridges *ts*; 12 pairs of notogastral setae; notogastral setae slightly expanded along length; sternal depression and circumpedal depression present; fixed digit of chelicera with medial tooth, movable digit toothless; ovipositor seta *k* about 10 μm long.

ADULT. Measurements. Mean total length: females ($n = 5$) 298 μm (range 292–311); males ($n = 7$) 291 μm (range 275–308). Mean notogastral width: females 200 μm (range 194–207); males 196 μm (range 185–227).

Integument. Microtuberculate over whole body and leg segments. In addition, humeral region of notogaster with granulate integument. Cerotegument granulate.

Prodorsum. Narrow carina extending laterally from seta *ro* present. Seta *ro* smooth, tapered, about 10–14 μm long. Lamella about 102–110 μm long, about 22–28 μm wide at base of lamellar cusp. Lamellar cusps about 45 μm long, tapered, narrow, well-separated, bearing seta *le* positioned about 16–24 μm dorsoposteriorly from tip. Seta *le* about 6–8 μm long, with many small barbs, tapered to plumose. Canal *xx* present. Distance between lamellae at base of cusps about 36 μm . Seta *in* about 8 μm long, barbed, tapered to plumose. Mutual distance of setal pairs *le*–*le* and *in*–*in*, approximately 44 and 72–80 μm , respectively. Sensillus about 54–57 μm long, clavate, head, short, about 18 μm , heavily barbed on lateral and dorsal surfaces, with minute barbs on ventral surface; stalk with minute barbs dorsally.

Lateral region. Tutorium about 54 μm long, surface with ridges. Tutorial cusp about 14–18 μm long, narrowly triangular. *PdIs* about 20 μm anteroposteriorly, about 5 μm dorsoventrally, tapered.

Notogaster. Slightly longer than wide; ratio 1.1:1. Humeral tubercles on anterior margin of notogaster rounded to subtriangular. Integument delimiting lenticulus thickened, but ridges (*ts*) absent. With pair of depressions (*fs*) on notogaster posterolateral to lenticulus; with tubercles overhanging depressions laterally (Fig. 49). Carina *eg* weakly developed, without granulate integument. Twelve pairs of notogastral setae: *c*, *h*, and row *p* 3–5 μm , subequal in size to seta *in*, tapered or blunt distally; other notogastral setae subequal in size, 28–34 μm long, minutely barbed, slightly expanded along length, tapered.

Ventral region. Epimere I with tectum extending from anterolateral margin posteriorly almost to acetabulum III. Sternal depression (*st*) at level of apodeme III present,

subtriangular, about 8 μm at widest part. Small medial depression at level of apodeme II present or absent. Epimeral setae smooth, *1a*, *2a* reduced to alveolus; *1b* thin, filiform, about 18–22 μm long; *3a* filiform, about 20 μm long; *3b* about 14 μm long; setae *4a*, *4b*, and *4c* acuminate, about 20 μm long. Carina *cm* extending laterally from posterior of level of acetabulum II to posterior of acetabulum IV. Tubercle present posterolateral to setae *4a* and *4b*. Carina *cob* present, curving anteriorly to form depression *cpd*. Genital, aggenital, anal, and adanal setae thin, acuminate, about 7 μm long. Lyrifissure *iad* 14–18 μm long, oriented parallel, but slightly angled, to lateral edge of anal plate, slightly anterior to seta *ad*₂ (Fig. 52). Genital plates (♀ and ♂) about 48 μm long by 58 μm wide; anal plates (♀ and ♂) about 43 μm long by 38 μm wide. Ratio length genital to anal plates, 1.11:1; ratio width genital to anal plates, 1.53:1.

Gnathosoma. Setae *a*, *m* and *h*, smooth, acuminate, about 16–18 μm long. Fixed digit of chelicera with single small tooth medially; movable digit toothless (Fig. 51).

Ovipositor. Seta *k* about 10 μm long.

Legs. Setation as for genus.

IMMATURES. Unknown.

Material Examined. *Holotype*: adult male, USA: LOUISIANA, Cameron Co., Hackberry Prairie, 23°58'26"N, 93°25'43"W, 21 February 1993 (VBP) from wet soil with thick grass cover; deposited in the CNC (Type No. 22218). *Paratypes*: 20 with same data as holotype; TEXAS, Patricio Co., Sinton, Welder Wildlife Foundation, 15 June 1978 (B. McDaniel) 1 from litter in riparian forest (RAN). Paratypes deposited in the FMNH, NHM, HNHM, RAN, and CNC.

Remarks. See remarks following description of *T. alas* sp.nov.

Etymology. This species is named for the Mississippi River, so important to the ecology of southeastern North America.

Tegeocranellus muscorum sp.nov.

(Figs. 57–69; Map 1B)

Diagnosis. Adult total length 421–448 μm ; with ridge extending laterally from seta *ro*; seta *le* positioned about 0–4 μm dorsoposteriorly of lamellar tip; lamellar cusps narrow, medial margins well-separated; sensillus barbed, clavate; notogaster with *fs*, usually with ridges *ts*; 12 pairs of notogastral setae; sternal depression and circumpedal depression present; fixed and movable digits of chelicera toothed; ovipositor seta *k* 8–12 μm long. Tritonymph prodorsum with three porose regions; opisthosoma with one pair of porose areas laterally. Larval hysterosoma with pattern of shallow grooves and foveae centrodorsally.

ADULT. Measurements. Mean total length: females ($n = 11$) 447 μm (range 421–472); males ($n = 5$) 438 μm (range 432–448). Mean notogastral width: females 290 μm (range 285–298); males 276 μm (range 252–296).

Integument. Microtuberculate over whole body and leg segments. In addition, humeral region of notogaster with granulate integument. Cerotegument granulate.

Prodorsum. Narrow carina extending laterally from seta *ro* present (Fig. 64). Seta *ro* minutely barbed, isodiametric along most of length, tapered, about 26–30 μm long. Lamella about 120–140 μm long, about 36 μm wide at base of lamellar cusp. Lamellar cusps about 58 μm long, tapered to point, narrow, well-separated, bearing seta *le* positioned about 0–4 μm dorsoposteriorly from tip. Seta *le* 16–24 μm long, minutely barbed, tapered. Canal *xx* not evident. Distance between lamellae at base of cusps about 42–46 μm . Seta *in* about 5–8 μm long, barbed, broadest medially. Mutual distance of setal pairs *le*–*le* and *in*–*in* approximately 36–40 and 82–90 μm , respectively. Sensillus about 72–80 μm long,

clavate; head short, about 18 μm , sparsely barbed with large barbs dorsally and laterally, smooth ventrally; stalk with minute barbs dorsally and laterally.

Lateral region. Tutorium about 110 μm long, surface with ridges (Fig. 64); cusp about 26 μm long, narrowly triangular. *Pdls* blunt to tapered distally, about 28 μm anteroposteriorly, about 8 μm dorsoventrally. Tectum of *Zl2* partially covering alveolus of seta *ex*.

Notogaster. Slightly longer than wide; ratio 1.06:1. Humeral tubercles on anterior margin of notogaster rounded (Fig. 62). Notogaster usually with ridges (*ts*) delimiting raised lenticulus (Figs. 62, 63); faint or absent in some specimens. With depressions (*fs*) on notogaster posterolateral to lenticulus (Fig. 63); with tubercles overhanging depressions laterally. Carina *eg* rounded anteriorly, with granulate integument. Twelve pairs of notogastral setae: *c*, *h*₁, and row *p* barbed, plumose, about 4, 8, and 8 μm long, respectively; other notogastral setae subequal in size, 30–40 μm long, smooth, isodiametric along most of length, distally tapered.

Ventral region. Epimere I with tectum extending from anterolateral margin posteriorly almost to acetabulum III. Sternal depression (*st*) at level of apodeme III present, diameter about 10 μm (Fig. 66). Small medial depression at level of apodeme II present, with narrow ridge extending anteriorly. Epimeral setae smooth, *1a*, *2a* about 2 μm long or reduced to alveolus; *1b* thin, filiform, about 20 μm long; *3a* filiform, about 46 μm long; *3b* about 8–12 μm long; setae *4a* and *4b* about 34 μm long, and seta *4c* acuminate, about 14–18 μm long. Carina *cm* short, positioned lateral to setae *4a* and *4b*. Carina *cob* present, curving anteriorly to form *cpd*, extending or not posteriorly as narrow depression (Fig. 66). Genital, aggenital, anal, and adanal setae thin, acuminate, about 7–10 μm long. Lyrifissure *iad* about 16 μm long, oriented parallel to posterolateral edge of anal plate, medial to seta *ad*₂. Genital plates (♀ and ♂) about 100 μm long by 120 μm wide; anal plates (♀ and ♂) about 90 μm long by 80 μm wide. Ratio length genital to anal plates, 1.11:1; ratio width genital to anal plates, 1.5:1.

Gnathosoma. Setae *a*, *m*, and *h* smooth, acuminate, about 22–26, 26–30, and 18–20 μm long, respectively. Fixed and movable digits of chelicera toothed (Fig. 58).

Ovipositor. Seta *k* narrow, tapered, about 8–12 μm long.

Legs. Setation as for genus.

IMMATURES. Measurements. Mean length: larva ($n = 10$), 192 μm (range 168–208); protonymph ($n = 10$), 245 μm (range 232–256); deutonymph ($n = 8$), 295 μm (range 280–304); tritonymph ($n = 10$), 376 μm (range 340–388).

Integument. Cerotegument not evident.

TRITONYMPH. Prodorsum. Rostrum with single row of foveae along margin; thin ridges extending posteriorly from foveae. Integument of prodorsum microtuberculate, except faintly micropunctate in central region medial to seta *le*, anterior and posterior to seta *ro*, and anterior to seta *in*. Prodorsum with three porose areas: single, semicircular porose area posteromedially, and pair posterior to bothridia (Fig. 67). Posteromedial porose area fused or not with pair posterior to bothridia. Seta *ro* smooth, tapered, about 10 μm long. Seta *le* tapered, 6–8 μm long. Seta *in* about 3 μm long, on tubercles. Seta *ex* reduced to alveolus. Mutual distance of setal pairs *ro-ro*, *le-le*, and *in-in*: 16, 38, and 50 μm , respectively. Sensillus fusiform, about 64 μm long.

Gastronotic region. Dorsum medial to δ faintly micropunctate, with faint foveae medially (Fig. 67). Integument lateral to δ primarily microtuberculate. Pattern of paired, shallow, surface grooves on anterior of gastronotic region, merging with δ anterolaterally (Fig. 67). All gastronotic setae, barbed, blunt, 4–6 μm .

Ventral region. Integument of mentum micropunctate. Integument on epimeral plate I micropunctate medially, microtuberculate laterally around seta *1c*. Epimeral plates II and III with small, diamond-shaped area of micropunctate integument medially. Integument of genital region microtuberculate, that of anal/adanal region faintly microtuberculate. Oval

porose area present surrounding opening of opisthosomal gland (Fig. 68). Adanal porose areas extending to posterior of anal/adanal region, projecting laterally posterior to genital region (Fig. 68). Development of epimeral, aggenital, genital, anal, and adanal setae as in Table 2. Epimeral setae filiform: *1a*, *1c*, *2a*, *3a*, *4a*, *4b*, *4c* about 6–8 μm long, *1b* and *3b* about 20 μm . Genital, aggenital, anal, and adanal setae about 6 μm long, acuminate.

Legs. Development of setae and solenidia as in Table 3. Porose areas not developed on femora III and IV.

LARVA. Integument microtuberculate except for centrodorsal gastronomic region, anal region, and leg segments. Microtuberculate integument both medial of and lateral of δ ; integument centrodorsally with pattern of shallow grooves and weak foveae (Fig. 69). Seta *in* not borne on tubercles, subequal in size to *ex*, about 4 μm . Gastronotal setae as in tritonymph, except seta *dm* (*d₂*) barbed, tapered, about 16 μm long; *dp* (*e₁*) barbed, tapered, about 12 μm long; (*h*) setae barbed, tapered, about 6 μm long. Prodorsal porose areas as in tritonymph. Adanal porose area present, porose area surrounding opening of opisthosomal gland not evident. Porose areas of trochanter III, and femora I–III not developed.

PROTONYMPH. Development of microtubercles and micropunctuation on integument as in tritonymph. Development of foveae on rostrum and puncta on gastronomic region as in tritonymph. Prodorsal and hysterosomal setae and porose areas as for tritonymph, except proportionally smaller. Porose areas on trochanters and femora III and IV not developed.

DEUTONYMPH. Development of microtubercles and micropunctuation on integument as in tritonymph. Development of foveae on rostrum and puncta on gastronomic region as in tritonymph. Prodorsal and hysterosomal setae and porose areas as for tritonymph, except proportionally smaller. Porose areas on femora III and IV not developed.

Material Examined. *Holotype*: adult ♀, USA: NORTH CAROLINA, Graham Co., Joyce Kilmer Memorial Forest, 13 mi NW Robbinsville, 8 August 1986 (EEL) from moss, herbs, and substrate on rocks at creek edge; deposited in the CNC (Type No. 22219). *Paratypes*: 18 with same data as holotype; NEW YORK, Madison Co., Nelson, "Cedar Swamp", 23 October 1986 (S. Palmer) 5 from moss under cattails in swamp (RAN); Courtland Co., Tully, Heiberg Forest, Pond 1, 13 November 1985 (R.A. Norton) 5 from wet sphagnum at edge of pond (RAN); MISSISSIPPI, Jackson Co., Pascagoula Wildlife Management Area, Cumbeast Bluff, W Pascagoula River, 30°37' N, 88°39' W, 15 March 1994 (VBP) 5 from clump of moss and grass in seepage area; FLORIDA, Highlands Co., Archibold Biological Station, 21 January 1975 (W. Suter) 2 from sphagnum from pond, FMHD 75-35 (RAN); Dade Co., Everglades National Park, Palma Vista Hammock, 16 January 1975 (W.S. Suter) 100 from dry log and litter at log; CANADA: ONTARIO, Long Point National Wildlife Area, Squires Ridge, 42°34' N, 80°14' W, 29 September 1981 (VBP) 15 from decaying vegetation at edge of slough in oak-maple parkland; Long Point Provincial Park, 7 August 1974 (EEL) 6 from wet pine and marshy litter, edge of marsh. Paratypes deposited in the FMNH, NHM, HNHM, RAN, and CNC.

Etymology. The specific epithet is the Latin for 'moss', and refers to the habitat of this species.

KEY TO ADULTS OF SPECIES OF *TEGEOCRANELLUS* FROM NORTH AND CENTRAL AMERICA

1. Notogaster with 10 pairs of setae, *d₂* (*dm*) and *e₁* (*dp*) absent 2
 - Notogaster with 12 pairs of setae, *d₂* (*dm*) and *e₁* (*dp*) present. 3
 2. Notogastral depressions (*fs*) and ridge (*ts*) present; lamellar cusps narrow, well-separated.
 - Notogastral depressions (*fs*) and ridge (*ts*) absent; lamellar cusps broad, touching medially ...
- *T. kethleyi* **sp.nov.**
 *T. mediolamellatus* **sp.nov.**

3. Notogastral depressions (*fs*) absent, sternal depression, if present, minute; sensillus smooth . . .
 *T. barbarae* **sp.nov.**
 — Notogastral and sternal depressions present, well-developed; sensillus barbed 4
4. Notogastral ridge *ts* present; teeth present on fixed and movable digits of chelicera
 *T. muscorum* **sp.nov.**
 — Notogastral ridge *ts* absent; fixed digit of chelicera with single small tooth medially, movable
 digit of chelicera toothless 5
5. Tutorium about 54 μm long; notogastral setae slightly expanded medially; southeastern North
 America *T. mississippii* **sp.nov.**
 — Tutorium about 78 μm long; notogastral setae isodiametric along length; Costa Rica
 *T. alas* **sp.nov.**

TABLE 4. Diagnostic table for adults of species of *Tegeocranellus* from North and Central America

| Character | <i>alas</i> | <i>barbarae</i> | <i>kethleyi</i> | <i>mediolamellatus</i> | <i>mississippii</i> | <i>muscorum</i> |
|---|----------------|-----------------|-----------------|--------------------------|---------------------|-----------------|
| Total length, μm | 292–330 | 454–531 | 363–376 | 428–441 | 275–311 | 421–448 |
| Lamellae | Separated | Separated | Separated | Medial margins touching | Separated | Separated |
| Sensillus length, μm | Clavate; 58–62 | Clavate; 48–60 | Fusiform; 66–70 | Narrowly fusiform; 72–76 | Clavate; 54–57 | Clavate; 72–80 |
| Notogastral setae | 12 pairs | 12 pairs | 10 pairs | 10 pairs | 12 pairs | 12 pairs |
| Notogastral depression (<i>fs</i>) | + | – | + | – | + | + |
| Notogastral ridge (<i>ts</i>) | – | – | + | – | – | +/- |
| Tutorium length, μm | About 78 | 106–114 | About 90 | About 105 | About 54 | About 110 |
| Sternal depression | + | – | + | Small indentation | + | + |
| Length genital plate: length anal plate | 1.13:1 | 0.9:1 | 0.78:1 | 0.73:1 | 1.11:1 | 1.11:1 |
| Width genital plate: width anal plate | 1.6:1 | 1.15:1 | 1.05:1 | 1.1:1 | 1.53:1 | 1.5:1 |
| Movable digit of chelicera | Toothless | Toothed | Toothed | Toothed | Toothless | Toothed |

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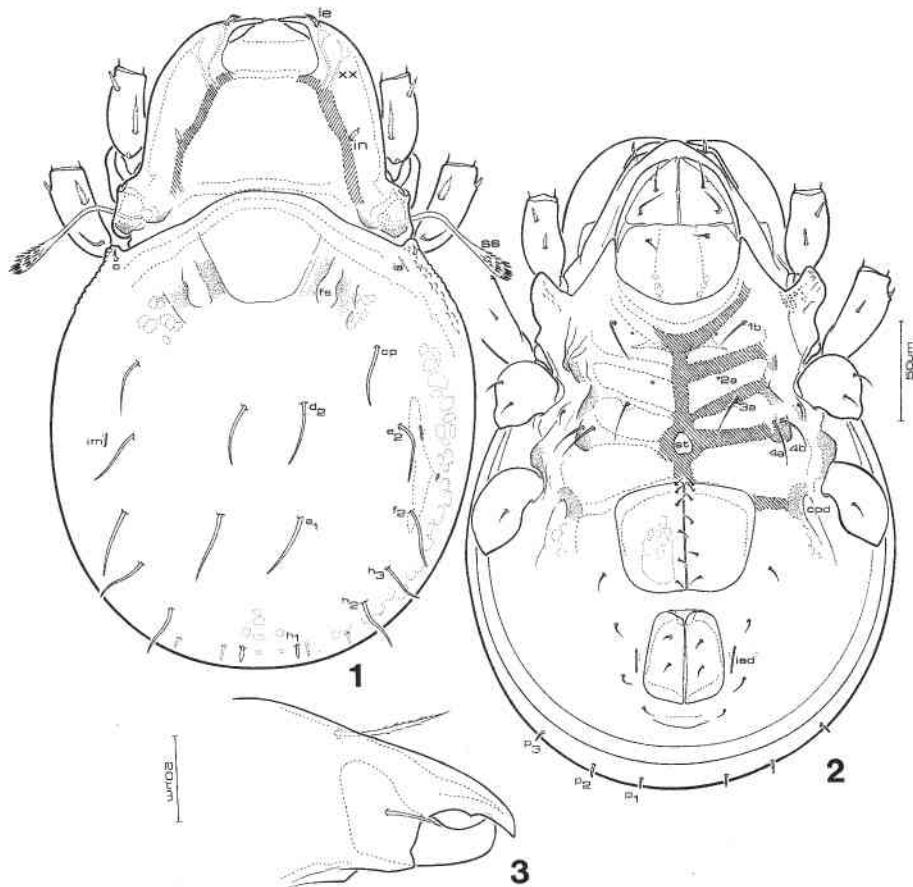
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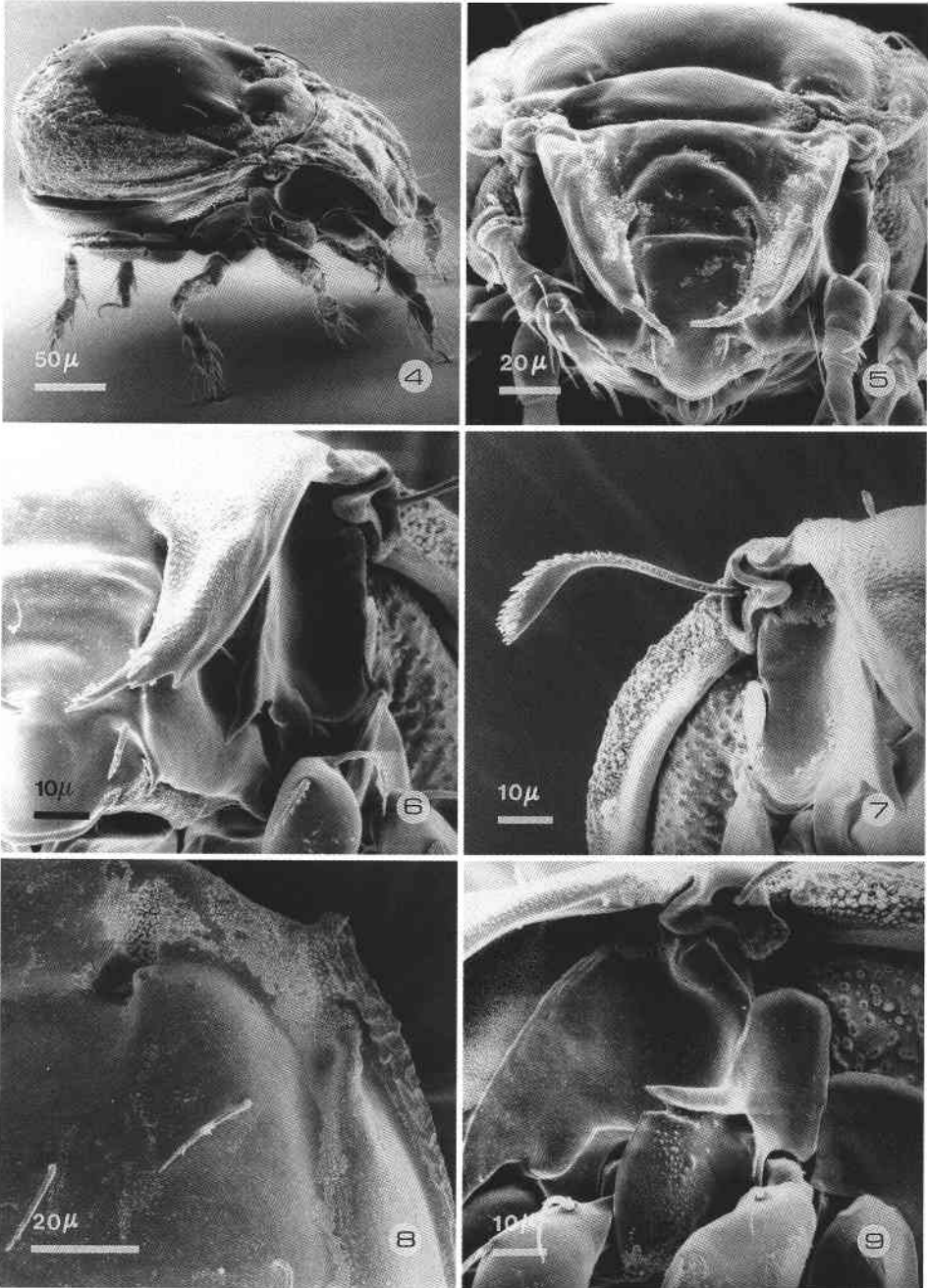
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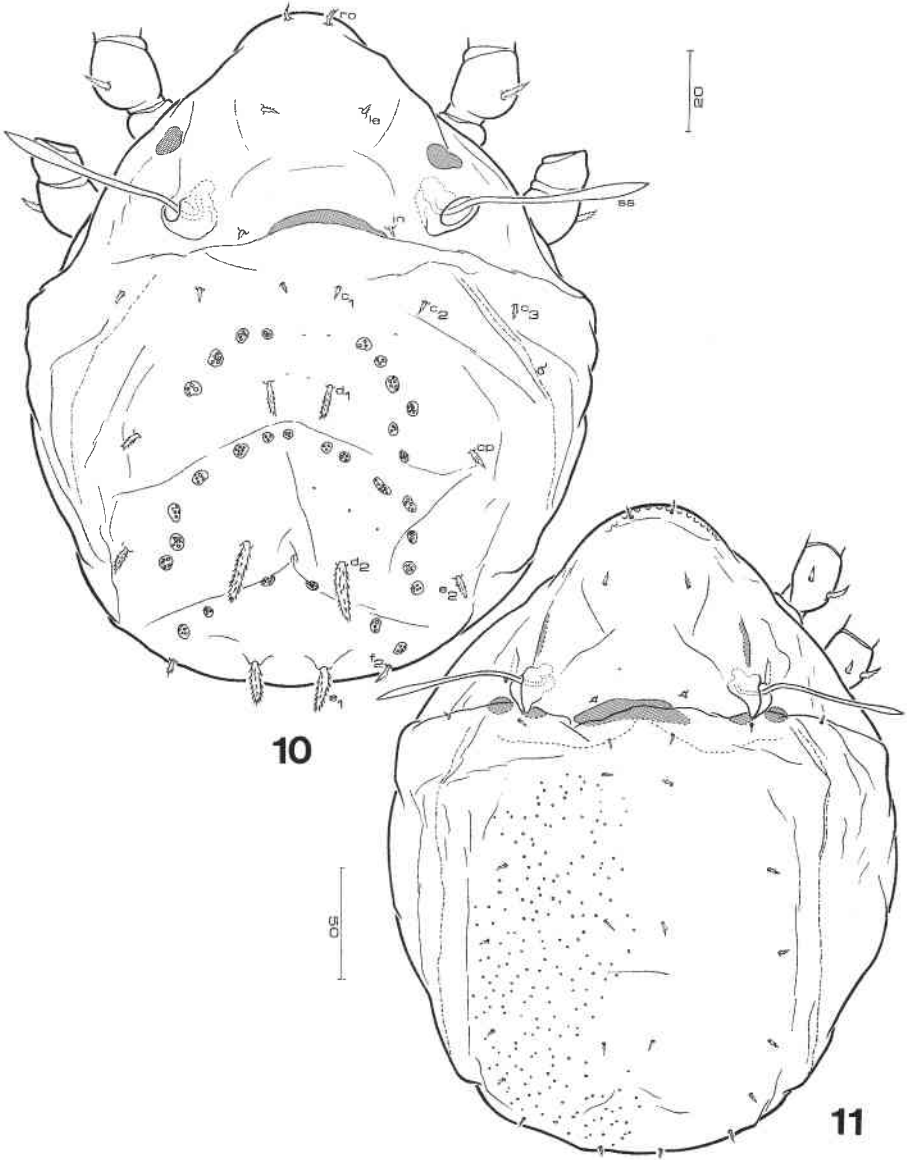
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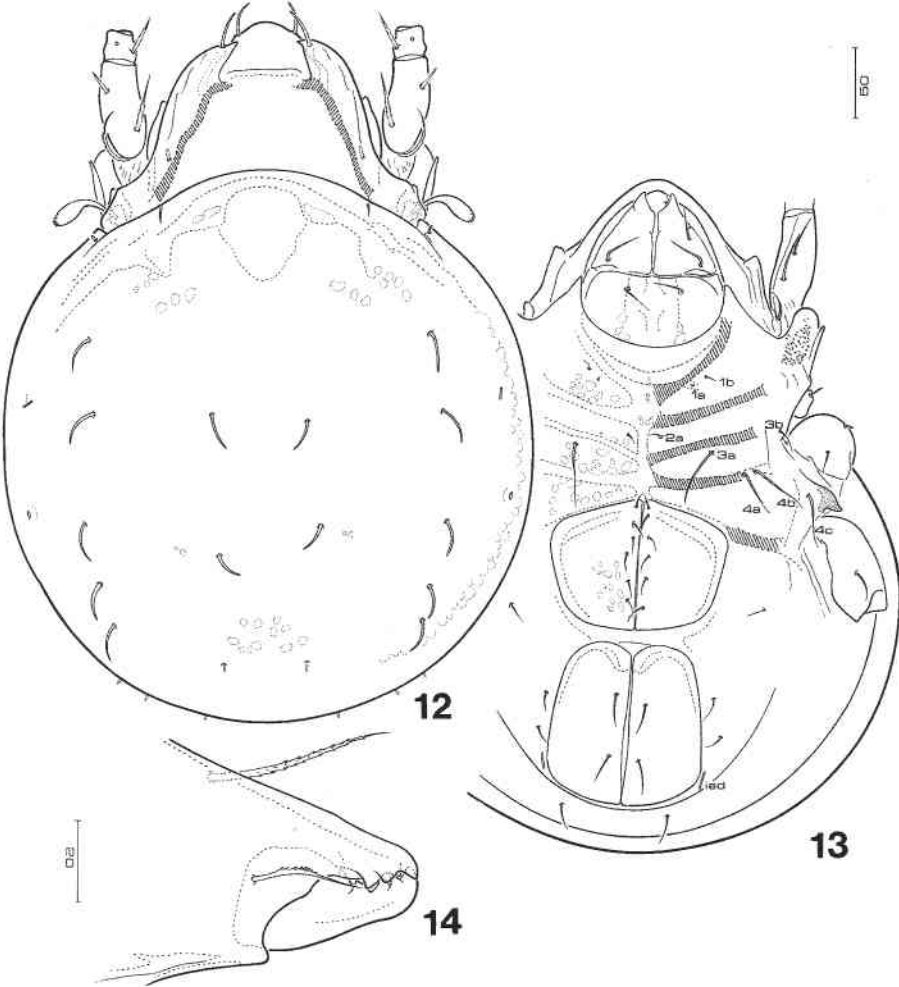
FIGS. 1–3. *Tegeocranellus alas* sp.nov., adult female: 1, dorsal aspect; 2, ventral aspect; 3, chelicera, antiaxial view.



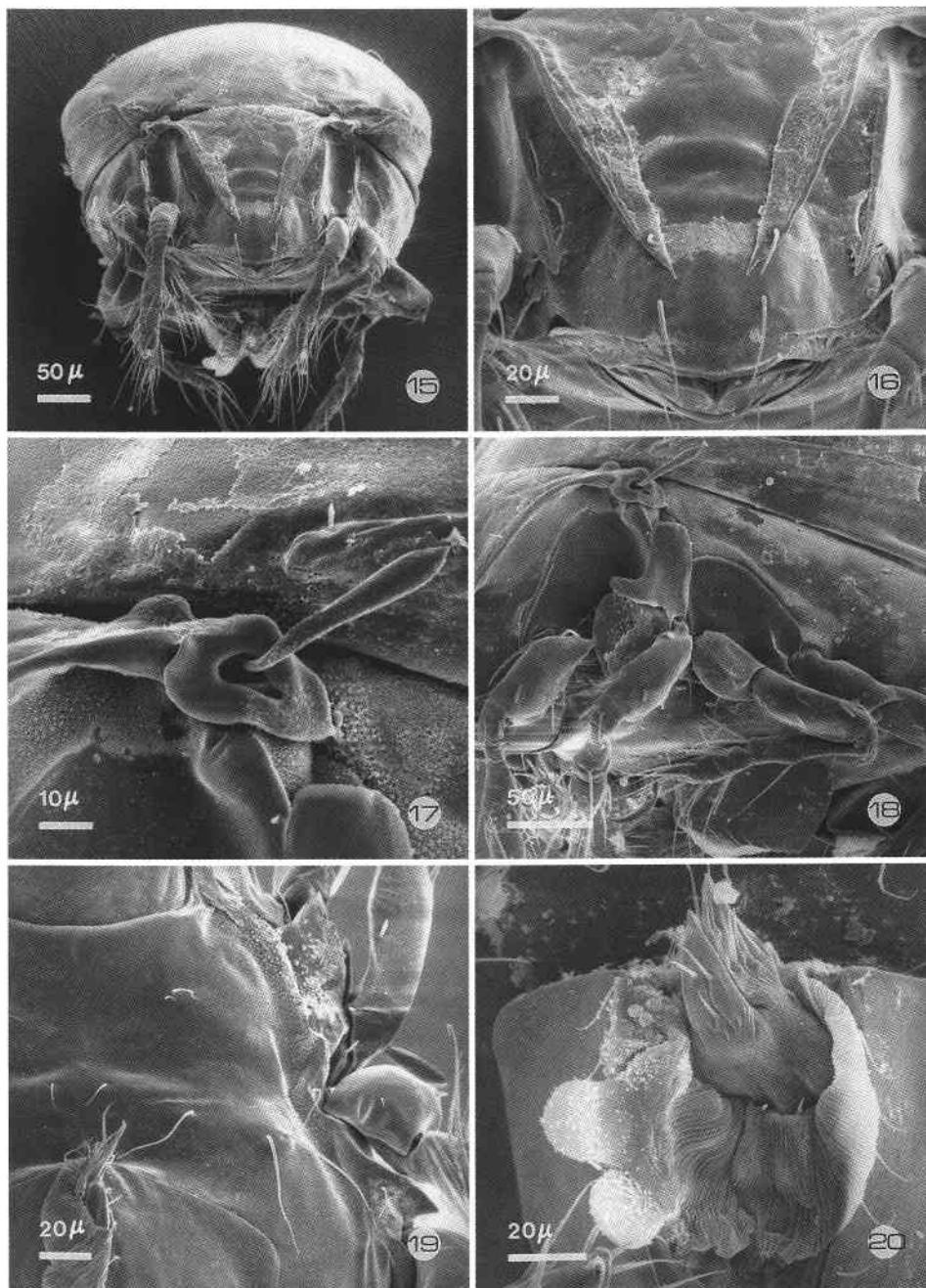
FIGS. 4–9. *Tegeocranellus alas* sp. nov., adult female: 4, lateral aspect; 5, anterior aspect; 6, detail of anterior of rostrum and lamella; 7, bothridium and sensillus, frontal aspect; 8, anterior of notogaster showing depression *fs* and carina; 9, lateral aspect of sejugal region showing tutorium, *Pds*, *ZI2*, and *ZI3*.



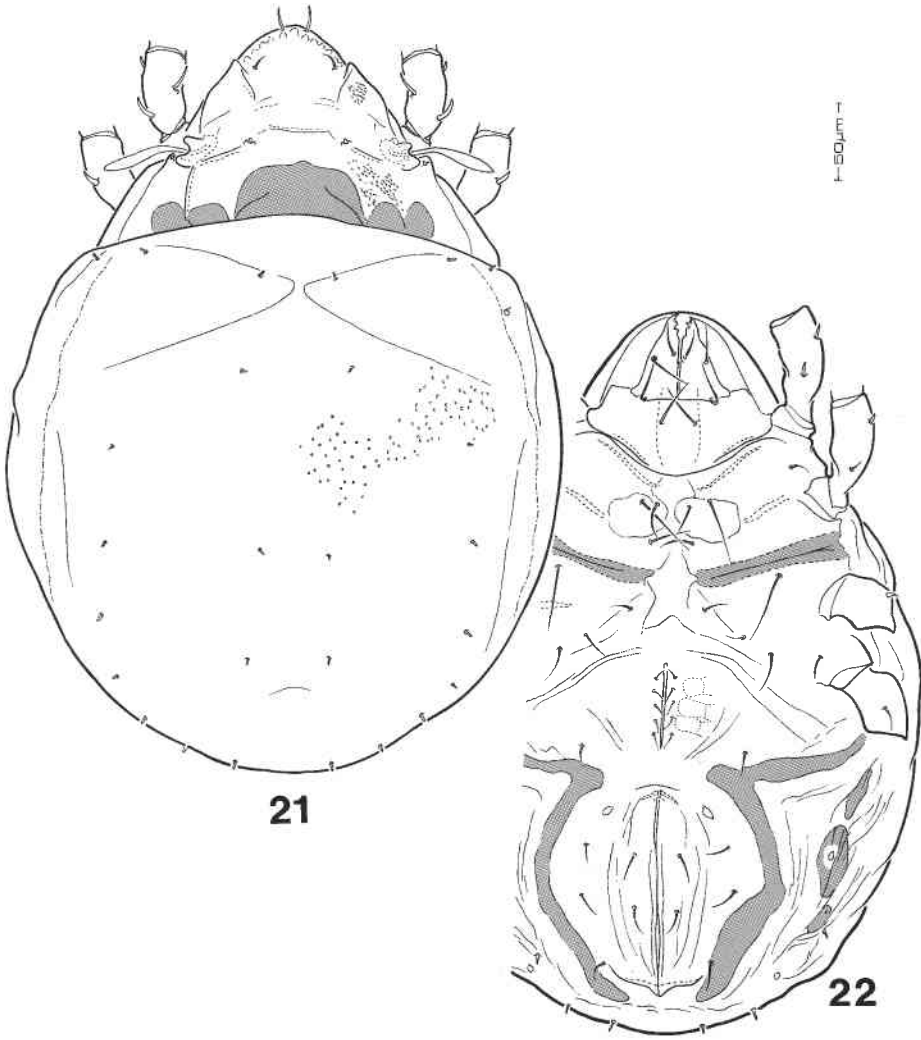
FIGS. 10, 11. *Tegeocranellus alas* sp. nov.: 10, larva, dorsal aspect; 11, tritonymph, dorsal aspect. Scale bars in μm .



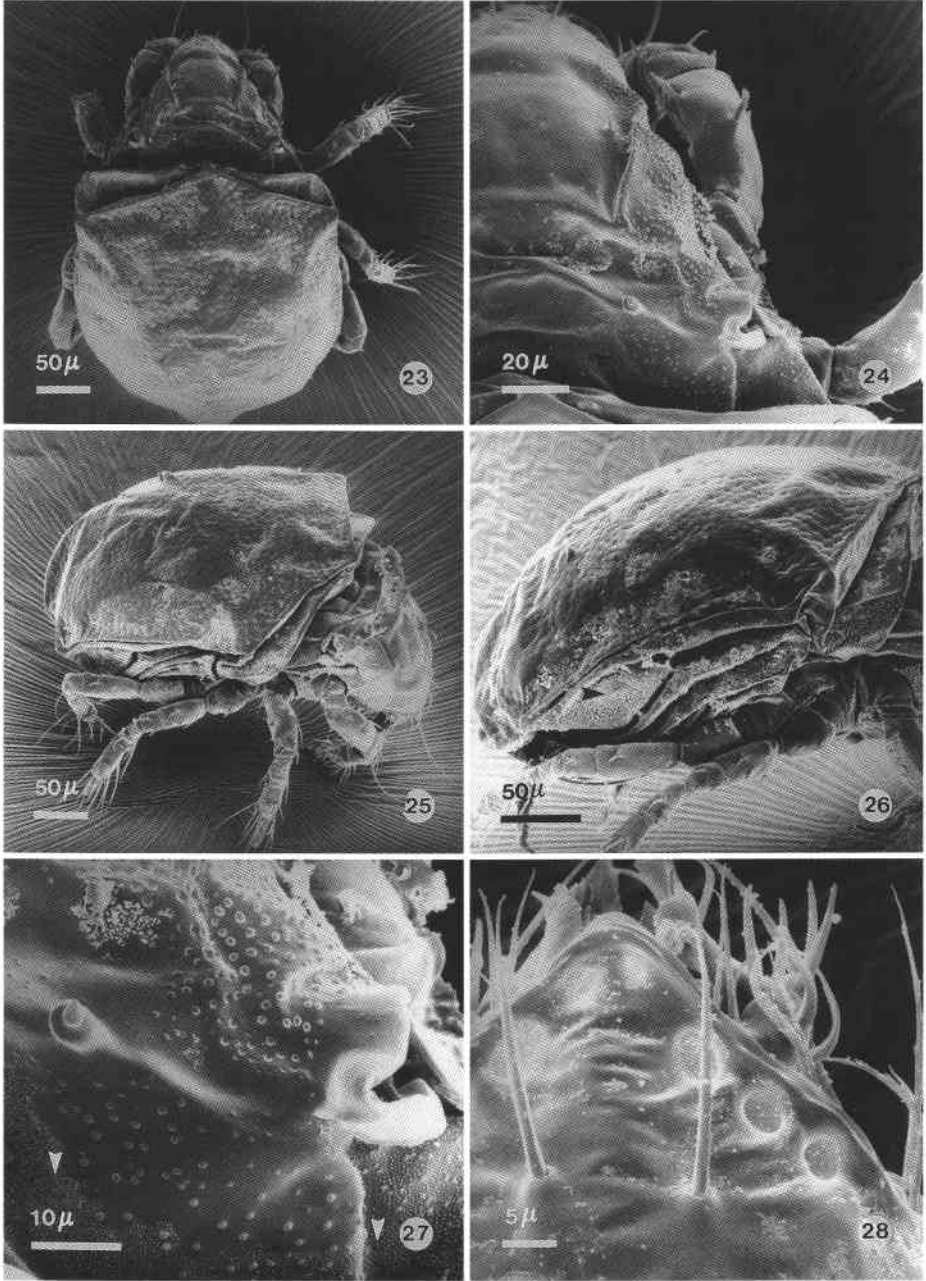
FIGS. 12–14. *Tegeocranellus barbarae* sp.nov., adult female: 12, dorsal aspect; 13, ventral aspect; 14, chelicera, antiaxial view. Scale bars in μm .



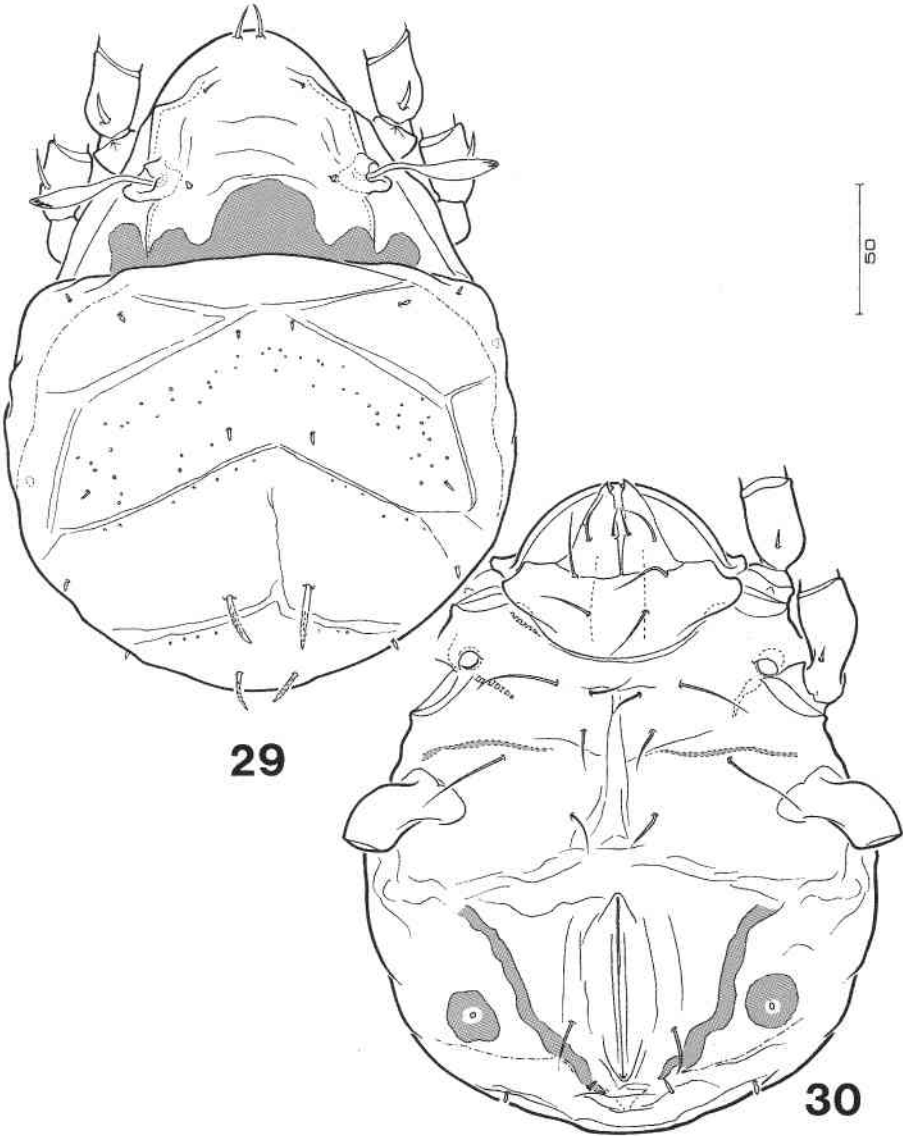
FIGS. 15–20. *Tegeocranellus barbarae* sp. nov., adult female: 15, frontal aspect; 16, detail of anterior of rostrum, tutorium, and lamellae; 17, bothridium and sensillus; 18, lateral aspect of sejugal region showing tutorium, pedotectum I, *Pdl*s, *Zl*2, and anterior of *Zl*3; 19, epimeral region, showing discidium; 20, genital papillae *Vm* and *Vp* and ovipositor.



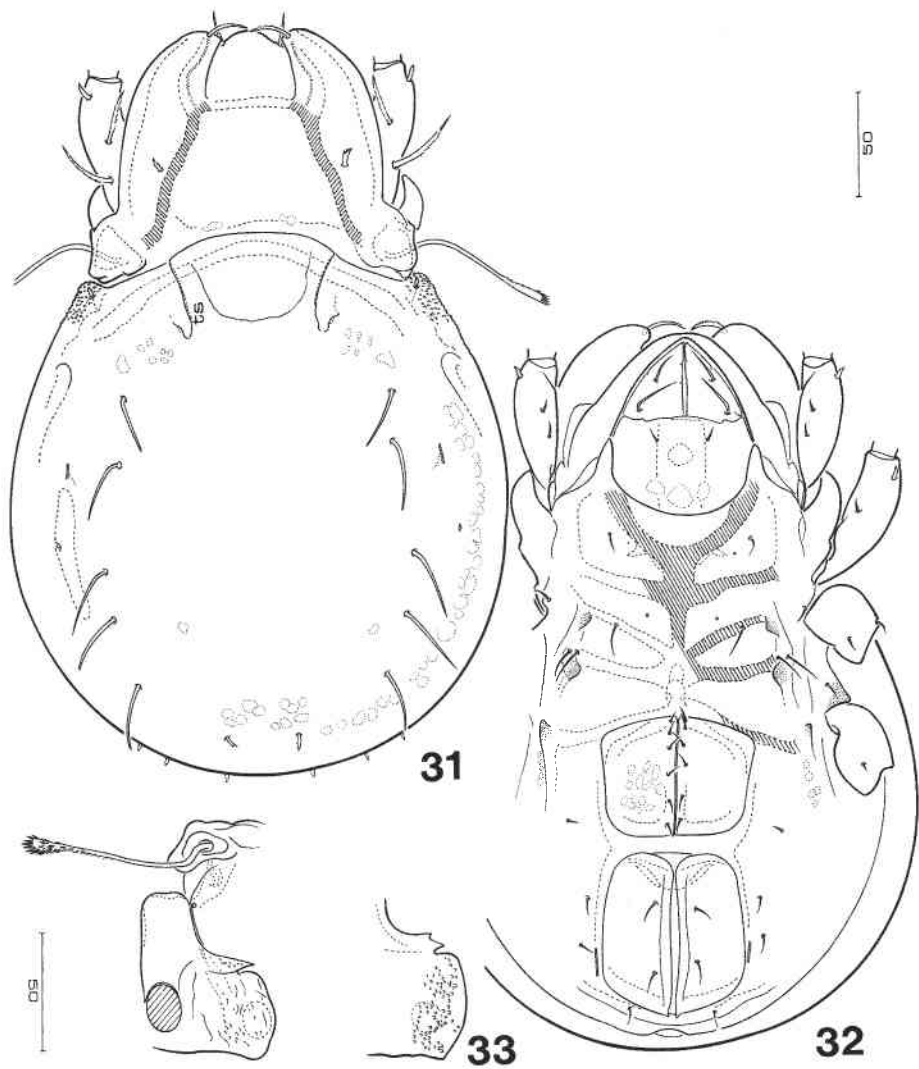
FIGS. 21, 22. *Tegeocranellus barbarae* sp. nov., tritonymph: 21, dorsal aspect; 22, ventral aspect.



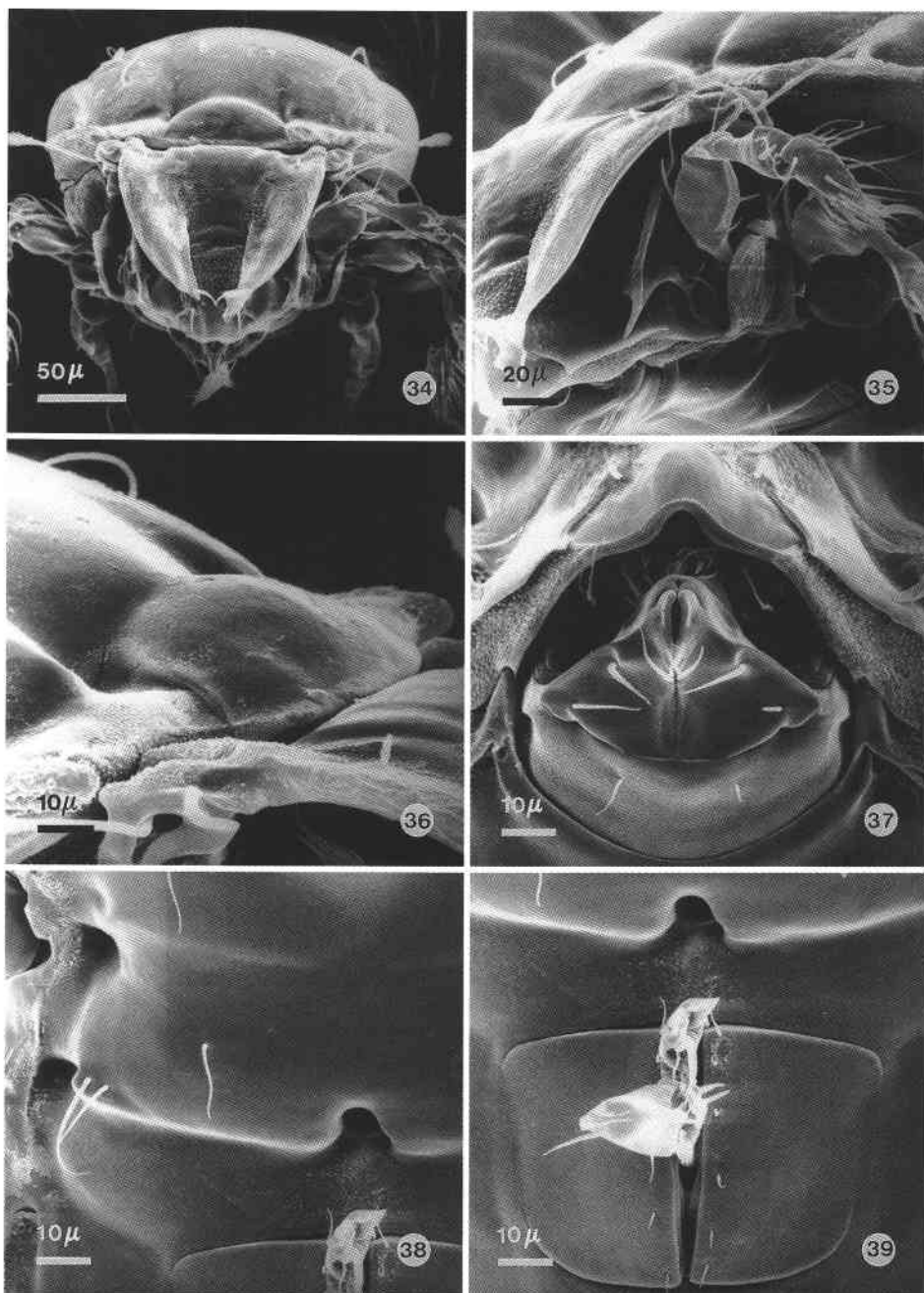
FIGS. 23–28. *Tegeocranellus barbarae* sp. nov., tritonymph: 23, dorsal aspect; 24, prodorsum; 25, lateral aspect; 26, lateral aspect of hysterosoma, opisthosomal gland indicated by arrow; 27, detail of prodorsum with posteromedial porose area and porose area posterior of bothridium indicated by arrows; 28, rostrum showing foveae.



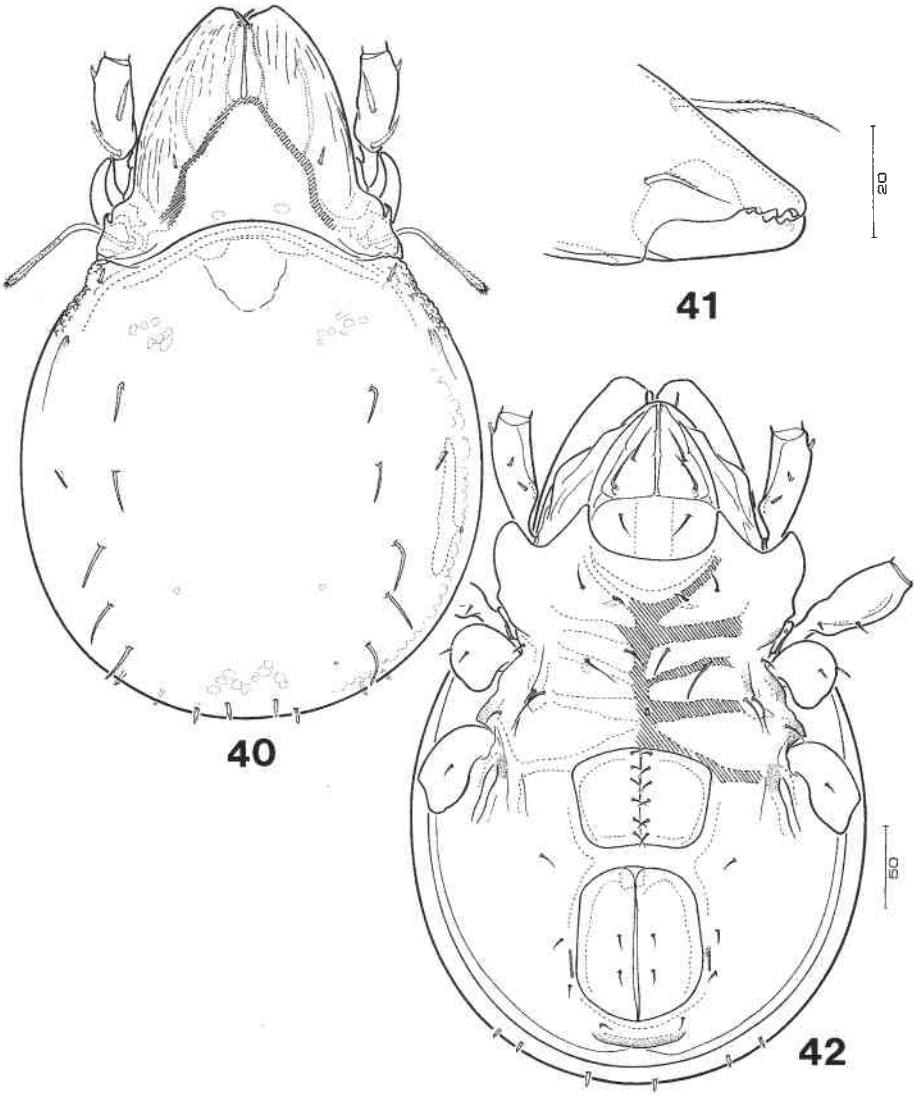
FIGS. 29, 30. *Tegeocranellus barbarae* sp.nov., larva: 29, dorsal aspect; 30, ventral aspect. Scale bar in µm.



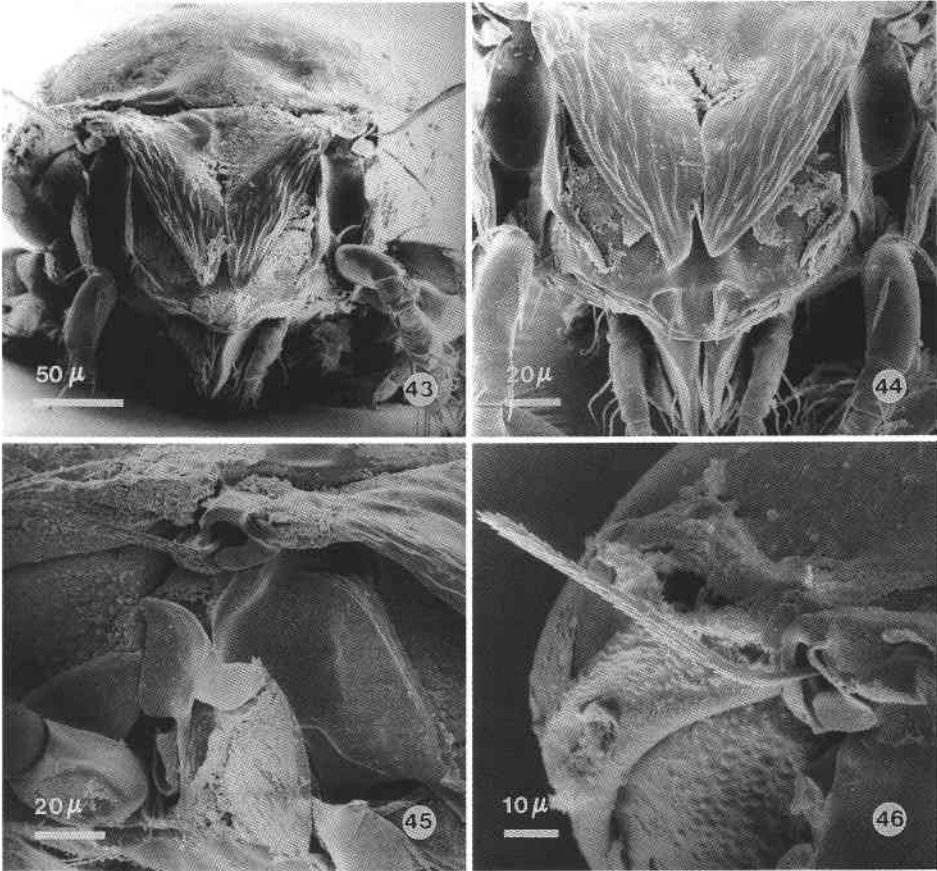
FIGS. 31–33. *Tegeocranellus kethleyi* sp. nov., adult female: 31, dorsal aspect; 32, ventral aspect; 33, detail of pedotectum I, showing variation in shape of *Pdl.s*. Scale bars in μm .



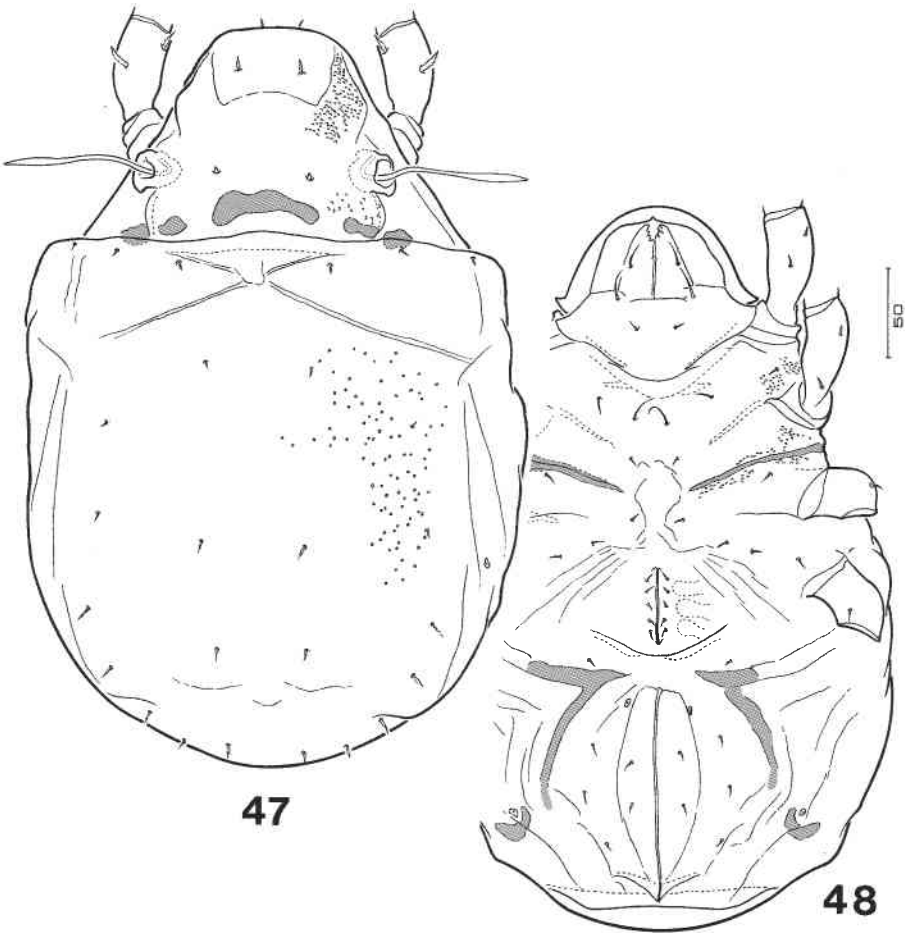
FIGS. 34–39. *Tegeocranellus kethleyi* sp. nov., adult female: 34, frontal aspect; 35, lateral region of podosoma showing tutorium, pedotectum I, *PdIs*, *ZI2*, and anterior region of *ZI3*; 36, anterior notogaster and posterior prodorsum showing domed lenticular region, carina *rs*, bothridium, and interlamellar seta; 37, gnathosoma, showing structure of rutellum; 38, epimeral region laterally; 39, epimeral region medially, detailing sternal depression (*st*) and genital plates.



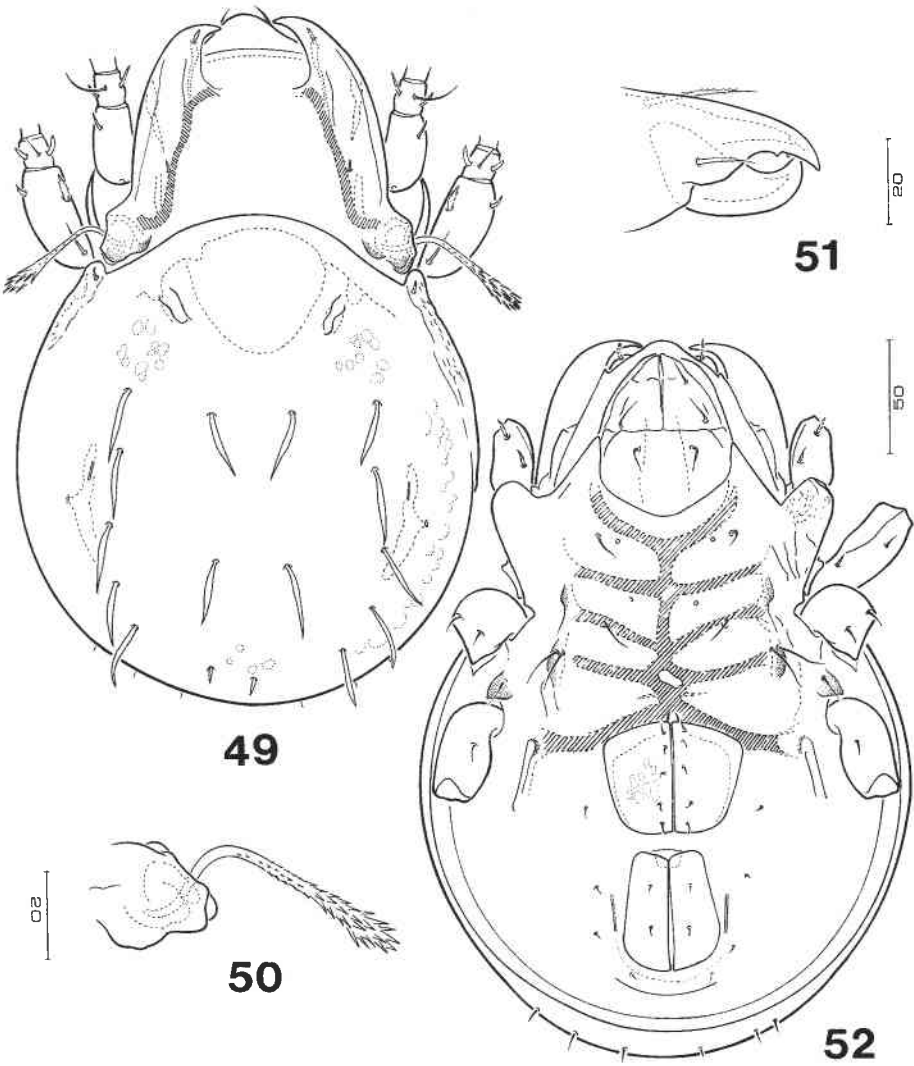
FIGS. 40–42. *Tegeocranellus mediolamellatus* sp. nov., adult male: 40, dorsal aspect; 41, chelicera, antiaxial view; 42, ventral aspect. Scale bars in μm .



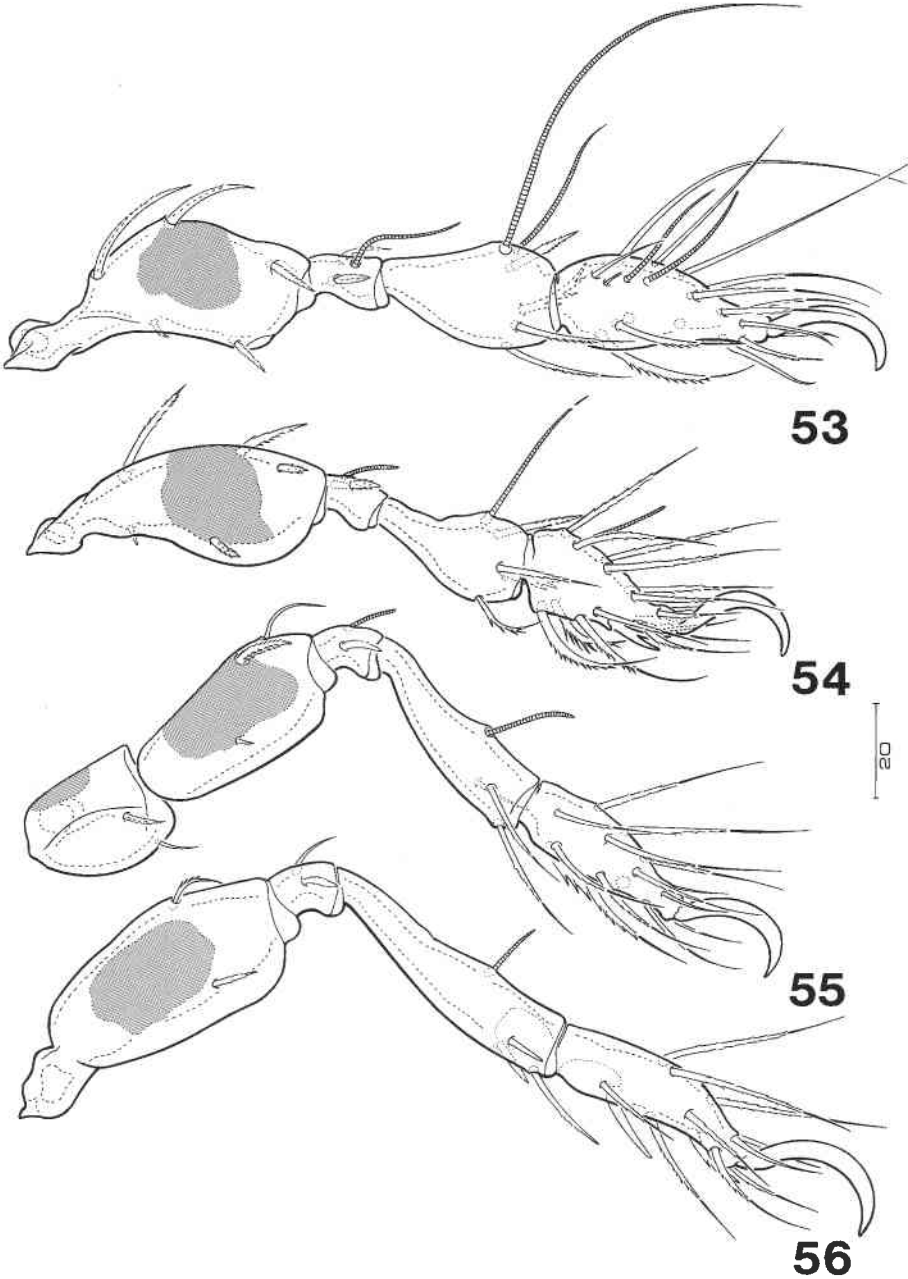
FIGS. 43–46. *Tegeocranellus mediolamellatus* sp.nov., adult male: 43, frontal aspect; 44, detail of rostrum and anterior lamellae; 45, lateral region of podosoma showing tutorium, pedotectum I, *Pdl1*, *Zl2*, and anterior of *Zl3*; 46, bothridium and sensillus.



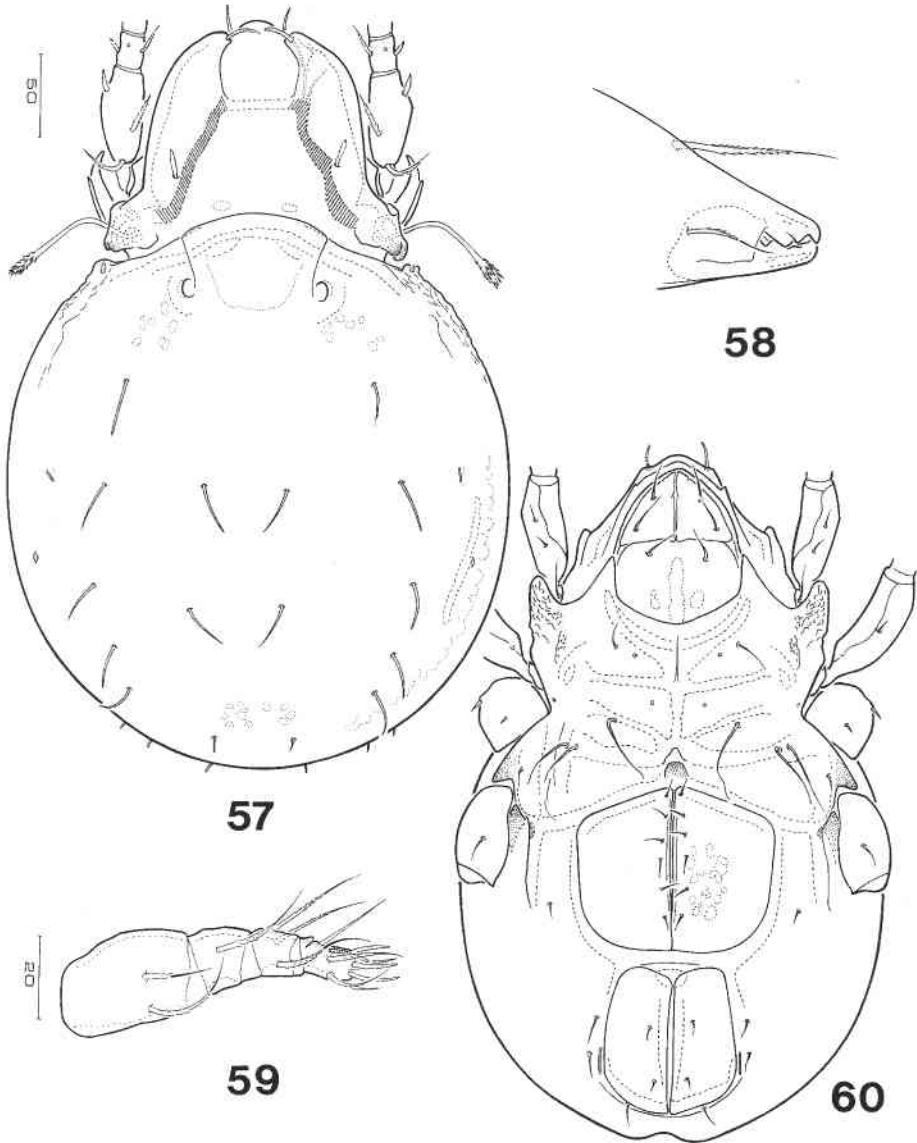
FIGS. 47, 48. *Tegeocranellus mediolamellatus* sp.nov., tritonymph: 47, dorsal aspect; 48, ventral aspect. Scale bar in μm .



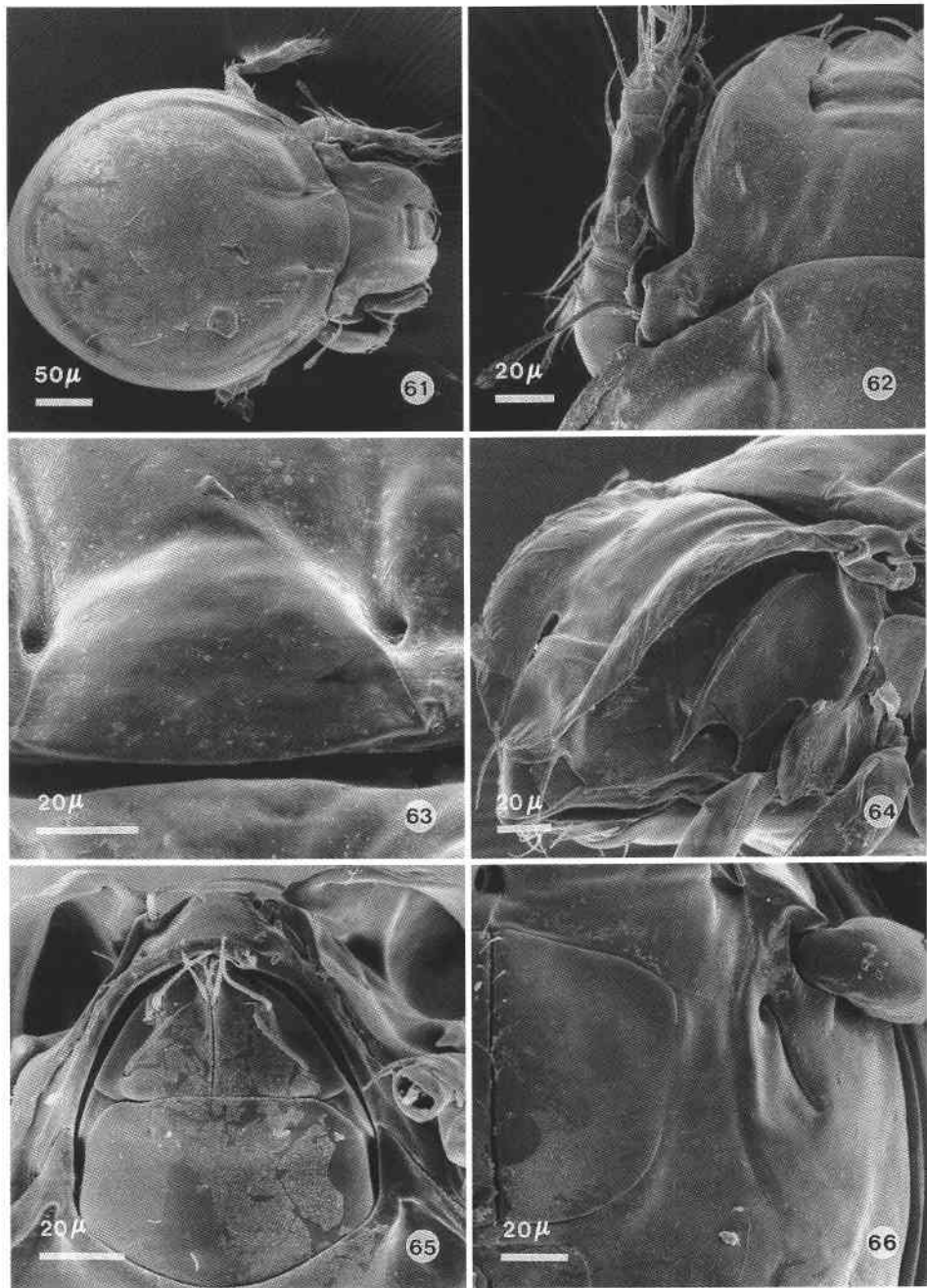
FIGS. 49–52. *Tegeocranellus mississippi* sp.nov., adult male: 49, dorsal aspect; 50, bothridium and sensillus; 51, chelicera, anti-axial view; 52, ventral aspect. Scale bars in µm.



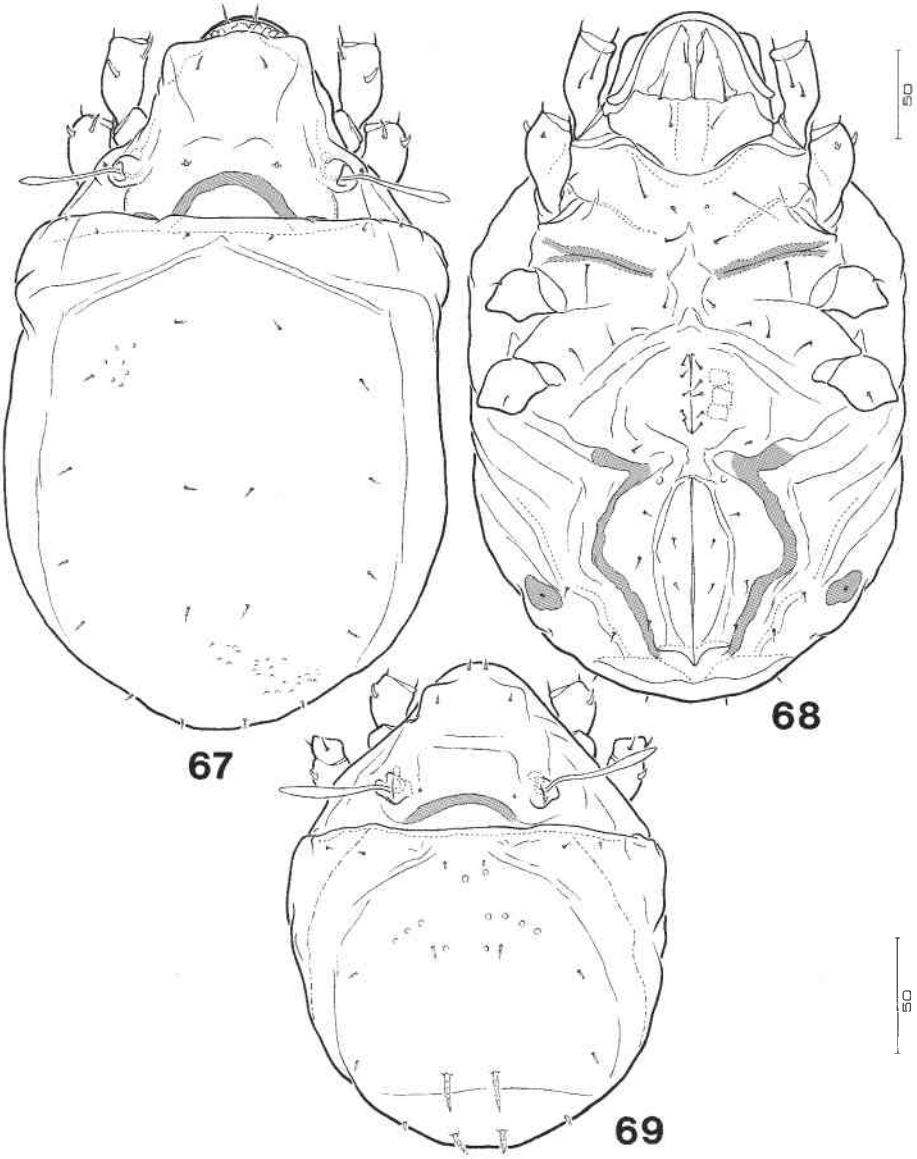
FIGS. 53–56. *Tegeocranellus mississippi* sp.nov., adult male: 53, leg I, trochanter removed; 54, leg II, trochanter removed; 55, leg III; 56, leg IV, trochanter removed. All legs in antiaxial view. Scale bar in μm .



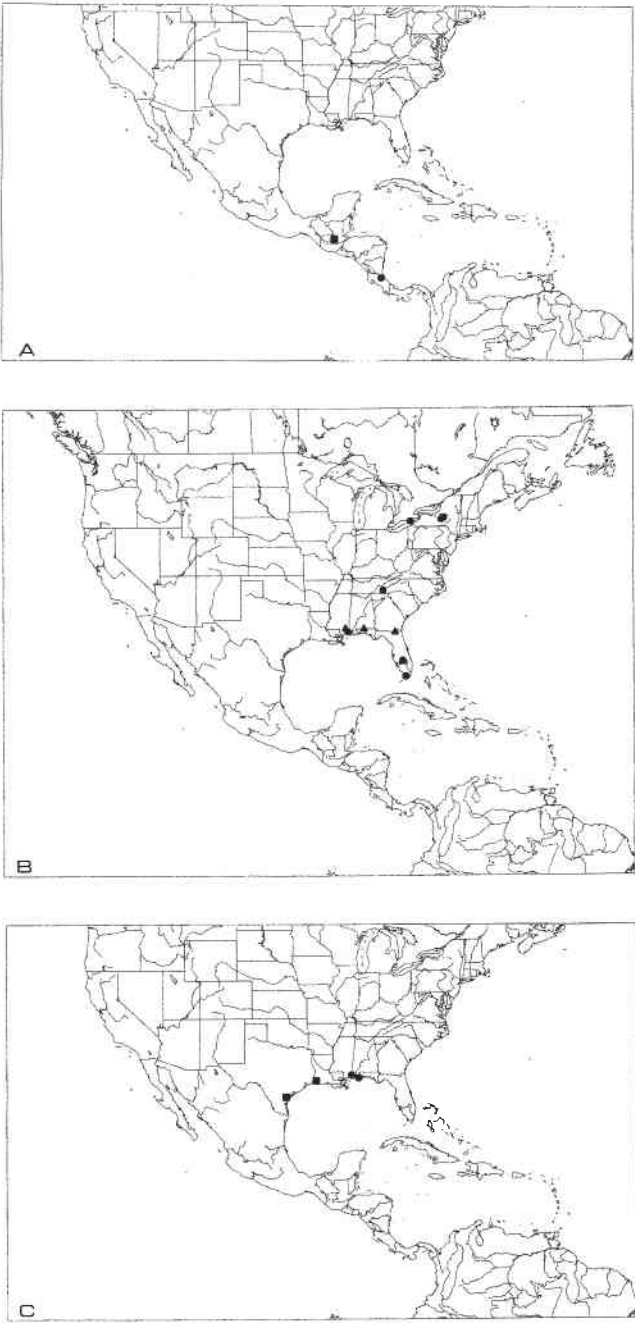
FIGS. 57–60. *Tegeocranellus muscorum* sp. nov., adult female: 57, dorsal aspect; 58, chelicera, antiaxial view; 59, pedipalp, antiaxial view; 60, ventral aspect. Scale bars in μm .



FIGS. 61–66. *Tegeocranellus muscorum* sp.nov., adult female: 61, dorsal aspect; 62, prodorsum and anterior of notogaster; 63, anterior of notogaster of another female showing variation in carina *ts* and shape of depression *fs* (prodorsum to the bottom of photo); 64, lateral region of podosoma (note: *PdIs* broken); 65, gnathosomal region and ventral surface of lamellar cusps; 66, ventral aspect showing sternal depression, genital plate, and circumpedal depression (*cpd*).



FIGS. 67–69. *Tegeocranellus muscorum* sp. nov.: 67, tritonymph, dorsal aspect; 68, tritonymph, ventral aspect; 69, larva, dorsal aspect. Scale bars in μm .



MAP 1. Known distribution of (A) *Tegeocranellus alas* sp.nov., ●; *T. mediolamellatus* sp.nov., ■; (B) *T. barbarae* sp.nov., ▲; *T. muscorum* sp.nov., ●; (C) *T. kethleyi* sp.nov., ●; *T. mississippii* sp.nov., ■.