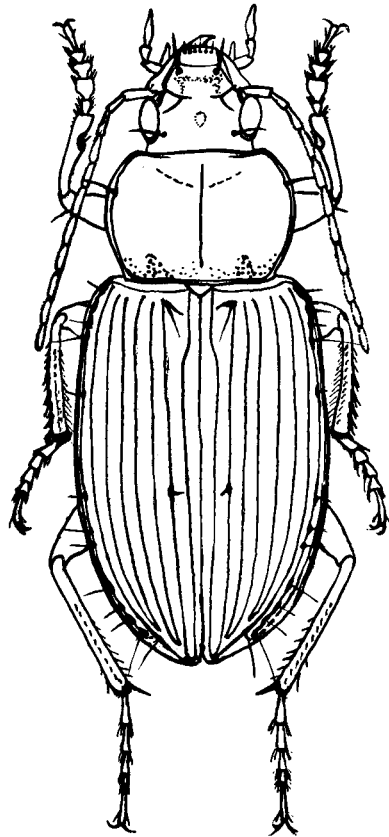




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*Pelmatellus nitescens* Bates, male, Mexico, Chiapas, Union Juarez. Size 7.1 mm.

CLASSIFICATION OF THE NORTH AND MIDDLE  
AMERICAN SPECIES OF THE GENUS *PELMATELLUS* BATES  
(COLEOPTERA: CARABIDAE: HARPALINI)

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*Quaestiones entomologicae*  
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*Based upon adult characteristics, this study includes a classification of, and a key to the North and Middle American species of Pelmatellus, descriptions, a discussion of variation of each species, phylogeny and zoogeography of the group. Nine of the 11 species are restricted to Middle America, and two are in southwestern United States. The new taxa described are P. nubicola, P. brachypterus, P. balli, P. infuscatus, P. rotundicollis, and P. stenolophoides parallelus. Thenarellus Bates and Pelmatellus are treated as subgenera. The genus is thought to have originated in South America from Antarctic Pelmatellina ancestors. Later, when Middle and South America were near each other, ancestors of extant species entered Middle America.*

*A l'aide des caractéristiques adultes, cette étude présente une classification, et une clef des espèces du genre Pelmatellus en Amérique du nord et du centre. Pour chaque espèce il y a une description et une brève analyse de la variation. Les relations phylogénétiques et la zoogéographie de ces espèces sont discutées. Neuf des onze espèces ne se rencontrent qu'en Amérique centrale, et deux se trouvent dans sud-ouest américain. Les nouveaux taxa décrits sont: P. nubicola, P. brachypterus, P. balli, P. infuscatus, P. rotundicollis, et P. stenolophoides parallelus. Thenarellus Bates est considéré comme sous-genre des Pelmatellus. Le genre probablement origina en Amérique du sud d'ancêtres des Pelmatellina antarctiques. Lors du rapprochement des Amériques centrale et du sud, les ancêtres des espèces actuelles pénétrèrent l'Amérique centrale.*

INTRODUCTION

The taxonomy of species of *Pelmatellus* has not been studied since the works of Bates (1882) and Casey (1914). The absence of recent taxonomic studies is due in part to the inconspicuousness of specimens of the species of *Pelmatellus* and to a lack of sufficient specimens for study. George E. Ball has collected over 700 specimens in Mexico, and a study of Middle and North American species is now possible.

MATERIALS

This study was based on examination of a total of 737 specimens from the University of Alberta (UASM); California Academy of Sciences (CAS); the Smithsonian Institution (NMNH); Museum National d'Histoire Naturelle (MNHP); and the British Museum of Natural History (BMNH). The specimens from the last named institution were examined by G. E. Ball who identified them by use of my key and comparison with a representative series of each species. I am selecting in this paper the types of the Bates' collection (BMNH) on the basis of recommendation from G. E. Ball who studied these types in 1970. I studied the type of *P. sinuosus* Casey (NMNH), but not the types of *P. turbatus* Fall and *P. lucidus* Casey. To complement this study, I examined representatives of the following genera and subgenera in Harpalini: *Notiobia* (*Notiobia*) spp. (UASM), *Notiobia* (*Anisotarsus*) spp. (UASM), *Anisodactylus*

(*Anisodactylus*) spp. (UASM), *Anisodactylus (Gynandrotarsus)* spp. (UASM), *Anisodactylus (Anadaptus)* spp. (UASM), *Anisodactylus (Amphasia) interstitialis* Say (UASM), *Anisodactylus (Pseudamphasia) sericeus* Harris (UASM), *Anisodactylus (Haplocentrus) laetus* Dejean (UASM), *Anisodactylus (Spongopus) verticalis* LeConte (UASM), *Xestonotus lugubris* Dejean (UASM), *Dicheirus* spp. (UASM), *Geopinus incrassatus* Dejean (UASM), *Harpalus chilensis* Solier (CAS), *Nemaglossa brevis* Solier (MNHP), *Trachysarus longicollis* Chaudoir (MNHP), *Trachysarus pallipes* Germain (MNHP), *Nemaglossa flavocincta* Blackburn (BMNH), *Nemaglossa (Lecanomerus) victoriensis* Blackburn (BMNH), *Thenarotes* sp. (BMNH), *Thenarotes discoidalis* Blackburn (BMNH), *Thenarotes tasmanicus* Bates (BMNH).

As most specimens are from the UASM collection, I recorded, in the distribution list for each species, the depository for those specimens from other collections only, holotypes and allotypes of new species are in the Smithsonian Institution collection (NMNH). The paratypes were deposited in the collections of the following institutions: University of Alberta (UASM), Instituto Politecnico Nacional de Mexico (IPNM), British Museum of Natural History (BMNH), Museum National d'Histoire Naturelle (MNHP), California Academy of Sciences (CAS), and the Canadian National Collection (CNC). The specimens seen by me are marked with this sign (!), those unmarked were seen by G. E. Ball.

## METHODS

*Description.* — Because members of this genus are similar to one another, descriptions are brief.

*Analysis of variation.* — I do not describe numerically the variation observed but present it in general terms.

*Measurements.* — The following measurements were made with an ocular micrometer in a stereoscopic binocular microscope. The total body length is the linear distance between the apex of the mandibles and the apex of the elytra of a straight specimen. Pronotal length is the distance along the midline from the basal to apical margins. Elytral length is the distance from the scutellar apex to the elytral apex. The maximum width of the first midtarsal article is the distance between the apical angles, length is the linear distance from the base of the article from just before the node to the apical angle. The midtibial width is measured slightly proximal to the apex as numerous setae and spines at the apex prevent accurate measurements. The maximum length of metasternum is measured along the elytral ventral margin, and the width is the distance between the two front angles.

*Illustration.* — Line drawings were prepared with the help of a grid in a stereoscopic binocular microscope. The structures of the everted internal sac of the median lobe are drawn with the right side facing the reader; the structures of the left side are shown by an interrupted line.

*Species discrimination.* — I accept for this study the biological species concept as discussed by Mayr (1969). This study is based on dead specimens, and the existence of gaps in color or structural characters is the best evidence for inferring gene flow. Geographical gaps may interrupt gene flow between allopatric populations and make it difficult to decide the classification status of structurally similar vicariant forms. Inferences concerning gene flow between allopatric populations are best made by comparing the proximal populations of both forms to geographically remote populations of the two forms. If proximal populations of the two forms exhibit convergence in color or structural characters, gene flow between them is probably recent (Whitehead, 1972).

## CLASSIFICATION

Because Pelmatellines are most closely related to Anisodactylina, as shown by the shared similarity of the type of vestiture on the ventral surfaces of the male front tarsi (Fig. 1), I have compared the characteristics of *Pelmatellus* to the characteristics of members of other genera and subgenera of these subtribes. My conclusions are that species of *Pelmatellus* as well as Australian and south American species (*Trachysaris longicollis*, *T. pallipes*, *Nemaglossa flavocincta*, *N. victoriensis*, *Thenarotes discoidalis*, *T. tasmanicus*) of related genera differ from Anisodactylina by the bisetose anterior margin of the penultimate article of the labial palpus (Fig. 2) and by the absence of setae from the apex of the prosternal intercoxal process. This is confirmed by Noonan (1973). I consider Pelmatellina (*Pelmatellus* and related genera) to be the sister group of the Anisodactylina. The subtribe Pelmatellina is the more plesiotypic of the two groups because of the bisetose penultimate article of the labial palpus.

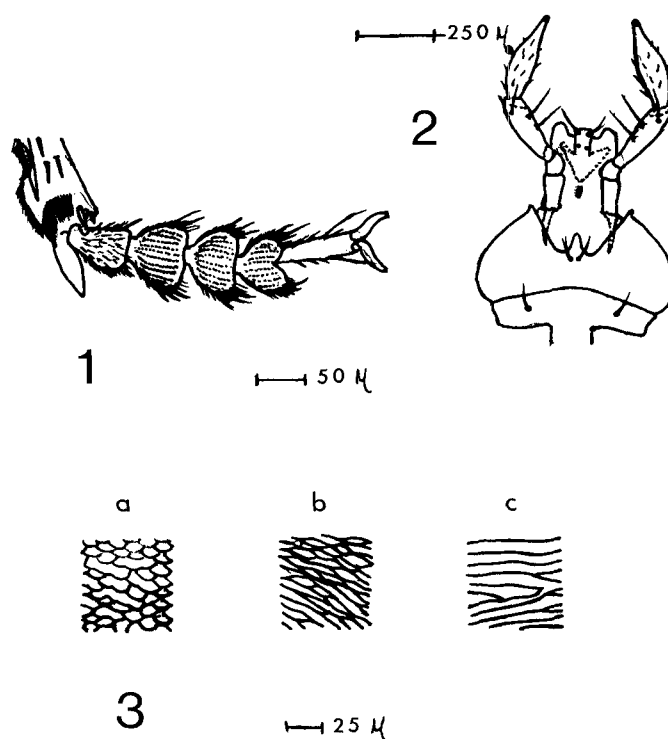


Fig. 1. Ventral view of male anterior tarsus of *Pelmatellus nitescens* Bates showing the spongy vestiture on articles 2-4. Fig. 2. Labium, ventral aspect, of *Pelmatellus nitescens* Bates. Fig. 3. Microsculpture types: (a) isodiametric meshes (*Pelmatellus obtusus* Bates), (b) slightly transverse meshes (*Pelmatellus stenolophoides stenolophoides* Bates), (c) very transverse meshes (*Pelmatellus nitescens* Bates).

Genus *Pelmatellus* Bates, 1882

*Pelmatellus* Bates, 1882: 68. — Casey, 1914: 234. — van Emden, 1953: 517. — Ball, 1960: 142.

TYPE SPECIES. — *Pelmatellus nitescens* Bates, 1882, here designated.

*Thenarellus* Bates, 1882: 69. TYPE SPECIES. — *Thenarellus leucopus* Bates, 1882, by monotypy.

*Description.*

*Color.* — Body of most specimens dark piceous, of a few specimens piceous or rufo-piceous. Appendages generally testaceous, infuscated in few specimens.

*Size.* — Body length 5 to 7 mm.

*Microsculpture.* — Head with isodiametric meshes, pronotum and elytra varied interspecifically from isodiametric to very transverse meshes, flat or convex.

*Chaetotaxy.* — Clypeus with one seta at each outer distal angle. Submentum with one seta on each side. Penultimate article of labial palpus bisetose on anterior margin. Mentum with one seta near middle on each side. Antennal scape with one large seta, article 3 with apical pubescence and setae, and articles 4 to 11 with pubescence and apical setae. Pronotum with one seta in anterior half of each lateral margin. Elytra: stria 2 with or without seta in apical half; scutellar stria with one seta in ocellate puncture; stria 7 with long preapical seta and short apical seta; umbelliculate series with a total of 11 to 14 setae in anterior and posterior groups. Sterna 3, 4, 5 of abdomen with single pair of setae on disc; sternum 6 with four marginal setae.

*Head.* — Basal clypeal margin clearly delimited or not. Clypeo-ocular prolongation clearly defined. Frons with small fovea, weakly defined in some specimens. Mentum with large tooth.

*Pronotum.* Wider than long in members of most species; lateral bead narrow and translucent, in members of most species extended along base of pronotum. Hind angles each with small denticle in members of most species.

*Pterothorax.* — Metepisterna elongate (2.5 times longer than wide) in macropterous forms or short (twice as long as wide) in brachypterous forms.

*Male genitalia.* — Median lobe asymmetrical; dorsal area mostly membranous; internal sac with or without right, left, and apical spines, each spine surrounded or not by smaller scale-like teeth. Parameres asymmetrical, conchoidal, and asetose.

*Female genitalia.* — Not studied.

Other characteristics not mentioned here are like those of generalized Anisodactylina.

#### Key to the adults of the Middle and North American species of the genus *Pelmatellus*.

1. Elytral stria 2 without discal puncture; male with vestiture on ventral surface of articles of front tarsi only . . . . . (Subgenus *Thenarellus*). 2
- Elytral stria 2 with single discal puncture; male with vestiture on ventral surfaces of articles of front and middle tarsi . . . . . (Subgenus *Pelmatellus*). 3
- 2 (1). Pronotum (Fig. 4) with hind angles well-defined; metepisternum elongate, 2.5 times longer than wide; macropterous . . . . . *leucopus* Bates, p. 85
- Pronotum (Fig. 5) with hind angles rather round; metepisternum shorter, twice as long as wide; brachypterous . . . . . *balli* new species, p. 85
- 3 (1). Male median lobe with ventrally directed hook at apex (Fig. 18-19); male with article 1 of middle tarsus about 1.2 times as wide as width of middle tibia near apex, sides of front and middle tarsi arcuate; female with article 2 of middle tarsus 1.2 times longer than wide . . . . . 4
- Male median lobe without hook at apex (Fig. 20-28); male with article 1 of middle tarsus about as wide as tibia near apex, articles with sides slightly arcuate; female with middle tarsus wider, article 2 as long as wide . . . . . 5
- 4 (3). Legs infuscated; pronotum with hind angles not denticulate (Fig. 7), basal lateral

- impressions impunctate or with few weak punctures; range — Mexico, Pacific coast north of the Isthmus of Tehuantepec . . . . . *infuscatus* new species, p. 90
- Legs testaceous; pronotum with hind angles denticulate, basal lateral impressions strongly punctate; range — southern Mexico and Guatemala . . . . . *nitescens* Bates, p. 88
- 5 (4). Elytral disc with microsculpture of isodiametric meshes (Fig. 3a) . . . . . *obtusius* Bates, p. 90
- Elytral disc with microsculpture of transverse meshes (Fig. 3b-3c) . . . . . 6
- 6 (5). Pronotal hind angles not denticulate (Fig. 10) . . . *rotundicollis* new species, p. 91
- Pronotal hind angles with well-defined denticles (Fig. 11-16) . . . . . 7
- 7 (6). Elytral disc with microsculpture of slightly transverse meshes (each mesh two to four times wider than long); pronotum coarsely punctate across base (Fig. 11-12) . . . . . 8
- Elytral disc with microsculpture of markedly transverse meshes (each mesh four to 20 times wider than long); pronotum with punctuation finer, restricted to the basal lateral impressions (Fig. 13-16) . . . . . 9
- 8 (7). Pronotum wider, hind angles distinctly angulate (Fig. 11); elytra with lateral margins not parallel in basal two-thirds . . . . . *s. stenolophoides* Bates, p. 91
- Pronotum narrower, hind angles less angulate (Fig. 12); elytra with lateral margins parallel in basal two-thirds . . . . . *s. parallelus* new subspecies, p. 93
- 9 (7). Metasternum shorter (ca. twice as long as wide); brachypterous; basal lateral impressions of pronotum impunctate or sparsely punctate . . . . . 10
- Metepisternum longer (ca. 2.5 times longer than wide); macropterous; basal lateral impressions of pronotum punctate . . . . . 11
- 10 (9). Pronotum with basal bead near hind angles only (Fig. 14), basal lateral impressions punctate . . . . . *nubicola* new species, p. 93
- Pronotum with basal bead extended mediad of basal lateral impressions (Fig. 15), latter sparsely and finely punctate . . . . . *brachypterus* new species, p. 94
- 11 (9). Pronotum with lateral margins posteriorly incurved evenly, hind angles each with smaller denticle (Fig. 13) . . . . . *vexator* Bates, p. 93
- Pronotum with posterior margins straight or sinuate, hind angles each with denticle very prominent (Fig. 16) . . . . . *cyanescens* Bates, p. 94

#### Subgenus *Thenarellus* Bates

*Pelmatellus leucopus* Bates, 1882: 69.

In addition to key characters, the members of this species are easily recognized by the combination of: piceous body, elytra of normal length, and well-developed hind wings. Microsculpture meshes very transverse on dorsal surfaces of elytra. Pronotal denticle prominent, hind angle rectangular (Fig. 4). Internal sac of male genitalia without spines (two males dissected).

*Distribution.* — The three males are from two localities in Costa Rica: Irazu, 6000 feet to 7000 feet (BMNH) !; Cache (BMNH) ! (Fig. 30).

#### *Pelmatellus balli* new species

*Type material.* — Holotype male and allotype female labelled: Mexico, Chiapas, Volcan Tacaná, s. e. slope 7800 feet, cloud forest, moss on trees, 23-VII-1972; G. E. Ball collector (NMNH). The paratypes from the same locality, three males and six females are in UASM,

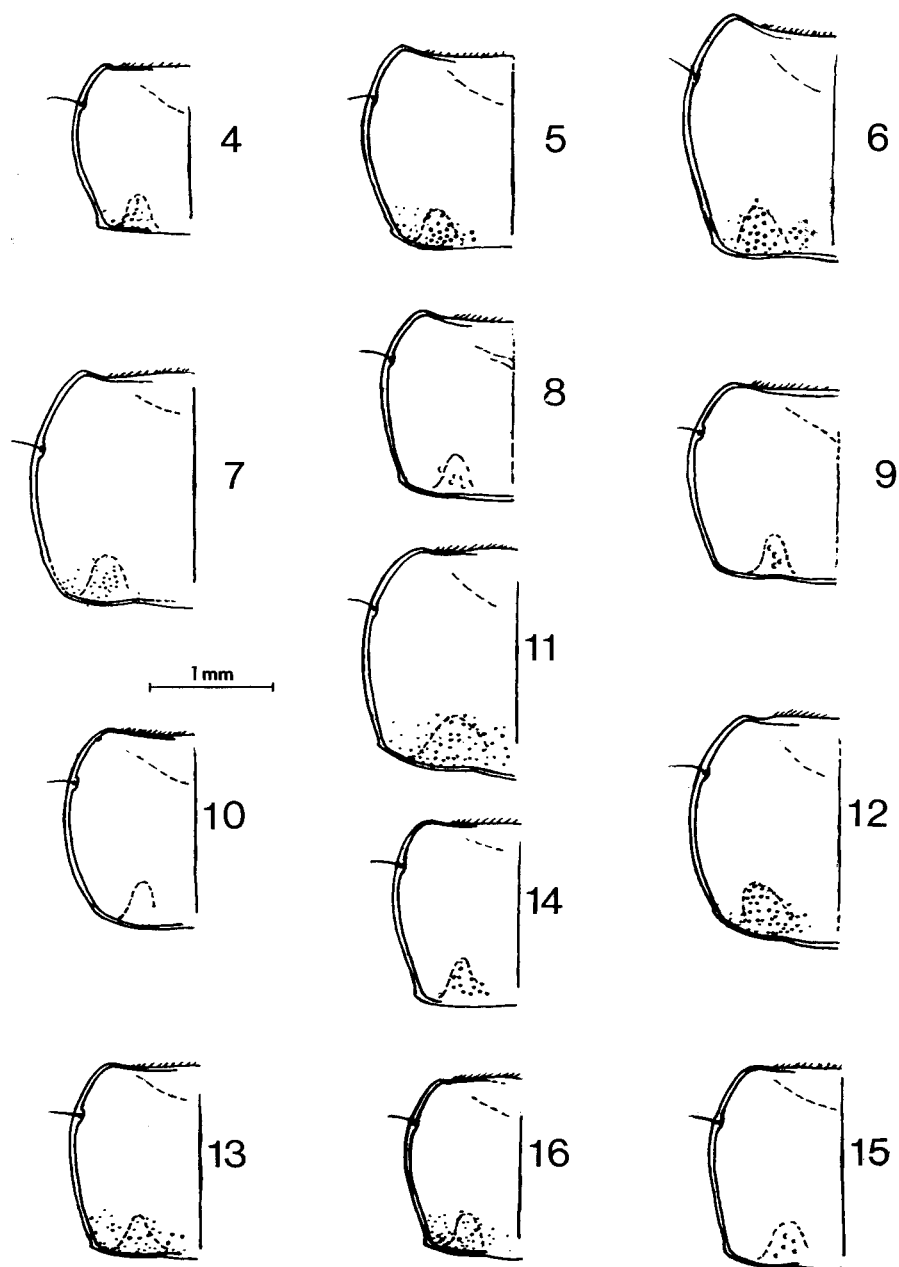


Fig. 4-16. Pronotum, right half, dorsal aspect, of species of the genus *Pematellus* in Middle and North America. 4. *Pematellus leucopus* Bates. 5. *Pematellus balli* new species. 6. *Pematellus nitescens* Bates. 7. *Pematellus infuscatus* new species. 8. *Pematellus obtusus* Bates. 9. *Pematellus obtusus* Bates (Oaxaca Stste). 10. *Pematellus rotundicollis* new species. 11. *Pematellus stenolophoides stenolophoides* Bates. 12. *Pematellus stenolophoides parallelus* new subspecies. 13. *Pematellus vexator* Bates. 14. *Pematellus nubicola* new species. 15. *Pematellus brachypterus* new species. 16. *Pematellus cyanesens* Bates.



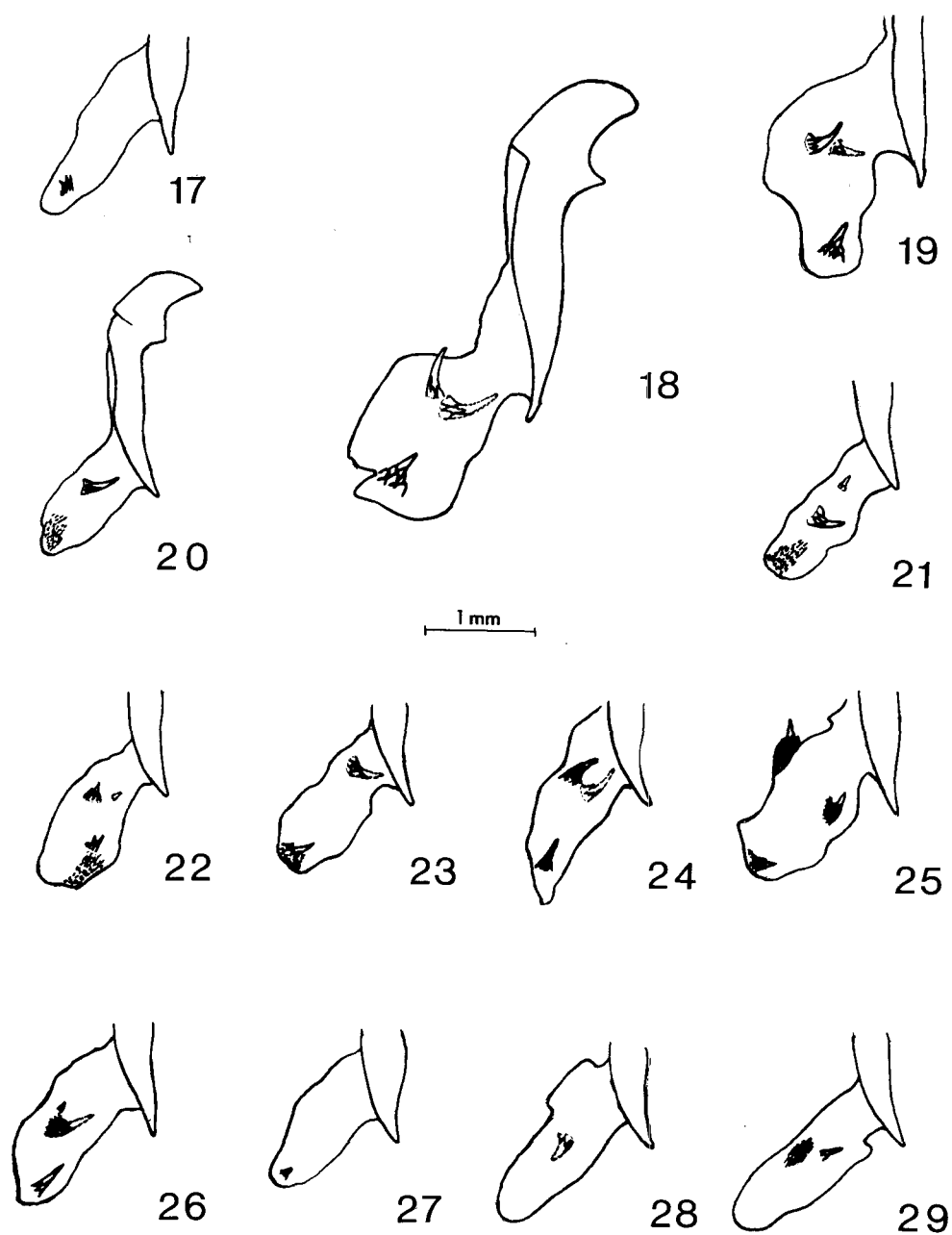


Fig. 17-29. Median lobe and internal sac, right lateral aspect, of species of the genus *Pelmatellus* in Middle and North America. 17. *Pelmatellus balli* new species. 18. *Pelmatellus nitescens* Bates. 19. *Pelmatellus infuscatus* new species. 20-23. *Pelmatellus obtusus* Bates. 24. *Pelmatellus rotundicollis* new species. 25. *Pelmatellus stenolophoides stenolophoides* Bates. 26. *Pelmatellus stenolophoides parallelus* new subspecies. 27. *Pelmatellus vexator* Bates. 28. *Pelmatellus brachypterus* new species. 29. *Pelmatellus cyanescens* Bates.

IPNM, CAS, and CNC.

Specimens of this species are recognized by the combination of: body rufo-piceous, elytra short rather ovate, and metepisterna and hind wings reduced. Pronotal denticle normal, hind angles obtuse (Fig. 5). Internal sac of male genitalia with apical group of spines (two males dissected) (Fig. 17).

*Derivation of specific epithet.* — *P. balli* is named in honor of G. E. Ball, who has contributed much to the knowledge of Mexican ground beetles.

*Geographical distribution.* — The four males and seven females I have seen are known from Volcan Tacaná on the Mexican-Guatemalan border, at the type locality and at Rancho San Antonio, Guatemala ! (Fig. 30).

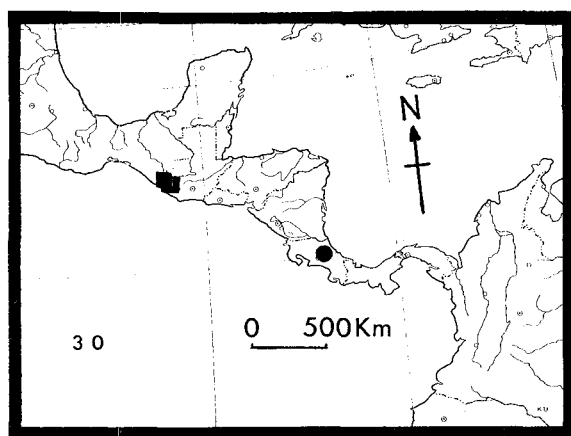


Fig. 30. Distribution of *Pelmatellus balli* new species (square), *Pelmatellus leucopus* Bates (circle).

*Notes on habitat.* — Specimens of this species were found under moss mats on tree trunks in tropical cloud forest at 7800 feet and at 9000 feet altitude.

#### Subgenus *Pelmatellus* Bates

This subgenus is characterized in the key. The nine Middle-North American species treated here are included in two species groups.

#### The *nitescens* group

Males of this group have wider front and middle tarsi, and females have narrower middle tarsi. The apex of the male median lobe is hooked in lateral view (Fig. 18). The meshes of microsculpture are very transverse. The species of this group include the largest specimens of the subgenus from Middle America.

#### *Pelmatellus nitescens* Bates

*Pelmatellus nitescens* Bates, 1882: 68. — Lectotype (here selected), male, labelled: Type HT

[circular label ringed with red]; Oaxaca Mexico Hoege; BCA Col. I, 1 *Pelmatellus nitescens* Bates; *Pelmatellus nitescens* [handwritten]. [BMNH].

Characteristics of this species are: color of body dark, dorsal surface of most specimens with blue or copper luster; pronotum with denticulate hind angles, well-defined and deeply punctate basal lateral impressions (Fig. 6); internal sac of male genitalia with three large spines (Fig. 18) (17 males dissected).

*Variation.* — Specimens south of the Isthmus of Tehuantepec are on average larger than those north of it. Those north of the Isthmus live at lower altitudes.

*Distribution.* — Members of this species occur along the Sierra Madre de Chiapas, Sierra Madre del Sur, Trans-volcanic Sierra, Sierra Madre Oriental and Occidental (Fig. 31). Eighty males and 89 females from the following states in Mexico have been studied: Chiapas !; Durango !; Distrito Federal !; Guerrero; Mexico !; Morelos !; San Luis Potosi !; Veracruz !.

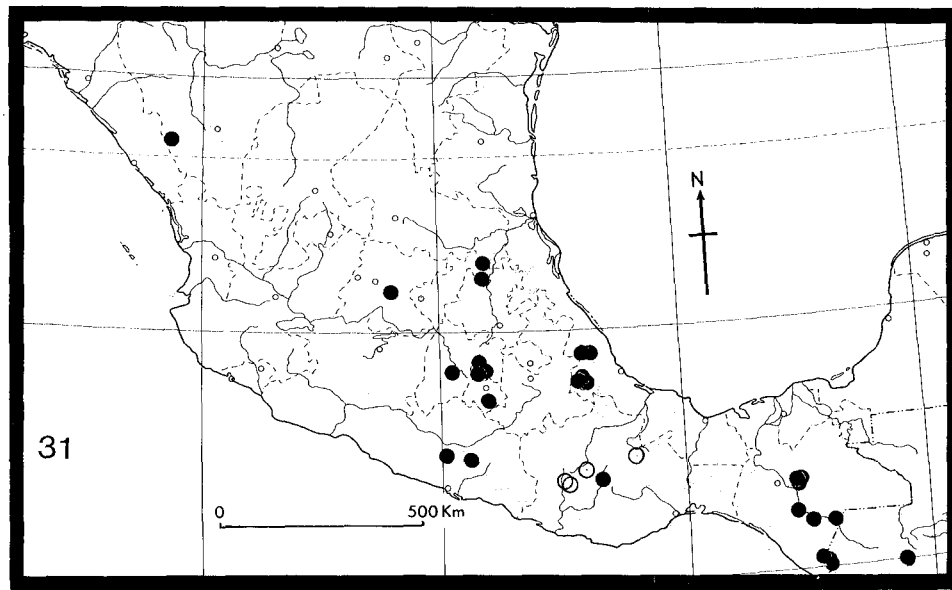


Fig. 31. Distribution of *Pelmatellus nitescens* Bates (black circle), and *Pelmatellus infuscatus* new species (open circle).

*Notes on habitat.* — Specimens were found in open habitat in forests (montane, montane tropical evergreen, temperate — dominated by *Liquidambar*, wet and dry oak-pine), along roadsides, in agricultural fields, around houses in small towns, and occasionally in bromeliads growing on trees in pastures. North of the Isthmus of Tehuantepec they were found from 2900 feet to 6600 feet (on average 5000 feet), and south of the Isthmus they occurred between 5200 feet and 7900 feet (on average 7100 feet). The beetles were collected from February until November, though they were more abundantly collected from June until November.

*Pelmatellus infuscatus* new species

*Type material.* — Holotype male and allotype female labelled: Mexico Oaxaca, 21.8 mi. n. Juchatengo, 7100 feet, 18-19 VII-1966; G. E. Ball, D. R. Whitehead collectors. The paratypes 6 males and 11 females are in UASM, IPNM, BMNH, MNHP, CAS, and CNC.

Specimens of this species are recognized by the combination of: infuscated legs, piceous body, and non-denticulate pronotal hind angles (Fig. 7). Median lobe and internal sac as in *P. nitescens* (Fig. 19) (two males dissected).

*Derivation of specific epithet.* — From Latin referring to the darkened appendages.

*Distribution.* — Specimens are known only from the Pacific slopes of the Sierra Madre del Sur, Oaxaca (Fig. 31). I have seen 7 males and 12 females from the following Mexican localities: Oaxaca, 21.8 mi. n. Juchatengo, 7100 feet !; Rte. 131, 21.6 mi. s. Juchatengo, 5500 feet !; Cerro Zempoalteptl, 7200 feet !; 6.6 mi. s. Sta. Catarina Juquila !.

*Notes on habitat.* — Specimens have been found under stones and in leaf litter on dry or wet slopes between 5300 feet and 7200 feet during July and August in oak-pine forests with Spanish moss.

The *vexator* group

Compared to specimens of the *nitescens* group, males of this group have narrower front and middle tarsi; females have wider middle tarsi. The apex of the median lobe is without a hook in lateral view (Fig. 27).

*Pelmatellus obtusus* Bates

*Pelmatellus obtusus* Bates, 1882: 68. — Lectotype (here selected) male, labelled: Type HT [circular label, ringed with red]; Ostuncalco, 500 feet [probably 8000 feet (Selander and Vaurie, 1962)] Champion; BCA Coll. I, 1 *Pelmatellus obtusus* Bates; *Pelmatellus obtusus* Bates [handwritten]. [BMNH].

*Bradycellus lucidus* Casey, 1884: 8. — Type locality: New Mexico, Cloudcroft. — [Junior primary homonym of *B. lucidus* Bates, 1874]. — Casey, 1914: 234 (*Pelmatellus*).

*Pelmatellus sinuosus* Casey, 1914: 235. Type locality: Mexico, Salazar ! — NEW SYNONYM.

This is a typical specimen of *P. obtusus* from central Mexico.

Specimens of this unusually variable species are readily recognized by the following: isodiametric meshes of microsculpture over elytral intervals (the seventh and/or eighth elytral intervals with transverse sculpture) (Fig. 3a); basal lateral impressions of pronotum punctate or with scattered poorly defined punctuations (Fig. 8); internal sac of male genitalia (Fig. 20, 21, 22, 23) with or without one to three spines (51 males dissected).

*Geographical variation.* — Specimens from southwestern United States are on average larger than specimens from more southern localities. However, the present material is not adequate to study the variation patterns in northern Mexico. Development of the pronotal denticles on the hind angles and of the basal angles themselves varies little from central Mexico northward, but varies clinally southward. In the central parts of the Trans-volcanic Sierra, most specimens show well-developed denticles and angulate angles (Fig. 8). Most specimens in the eastern parts of the Trans-volcanic Sierra, eastern Oaxaca, and Chiapas have reduced denticles and more rounded angles. In the western parts of the Sierra Madre del Sur in most localities, the angles are rounded and without denticles (Fig. 9). The number of spines on the internal sac varies geographically. In southwestern United States, the right spine is missing from all specimens examined, and the apical spine is absent from some specimens

(Fig. 23). In Mexico north of the Isthmus of Tehuantepec, the number varies from one to three (Fig. 20, 21, 22), but the right spine is present in all specimens examined. I have seen three specimens from south of the Isthmus without spines.

*Distribution.* — This species ranges from the southwestern United States to Guatemala. In Mexico it is represented in the Sierra Madre del Sur, Sierra Madre Oriental, Trans-volcanic Sierra, and Sierra Madre de Chiapas (Fig. 32). I have seen 150 males and 160 females from the following countries and states: Guatemala; Mexico — Chiapas !, Durango !, Guerrero !, Hidalgo !, Mexico !, Michoacan !, Morelos !, Oaxaca !, Puelba !, United States — Arizona !, New Mexico !.

*Notes on habitat.* — Specimens were found commonly under stones and debris in agricultural lands and open areas in temperate oak-pine forests; a few specimens were found along creek valleys and meadows. The altitude range is from 6600 feet to 11175 feet. Adults were collected from March until September; most were obtained in July and August (specimens from the southwestern United States were more abundantly collected in September).

*Pelmatellus rotundicollis* new species

*Type material.* — Holotype male labelled: Mexico, Nuevo Leon, Cerro de Potosi, 12.2 mi. n. w. Galeana, 7200 feet, e. slope, 17-X-1965; D. R. Whitehead, G. E. Ball collectors. [NMNH].

The specimen is readily recognized by its unusually round pronotum (Fig. 10). It is distinguished from *P. obtusus*, closest relative, by the round pronotal hind angles; the evenly curved pronotal lateral margins; and only the first and second intervals of the elytra with isodiametric meshes of microsculpture. Internal sac with three large spines (Fig. 24).

*Derivation of the specific epithet.* — From Latin meaning round neck, referring to the round pronotum.

*Distribution.* — The single specimen is known from the mountain of Cerro de Potosi in northeastern Mexico (Fig. 32).

*Notes on habitat.* — The holotype was found under a stone in an oak-pine forest along a canyon bottom at 7200 feet.

*Pelmatellus stenolophoides* Bates

*Pelmatellus stenolophoides* Bates, 1882: 68. Lectotype (here selected) male, labelled: Type HT [circular label, ringed with red]; Capulalpam; Mexico Sallé Coll.; BCA Coll. I, 1 *Pelmatellus stenolophoides* Bates; *Pelmatellus stenolophoides* Bates [handwritten]. [BMNH].

Members of this species are characterized by: slightly transverse meshes of microsculpture on the elytra (Fig. 3b); and extensive development of scales at base of one or two basal spines in the internal sac (Fig. 25, 26). Externally, the deep and extended punctuation of the pronotal base permits ready identification (Fig. 11, 12). Pronotal length relative to the elytral length is greater than in other species (ratio more than 2.6).

*Pelmatellus stenolophoides stenolophoides* Bates

Specimens of this subspecies have a wider pronotum (Fig. 11), with more angulated hind angles. The three spines of the internal sac in all of the 30 males I dissected are average in position.

*Variation.* — Specimens west of the Rio Balsas are generally wider than those east of it.

*Distribution.* — Members of this species are found along the Sierra Madre Occidental, the Sierra Madre del Sur, and the Trans-volcanic Sierra (Fig. 33). One hundred and three males

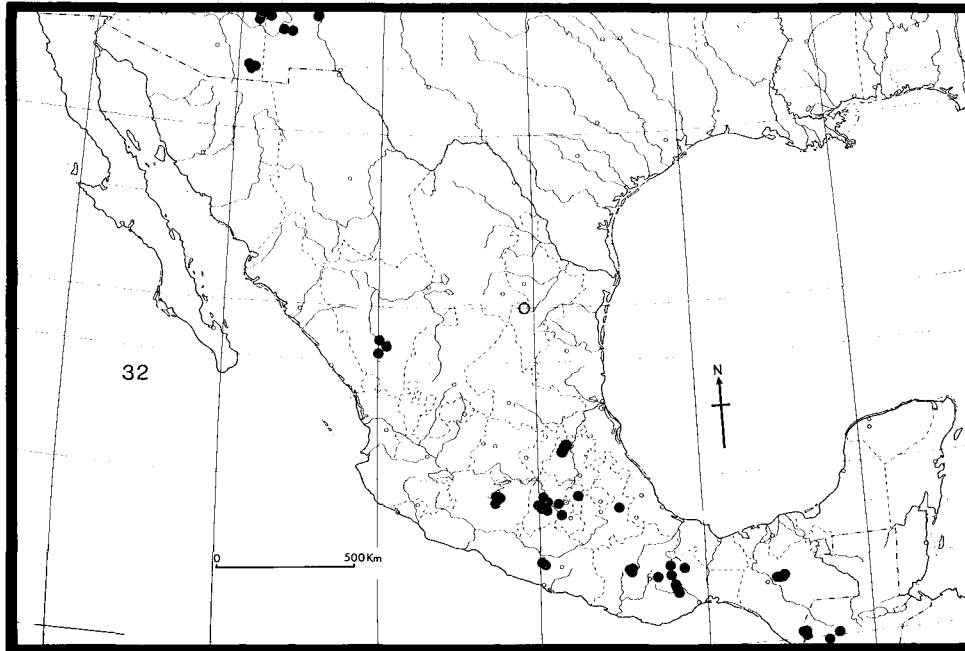


Fig. 32. Distribution of *Pematellus obtusus* Bates (black circle), and *Pematellus rotundicollis* new species (open circle).

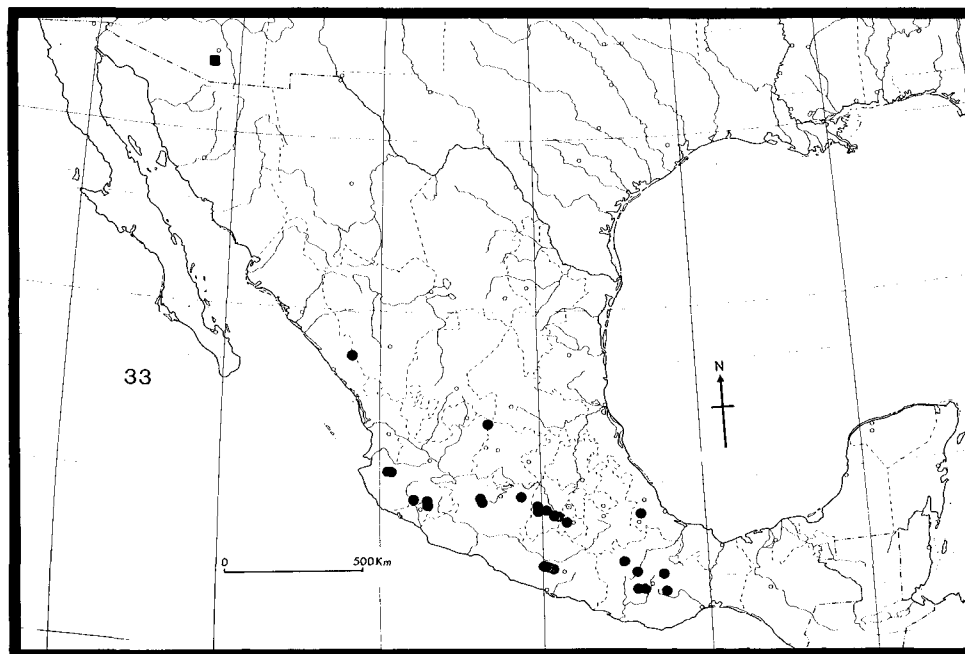


Fig. 33. Distribution of *Pematellus stenolophoides stenolophoides* Bates (circle) and *Pematellus stenolophoides parallelus* new subspecies (square).

and 85 females from the following states in Mexico were seen: Guerrero !, Jalisco !, Mexico !, Michoacan !, Morelos !, Oaxaca !, Veracruz !.

*Notes on habitat.* — Specimens were collected in open places near roadsides, agricultural fields, and near houses in small towns. Most were found in open places in the temperate oak-pine forests and a few were collected in cut-over temperate cloud forests and acacia grasslands. Adults were obtained between 5200 feet and 8000 feet from March to September; most were collected in August.

*Pelmatellus stenolophoides parallelus* new subspecies

*Type material.* — Holotype male labelled: Arizona, Mt. Lemmon, Catalina Mts. 9150 feet, 17-VI-12, J. R. Slevin. [CAS].

This subspecies is known from a single specimen which differs from all others in the following details: pronotum less transverse and hind angles less angulate (Fig. 12); elytra narrower and with parallel margins; and right spine in internal sac reduced to tiny scale (Fig. 26). Because none of the northernmost samples of *P. s. stenolophoides* in Mexico (Sinaloa) even suggests a trend toward this character combination, I describe this form as a new subspecies.

*Derivation of the specific epithet.* — From Latin referring to the parallel margins of the elytra.

*Distribution.* — This subspecies is known only from the type locality (Fig. 33).

*Pelmatellus vexator* Bates

*Pelmatellus vexator* Bates, 1882: 68. Lectotype (here selected) female, labelled: Type HT [circular label, ringed with red]; Totonicapam, 85-10500 ft. Champion; BCA Coll. I, 1 *Pelmatellus vexator* Bates [handwritten]. [BMNH].

Specimens of this macropterous species have: very transverse meshes of microsculpture on the elytra (Fig. 3c); pronotum with denticulate hind angles and fine to coarsely punctate posterior lateral impressions; and moderately wide microsculpture meshes on elytra (5-9 $\mu$ ). The elytra are ovate and resemble those of brachypterous specimens. The single known male of this species has one small apical spine on the internal sac of the male genitalia (Fig. 27).

*Distribution.* — This species is known only from the type locality in northern Guatemala (8500 to 10500 ft) (Fig. 34). I have seen only one male and one female from the type series.

*Pelmatellus nubicola* new species

*Type material.* — Holotype male, labelled: Mexico, Chiapas, Yerba Buena Hosp., 1.5 mi. n. Puebla Nuevo, 7200 feet, cloud forest, 12-VI-1972; G. E. Ball, P. A. Meyer collectors. [NMNH]. The other two specimens are paratypes and are deposited in UASM and IPNM.

This species is related to *P. vexator*; but individuals are brachypterous, and the pronotal lateral bead does not extend basally beyond the basal lateral impressions. (Fig. 14). Elytra more ovate because of narrowed shoulder and short metepisterna. Transverse meshes of elytral microsculpture very fine (4.5-5.2 $\mu$  in width). Internal sac with two large spines and an apical field of smaller spines (two specimens dissected).

*Derivation of the specific epithet.* — From Latin meaning living in clouds, referring to the cloud forest habitat of these beetles.

*Distribution.* — This species is known only from the type locality (Fig. 34).

*Notes on habitat.* — Specimens were found under stones and logs in shaded places in a

tropical cloud forest on a mountain top (7200 feet).

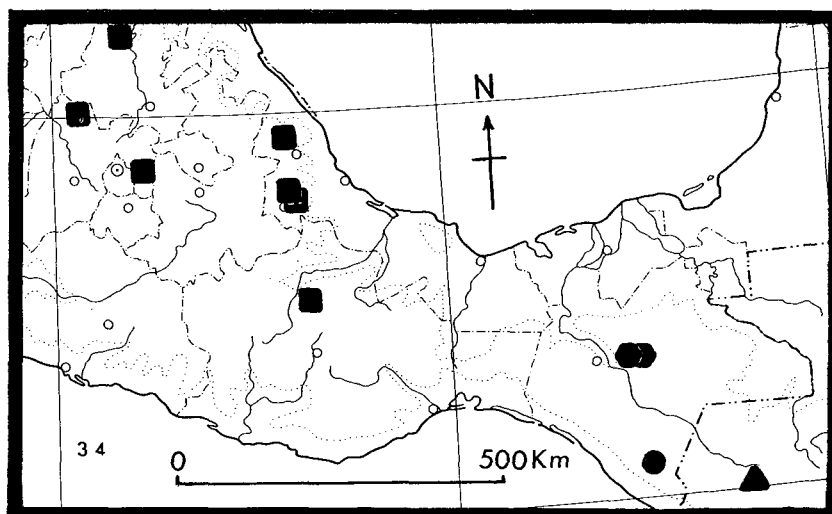


Fig. 34. Distribution of *Pelmatellus cyanescens* Bates (square), *Pelmatellus brachypterus* new species (hexagon), *Pelmatellus nubicola* new species (circle), and *Pelmatellus vexator* Bates (triangle).

#### *Pelmatellus brachypterus* new species

*Type material.* — Holotype male and allotype female, labelled: Mexico, Chiapas, Mt. Zontehuitz nr. San Cristobal las Casas, 9200 feet, 30-VIII-1965; G. E. Ball, D. R. Whitehead collectors. [NMNH]. The remaining three specimens are paratypes and are in UASM, IPNM and BMNH.

Specimens of this species share with those of *P. nubicola* short and ovate elytra and brachyptery, but the pronotal lateral bead is extended basally at least across the basal lateral impressions (Fig. 15). Meshes of elytral microsculpture narrow (width 4.8-5.7 $\mu$ ). Internal sac with left basal spine only (Fig. 28) (three males dissected).

*Derivation of the specific epithet.* — From Greek meaning short wings, referring to the very reduced hind wings.

*Distribution.* — This species is known only from neighbouring mountain localities in the Sierra Madre de Chiapas: Mt. Zontehuitz nr. San Cristobal de las Casas !; and 8.6 mi. e. San Cristobal, rte 190 ! (Fig. 34).

#### *Pelmatellus cyanescens* Bates

*Pelmatellus cyanescens* Bates, 1882: 68. Lectotype (here selected) male, labelled: Type HT [circular label, ringed with red]; Cordova; Mexico, Sallé Coll.; BCA Coll. I, 1 *Pelmatellus cyanescens* Bates; *Pelmatellus cyanescens* Bates [handwritten]. [BMNH].

Members of this species are recognized by the combination of: pronotum rather cordate with very prominent denticle on each hind angle, and straight or slightly sinuate lateral margin in basal half (Fig. 16); elytra long; hind wings well-developed; transverse meshes of micro-



sculpture on elytral disc moderately fine (5.8-6.1  $\mu$  in width); internal sac without apical spine (Fig. 29), right basal spine well-developed, left one present as field of long fine spines (six males dissected).

*Distribution.* — This species is known from central Mexico, and is rare and localized in the Sierra Madre Oriental, Trans-volcanic Sierra, and Sierra Madre de Oaxaca (Fig. 34). Seventeen males and five females from the following Mexican localities were seen: Hidalgo, Barranca de los Marmoles, 0.4 mi. s. San Vicente, Rte 85 !; Mexico, San Miguel; Mexico, Real del Monte; Oaxaca, 27.5 mi. s. Valle Nacional !; Veracruz, 10 mi. s. w. Cd. Mendoza !; Veracruz, Cofre de Perote, n. slope nr. Tembladera !; Veracruz, Cordova [= Cordoba].

*Notes on habitat.* — Specimens of this species were collected from June to October in open places in oak-pine forests and along roadsides at various altitudes from 5000 feet to 13500 feet.

## PHYLOGENY

Middle American species of *Pelmatellus* are closely related and therefore probably recently evolved. Most other Pelmatellina are found in South America, New Zealand, and Australia, but in these regions they are diverse and not well-known (G. E. Ball, pers. comm.). I have examined representatives of Australian and South American genera and believe that *Pelmatellus* probably originated in South America.

Figure 35 summarizes my views on the phylogeny of Middle and North American *Pelmatellus* and Table 1 explains characters and character states employed in construction of the figure. The ancestor of *Pelmatellus* can be tentatively characterized by the plesiotypic character states in Table 1.

Each character state is designated as plesiotypic or apotypic. A plesiotypic character state is one which was evolved relatively early in the evolution of a group while an apotypic character state is one which was evolved relatively recently. In my analysis I followed Hennig's principles as clearly outlined by Kavanaugh (1972). For each character I determined if the various states shared by different taxa are homologous, convergent or parallel. If homologous, I determined the position of each state in its transformation series. If the position of a state was not clear, I correlated it with other series of transformation or based it on chorological evidence. Monophyletic taxa were recognized only where synapotypy for one or more characters was recognized.

I considered the following character states as plesiotypic because they are widespread in the Pelmatellina: one setigerous puncture on stria two of elytron; spongy vestiture on ventral surfaces of middle tarsal articles; hind wings fully developed; metepisterna long; median lobe apex in lateral view without hook; pronotal lateral bead extended over most of base; and elytral intervals with transverse microsculpture meshes. Other states considered plesiotypic because they are commonest among species of *Pelmatellus* are: dark testaceous body and testaceous appendages; base of spines in internal sac with few scales; each spine of one spike; scales not shaped like a spine; pronotum transverse, hind angles denticulate, and the basal lateral impressions punctate. A character state was considered plesiotypic after being correlated with plesiotypic states in better understood transformation series (e.g. narrow male tarsi and wide female tarsi relative to the not-hooked apex of the median lobe). Some apotypic states evolved in parallel: pronotal basal impressions impunctate (appears independently twice); pronotal hind angles without denticle (three times); and brachyptery and reduced metepisterna (three times).

Table 1. Plesiotypic and apotypic character states used in Fig. 35.

| No. | Character                             | Character State                  |                                     |
|-----|---------------------------------------|----------------------------------|-------------------------------------|
|     |                                       | Plesiotypic                      | Apotypic                            |
| 1.  | Puncture of second elytral stria      | Present                          | Absent                              |
| 2.  | Mid-tarsal vestiture of male          | Present                          | Absent                              |
| 3.  | Hind wings                            | Present                          | Absent                              |
| 4.  | Abdomen                               | Normal                           | Short                               |
| 5.  | Median lobe apex                      | Simple                           | Hooked                              |
| 6.  | Male tarsi                            | Normal                           | Very wide                           |
| 7.  | Female tarsi                          | Normal                           | Narrower                            |
| 8.  | Pronotal hind angle denticle          | Present                          | Absent                              |
| 9.  | Leg color                             | Testaceous                       | Infusate                            |
| 10. | Isodiametric meshes of microsculpture | On first elytral interval only   | On more than one interval           |
| 11. | Punctuation on pronotal base          | Well-developed                   | Absent                              |
| 12. | Isodiametric meshes of microsculpture | Two first elytral intervals only | More widespread                     |
| 13. | Elytral meshes of microsculpture      | Very transverse                  | Slightly transverse                 |
| 14. | Basal spines in internal sac          | With few scales                  | With many scales                    |
| 15. | Pronotal hind angle denticle          | Normal                           | Very prominent                      |
| 16. | Pronotum ratio                        | Wide                             | Narrower                            |
| 17. | Basal bead of pronotum                | Complete                         | Interrupted                         |
| 18. | Apical spine of internal sac          | Single                           | Subdivided into many smaller spines |

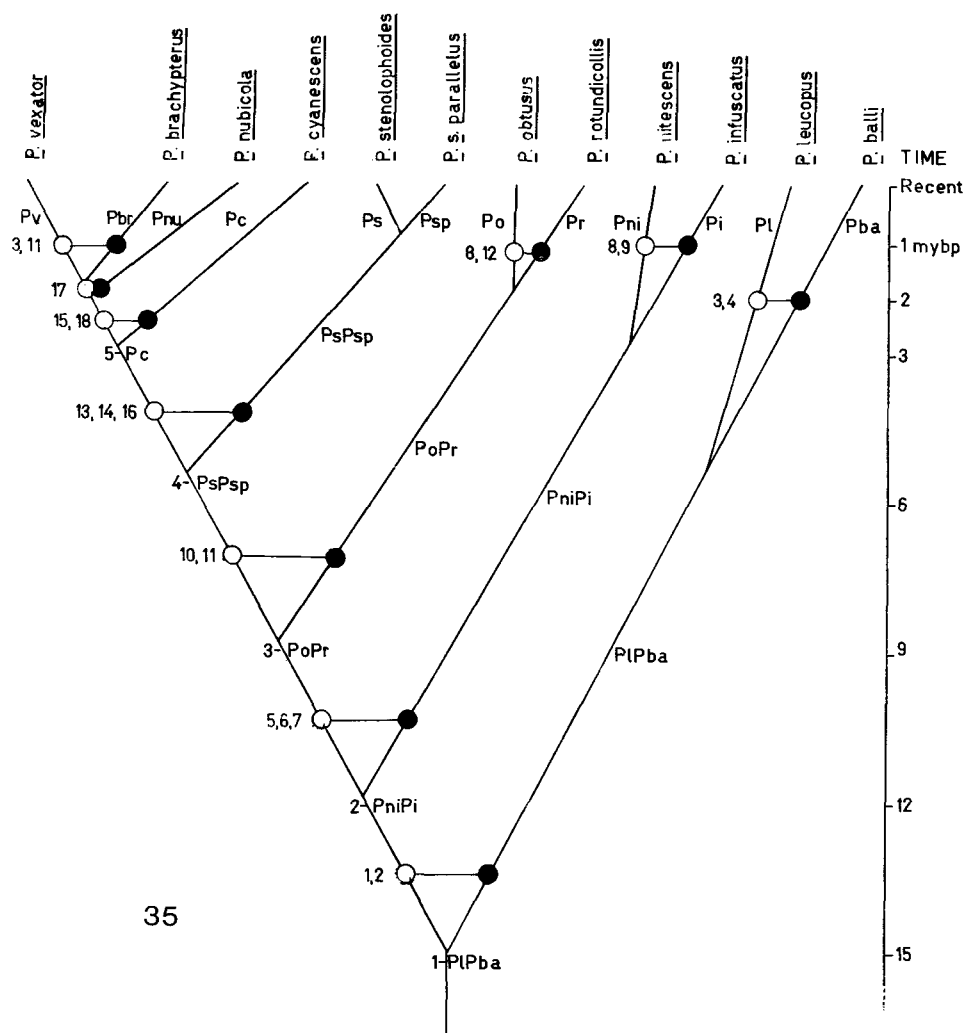


Fig. 35. Hypothetical phylogeny for species of North and Middle American species of the genus *Pelmatellus*. Note that the open circles represent plesiotypic states, and the black ones the apotypic states. The number near each state can be referred to in Table 1. Ancestral forms were given symbolic names derived from abbreviated names of extant species. mybp = million years before present.

## ZOOGEOGRAPHY

Before elucidating the past history of the genus in Middle and North America, it is important to summarize facts about geographical ranges, phenology and habitat requirements.

*Geographical range.* — Members of *Pelmatellus* are found from Costa Rica in southern Middle America to southwestern United States in North America (not having seen the few

Ecuadorian species described by Bates, I feel uncertain about their generic identity). The ranges of most species are not continuous because populations are restricted to highland areas (usually above 5000 feet). I recognized five regions of highlands: Costa Rica, Guatemala, Mexico excluding the northern part of the Sierra Madre Oriental, sub-Mogollon-southern Rocky mountains and Cerro de Potosi. The last named region is part of the Sierra Madre Oriental but is isolated by arid country.

*Habitat requirements.* — The beetles generally live between 5000 and 9000 feet, but some occur at lower elevations in protected ravines (2900 feet) or at very high altitude (11000 feet). Two main ecological groups of beetles can be defined: those living in association with the oak-pine forest (in the forest litter or in natural or artificial openings), and those restricted to tropical cloud forests. Since most species live in a wide range of altitudes, there is no evidence of altitudinal segregation. One form of *P. nitescens* north of the Isthmus of Tehuantepec occurs generally at lower altitude than any other species, but there is still a wide overlapping of altitudinal range. Adults are found in the same period from March to November, and are probably not segregated in time.

*Sympatry, parapatry, and allopatry.* — Extant sister species are clearly allopatric. Occurrence in the same locality and habitat (sympatry) has been observed for the following more distantly related species: *P. obtusus* and *P. nitescens* (Volcan Tacaná, Chiapas); *P. obtusus* and *P. s. stenolophoides* (many localities in the following Mexican states: Chiapas, Oaxaca, Guerrero, Michoacan, and Mexico); *P. obtusus* and *P. cyanescens* (Barranca de los Marmoles, Hidalgo). *P. balli* relative to *P. nitescens* and *P. obtusus* is parapatric, with samples of the former having been collected within 100 meters of the latter two species. I suspect that *P. infuscatus* is parapatric to *P. s. stenolophoides*, and *P. obtusus* is apparently restricted to forest litter while *P. infuscatus* and *P. s. stenolophoides* are restricted to open habitats.

*Power of dispersal.* — Macropterous specimens probably can fly. However, fairly direct evidence is available only for *P. s. stenolophoides*, specimens of which have been captured at night at black light. I suspect that other macropterous forms are good flyers. The known ranges of most macropterous species are much more extensive than are the known ranges of most brachypterous ones. *A. priori*, one would expect species whose members can fly to be more widespread than species whose members cannot fly (see also Ball and Nègre, 1972). Also, species represented by markedly similar populations on both sides of the Isthmus of Tehuantepec suggest that this barrier was crossed recently. The most likely way that temperate-adapted stocks would cross the tropical lowlands is by flight (see also Ball, 1970).

*Historical zoogeography.* — The genus *Pelmatellus* is probably a derivative of the South American Andean fauna, an element not well-represented in Middle America. The absence of lowland species of *Pelmatellus* suggests that invasion of Middle America was by flight of a montane, temperate-adapted ancestor, which probably crossed a narrow sea gap and tropical lowlands of Panama. The sea barrier between South and Middle America persisted until at least late Pliocene (Herskovitz, 1969). Figure 36 summarizes my views on the zoogeographical events of Middle and North American *Pelmatellus*.

Members of the ancestral stock probably made short stops in tropical lowland habitats for rest and feeding. This mode of dispersal is suggested by analogy with behaviour of some Canadian carabids of the genus *Elaphrus* which I have observed flying away in a matter of a few hours after landing in a slightly unsuitable habitat. The sea gap was probably not too difficult to cross as it was narrow during the Miocene (Herskovitz, 1966), when the *Pelmatellus* stock probably dispersed northward.

The time at which the gap between the northern Colombian mountains and Costa Rican highlands was crossed is not certain. However, the estimated rate of speciation would suggest middle Miocene rather than late Pliocene when the sea gap was closed between the two

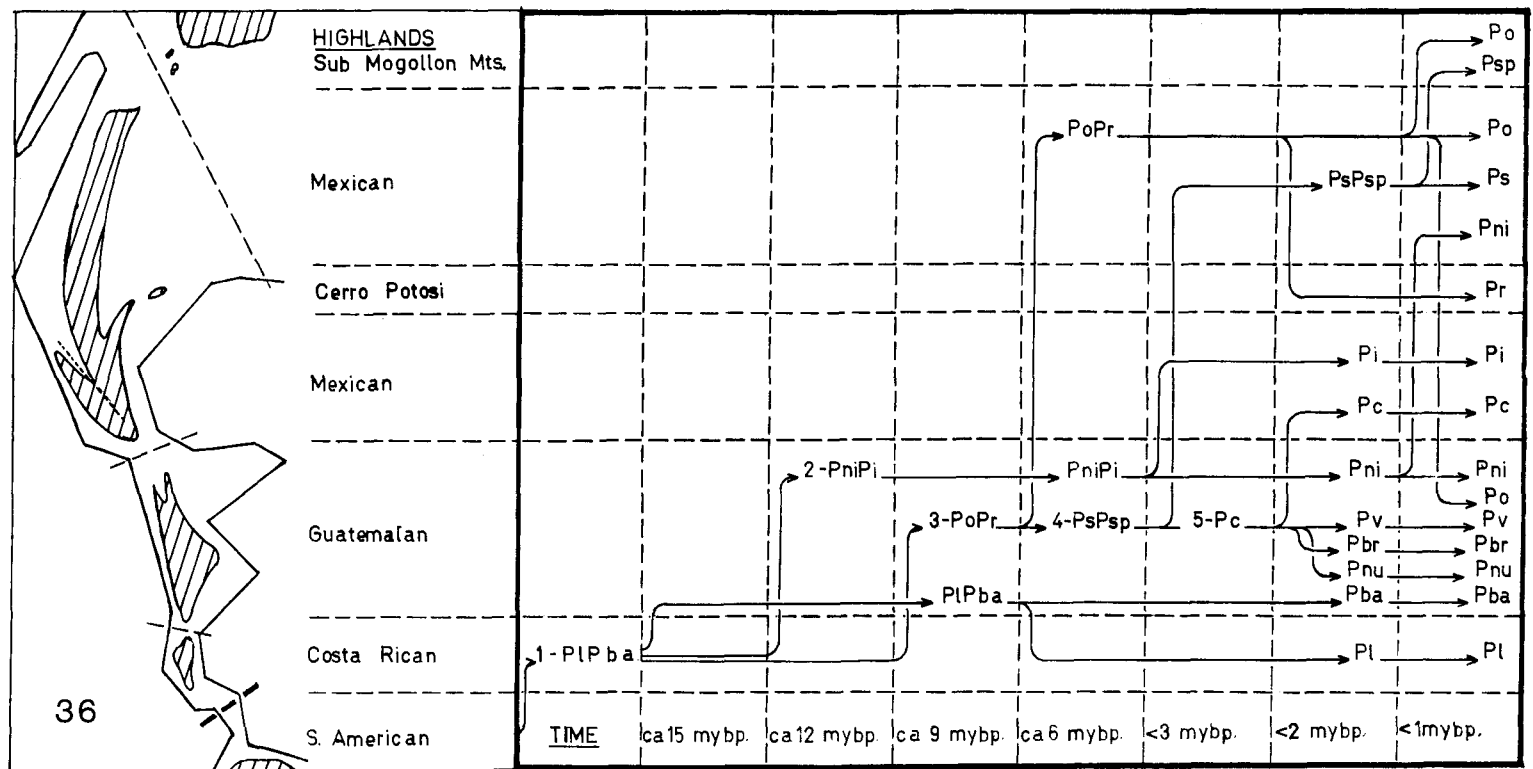


Fig. 36. Summary of probable zoogeographical events during evolution of genus *Pelmatellus* in Middle and North America. The symbolic name of the ancestral form is derived by juxtaposition of abbreviated names of extant species, and their phyletic position is shown in Fig. 35. mybp = million years before present.

continents. Whitehead (1972) in postulating three million years on average between each dichotomy for continental fauna showed that it fitted geological events not only in the group he studied (*Schizogenius*) but even for *Brachinus* and *Evarthrus*. G. E. Ball and J. Nègre in their revision of the Nearctic *Calathus* (1972) arrived at a similar conclusion. Thus, in this study, I subtracted the non-continental species and counted five dichotomies from the presumed ancestor to the extant species. This would suggest about 15 million years. This estimate correlates well with the crossing of the sea gap by mammals (Herskovitz, 1969). Moreover, this period coincides well with the arrival of numerous Nearctic elements (Ball, 1972) in the Mexican highlands, suggesting probably the existence of unoccupied niches perhaps because of the general cooling trends in process at the time (Ball, 1972).

The great trek could have been achieved in numerous ways. I think the following explanation is the most plausible in the light of the present knowledge of these beetles and general information is now available on carabid biology. During rains, mountain torrents chewed banks, and carried numerous beetles from the highlands. Many of these died; a few managed to survive on floating debris. As the tropical lowlands were unsuitable, many flew away, some toward Middle America. Probably one or a few individuals reached the Costa Rican highlands and became established. I cannot say if this was the only invasion as we know nothing of the Colombian and Venezuelan fauna, but on the basis of parsimony, I assume that there was only one invasion.

Speciation of Middle and North American species of *Pelmatellus* probably started in Costa Rica. The past history is summarized in Fig. 36. After successfully colonizing the Costa Rican highlands, some individuals reached the Guatemalan highlands. This isolated population was the common ancestor for the species of the subgenus *Thenarellus* (1-PIPba). Later, another invader arrived on the Guatemalan highlands and became the ancestor of the *nitescens* group (2-PniPi). Finally, another invasion came from the Costa Rican highlands. These last invaders comprised the ancestral stock of all other *Pelmatellus* (the *vexator* group 3-PoPr). Meanwhile, some populations of the *Thenarellus* group shifted their ranges to include the Costa Rican highlands and in time evolved into *P. leucopus* (P l) while the remaining ones in the Guatemalan highlands evolved as *P. balli* (Pba). A great barrier, the Isthmus of Tehuantepec, was also crossed during that period by a member of the *vexator* group. The ancestor of this successful colonizer gave rise to the proto-*P. obtusus* (PoPr) on the Mexican highlands. Another invasion by a member of the *vexator* group (4-PsPsp) of the Mexican highlands produced *P. stenolophoides* (Ps). Thereafter, specimens of the *nitescens* group invaded the Mexican highlands and gave rise to *P. infuscatus* (Pi) which specialized in living in forest litter habitats, probably to avoid competition with the already established species of *Pelmatellus*. The Isthmus was crossed again by specimens of the *vexator* group (5-Pc) resulting in *P. cyanescens*. As there were many species already in the Guatemalan highlands, competition among them probably forced some populations to invade unoccupied niches such as those in cloud forests. This resulted in the evolution of *P. nubicola* (Pnu), *P. brachypterus* (Pbr), and *P. vexator* (Pv). During that period, members of the proto-*P. obtusus* group invaded the area of Cerro Potosi and evolved into *P. rotundicollis* (Pr). (This region has already yielded several endemics: *Carabus hendrichsi* Bolívar, Rotger and Coronado, *Calathus potosi* Ball and Nègre, and one undescribed species of *Dicaelus* (Ball, pers. comm.)). The source of the invasion is not clear as the three other species suggest invasion from the north, the west, and the Trans-volcanic Sierra. Martin (1958) suggests a northeast Madrean and Trans-volcanic route for cold-blooded vertebrates. The former is more probable, but I do not have data to prove or disprove any route. Meanwhile, the proto-*P. obtusus* evolved into *P. obtusus* (Po).

During recent glacial periods, the effectiveness of lowland barriers was reduced as semi-desert areas became narrower due to the development of oak-pine forests, with the lowland

tropical forests being at lower elevations than they are now. Thus *P. obtusus* and *P. stenolophoides* crossed the gap between the Mexican and sub-Mogollon mountains of Arizona. The northern population of *P. stenolophoides* became sufficiently differentiated to warrant sub-specific rank as *P. s. parallelus* (Psp), but *P. obtusus* apparently remained the same. Further south, *P. obtusus* crossed from the Mexican Highlands to the Guatemalan highlands, and today both populations are similar. Finally, *P. nitescens* invaded the Mexican highlands from the Guatemalan highlands. This last invasion produced a form which remained at lower altitude, probably to avoid competition with other *Pelmatellus*. Thus, speciation proceeded through isolation of populations on isolated highlands. The ecological barriers were mainly tropical lowlands, and to some extent semi-desert and desert areas in the north.

This postulated scheme of evolution and dispersal is probably correct for the five wide-spread species. Bates found four of these, but Ball in 1967 found the fifth. Of the five species described here, one was found by Rogers a century ago, two by Ball in 1967, and two more by Ball in 1972. Most of the Costa Rican and Guatemalan highlands (except in Chiapas) were little investigated. Isolated mountains in the northeast and cloud forests may contain additional undescribed forms. Finally, northern Mexico was not adequately sampled. Thus, this account of the past history is a first attempt to explain a series of events of probably greater complexity than suggested by the presently available data.

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