

# TAXONOMY AND PHYLOGENY OF THE NEOTROPICAL GENUS *BIBIONELLUS* (DIPTERA, BIBIONIDAE)<sup>1</sup>

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## ABSTRACT

The four known species of the Neotropical genus *Bibionellus* Edwards are redescribed, *B. aczeli* Hardy, *B. barrettoi* Lane & Forattini, *B. paulistensis* Lane & Forattini, and *B. tibialis* Edwards. Head, antenna, thorax, legs, wing, halter, female and male terminalia are illustrated. A phylogeny for the species is proposed, based on 20 transformation series, with a total of 22 characters, mainly from male terminalia. No homoplastic conditions were found. Autapomorphies for *B. aczeli* and *B. tibialis* were found. *B. barrettoi* and *B. paulistensis* still remain with undiscovered autapomorphies and the names may not apply to historical entities. The monophyly of the genus is confirmed, based on eight synapomorphies. *B. aczeli* is considered the sister group of the remaining species of the genus. *B. barrettoi* is considered the sister group of *B. paulistensis* + *B. tibialis*. The age of origin attributed to the ancestral stem of *Bibionellus*, possibly Late Jurassic or Early Cretaceous, and the small number of species known in the region suggest that an unadvised biogeographical analysis of the biological area cladogram could generate false biogeographical components.

KEYWORDS. Diptera, Bibionidae, Phylogeny, *Bibionellus*, Neotropical.

## INTRODUCTION

The genus *Bibionellus* was erected by EDWARDS (1935) to include *B. tibialis* Edwards. LANE & FORATTINI (1948) added *B. barrettoi* and *B. paulistensis*, and an identification key for the three species known at that time. HARDY (1951) later described *B. aczeli*, improving the key for the genus.

In the Bibionidae system, *Bibionellus* has been included in the Bibioninae by most authors (EDWARDS, 1935; HARDY, 1945, 1951, 1959, 1966; LANE & FORATTINI, 1948). PINTO (1992), in a phylogenetic analysis of the family, confirmed the

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monophyly of the Bibioninae and presented the phylogenetic relationships among the members of the Bibioninae: (*Bibio* (*Bibionellus* (*Bibiodes* + *Enicoscolus*))). Still according to PINTO (1992), the phylogenetic relationships among the Bibionidae can be represented as follows: (Hesperinae (Penthetriinae (Pleciinae + Bibioninae))). The first three subfamilies are monotypic.

*Bibio* Linnaeus, *Plecia* Wiedemann, and *Dilophus* Meigen have wide distribution over the world, although *Plecia* is mainly known from fossils in the Holarctic region. *Hesperinus* Walker is restricted to the Holarctic region, and *Penthetria* Meigen has a similar distribution, except for some few Neotropical and Oriental species. *Bibiodes* Coquillett is restricted to southern North America, while *Enicoscolus* Hardy is known to occur only in the Australian region and southwestern North America. *Bibionellus* is restricted to central and southeastern South America. Although there is rather extensive fossil collections of Bibionidae, no fossils are known of *Bibionellus* or *Enicoscolus* Hardy (see EVENHUIS, 1994).

The purpose of this paper is to review the known species of *Bibionellus* and to establish a phylogeny for the species of the genus based on examination of type-material and on additional specimens collected in South America.

#### MATERIAL AND METHODS

The material analyzed is deposited in the Museu de Zoologia, Universidade de São Paulo, São Paulo, SP (MZSP); Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras, Ribeirão Preto/USP, Ribeirão Preto, SP (DBRP), Brazil; and Instituto Fundación Miguel Lillo, Tucumán (IFML), Argentina. Male and female specimens of each species were dissected and prepared on permanent slide mountings for detailed examination of sclerite morphology.

The phylogenetic analysis was made following the methodology proposed by HENNIG (1966) using non-numerical methods (AMORIM, 1994). Numerical methods were not employed since there were not incongruence in the data matrix. The group+ artifact to name is employed to refer to inclusive taxa in sequenced phylogenetic classifications (AMORIM, 1982).

#### *Bibionellus* Edwards

*Bibionellus* EDWARDS, 1935:19. Type species, *Bibionellus tibialis* Edwards, 1935 (by original designation).

Total length, between 3.0 and 4.0 mm, females (fig. 2) slightly stronger than males (fig. 1), but not too longer. On the genus ground plan, males are most certainly dark reddish brown; females, as in other bibionid genera, present lighter, yellowish brown colors than males, especially on head, thorax, and legs.

Setae quite scarce on head (figs. 5-7), except on antenna and palpus. Flagellomeres with a rather regular crown of setae. Eyes always bare of setae between ommatidia. A pair of rows of rather large setae on scutum. As in all Bibionidae except *Hesperinus*, there is sexual dimorphism, particularly on the shape of the head. Females show head rather elliptical with strongly dichoptic small eyes placed fronto-laterally (figs. 5, 7). Males holoptic, with eyes largely developed, giving a rounded shape to the head (fig. 6). A slender, sclerotized area separates larger ommatidia dorsally from smaller ommatidia ventrally on each eye of the males, a synapomorphy of the Bibioninae. Ocelli placed on a projected

vertical protuberance, like other Penthetriinae<sup>+</sup>. Maxillary palpus with four articles, as in the ground plan of the family. Antenna considerably reduced, shorter than the palpus, placed at the ventro-anterior margin of the eyes. The flagellomeres are wider than long, except the first, and all have a short basal peduncle; first flagellomere longer than the remaining articles (figs. 3, 4).

Thoracic sclerites rather similar to those of other Bibionidae, although scarcely pubescent (fig. 8). Pronotum setose laterally. Epimeron I quite well developed. Katepisternum slightly higher than in other genera; suture between katepisternum and anepisternum anteriorly incomplete. Epimeron II high. Episternum III with an unusual group of conspicuous setae ventral to the spiracle. Halter considerably developed (fig. 11). Wing venation (figs. 9, 10) similar to that of *Bibio*, with m-cu moved to an anterior position, usually in contact with the base of  $M_2$ , but in some cases attached right to the fork or to the end of  $M_{1+2}$ . r-m length variable, sometimes shorter, but others larger than the base of Rs. Sc incomplete. C typically well developed beyond  $R_{4+5}$ , extending at least half way to  $M_1$ , an apomorphic condition at this level.  $A_1$  never complete, but always present and well produced on its basal half. Alar stigma obvious.

Anterior coxa slightly enlarged, as in other Bibioninae, more than half the anterior femur length (fig. 12); anterior femur strong, with a distal inner projection bearing a row of teeth in *Bibionellus* (fig. 13); anterior tibia with an additional inner protuberance (fig. 12), synapomorphic for the genus, in addition to the long mucron, present in *Bibio* and *Bibiodes*; tibial spur short but strong (fig. 14). First tarsomeres about twice the length of the remaining tarsomeres. Pulvilli scarcely sclerotized (fig. 18). Mid leg (figs. 15, 16) without any striking differentiation. Hind femur and tibia with the typical distal half enlarged (fig. 17), as seen in other Bibioninae, but more conspicuous than seen in *Bibio*, *Bibiodes*, and *Enicoscolus*. Mid and hind apical tibial spurs strong (figs. 16, 17). Males with more numerous setae on abdominal tergites than the female.

Female terminalia of *Bibionellus*, as in other Diptera, with sternite 8 fused with the short gonapophyses 8, resulting in a single plate with a mesal posterior incision and a pair of lobes projecting over sternite 9, which becomes an internal sclerite (figs. 19-21). Behind the lobes is the labium (projecting from sternite 9) and the postgenital plate, the gonopore between them. Genital furca rather long and wide, as in other Bibionidae, scarcely sclerotized, hard to visualize. Sternite 10 poorly sclerotized, although well developed, triangular-shaped, covered with microtrichia. Tergite 8 well developed, with setae and wider than long. Tergite 9 considerably short, possibly fused to tergite 10, which is absent as an independent plate. As the remaining Pleciinae<sup>+</sup>, cerci 1-articulated.

Gonocoxites in the male terminalia fused to sternite 9, as in other Bibionidae, forming a synsternogonocoxite. Gonocoxites with a dorsal "gonocoxal bridge" also found in other Bibionomorpha. In the ground plan of the Bibionidae, the gonocoxites are produced beyond sternite 9 posterior margin, feature still found in *Bibio* and *Bibiodes* (the males of *Enicoscolus* are unknown). In *Bibionellus*, particularly, sternite 9 is produced posteriorly between the gonocoxites, so a single ventral plate is present on the terminalia to which the gonostyles distally articulate. Meso-posterior margin of the synsternogonocoxite produced to form a

structure maybe improperly named “mesosome” by LANE & FORATTINI (1948). This plate presents a mesal projection with a pair of lateral “wings”, separated from it by a furrow on each side. The surface of this plate is covered by macrotrichia modified in small spines, except laterally where the typical macrotrichia are maintained. Gonostyles considerably elongated; its base is latero-dorsal to the synsternogonocoxite plate, with a strong mesal fold, then projecting posteriorly. Their apex is strongly sclerotized and it is usually possible to visualize an inner apical tooth on each gonostyle; scattered setae cover its surface. Behind the synsternogonocoxite is the aedeagus, not tubular, but rather a slender, elongated plate with long microtrichia distally. A pair of long, curved parameral plates present laterally to the aedeagal plate; parameres quite larger basally, slender distally, the pointed apex oftenly arising from the terminalia. Gonocoxal bridge in a rather anterior position, extending anteriorly on a pair of gonocoxal apodemes. Tergite 9 twice wider than long, shorter than the synsternogonocoxite, with a quite concave anterior margin and a pair of lobes on posterior margin. Cerci 1-articulated, rectangular, projecting from the posterior margin of tergite 9. A light sternite 10 is sometimes visible.

The distribution of the *Bibionellus* species is presented in fig. 44.

### ***Bibionellus aczeli* Hardy**

(Figs. 5, 11-18, 22-27, 44,45)

*Bibionellus aczeli* HARDY, 1951:345, figs. 1a-c. Type locality: Argentina, Jujuy, Palpala. Types, IFML.

Material examined. ARGENTINA, **Tucumán**, San Pedro de Calalao, 2♂, I.1953, Duret col., E. Hardy det. (MZSP); 3♂, 1♀, same locality, except II.1949, M. Arnau col. (IFML).

**Redescription.** Male (figs. 11-18): entirely dark reddish brown with brown macrotrichia. Ocelli shining black. Wing slightly smoky and alar stigma dark. Terminalia as in figs. 22-27.

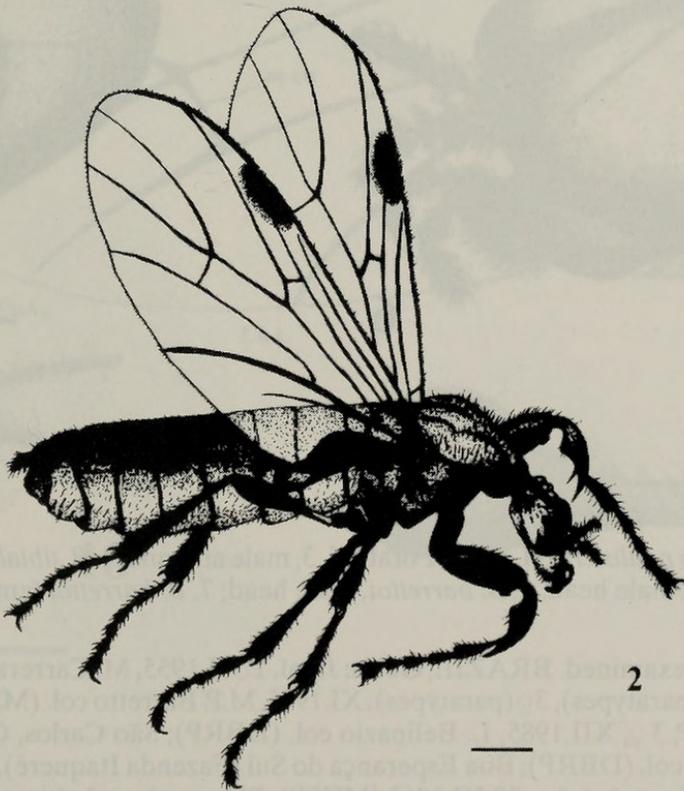
Female (fig. 5): head light brown. Ocelli shining jet black. Thorax entirely light brown, with yellowish macrotrichia. Legs light brown, except for the tarsi, dark brown. Abdomen dark brown with light brown pilosity. Otherwise as males.

**Comments.** The female of *B. aczeli* was unknown to HARDY (1951). Body general coloration is darker than the female of any other *Bibionellus* species. *B. aczeli* can be readily separated from other species in the genus by the entirely dark color of the males and by the shape of the “mesosome” (fig. 24), which is short and with rather wide lateral projections. The synsternogonocoxite (fig. 22) has a median rift separating two lobose areas on the posterior margin. The holotype of this species was not seen, but the specimens we examined match very closely that illustrated by HARDY (1951). Moreover, the material studied was collected near the type locality.

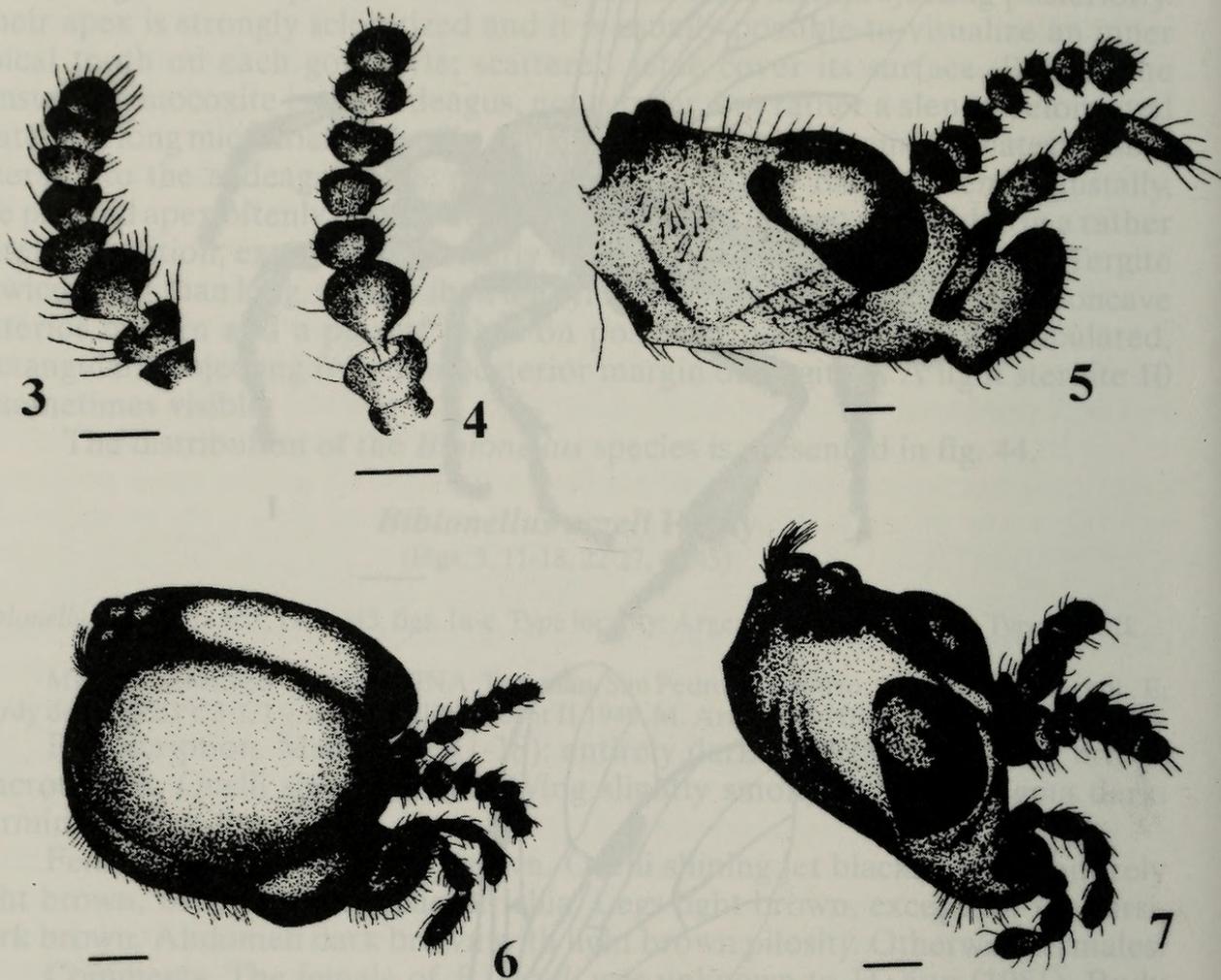
### ***Bibionellus barretto* Lane & Forattini**

(Figs. 1-2, 6-10, 19-21, 28-32, 44,45)

*Bibionellus barretto* LANE & FORATTINI, 1948:569. Type locality: Brazil, State of Goiás, Corumbá. Types: MZSP. HARDY, 1951:344.



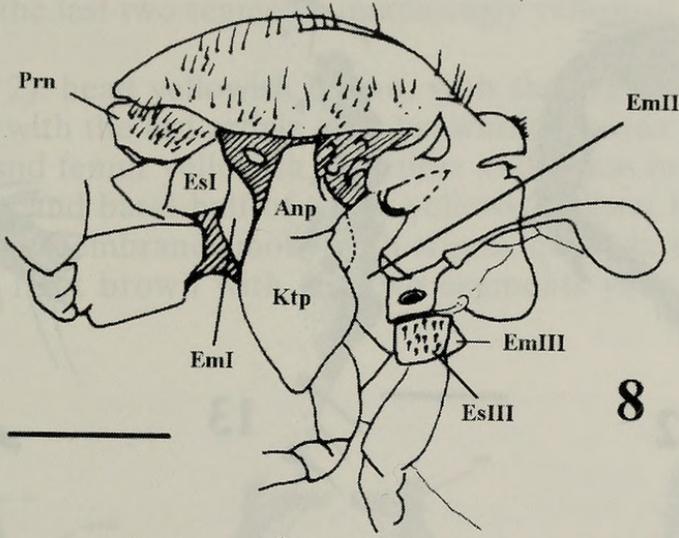
Figs. 1-2. *Bibionellus barrettoii* Lane & Forattini, habitus. 1, male paratype; 2, female paratype. Scales, 0.5 mm.



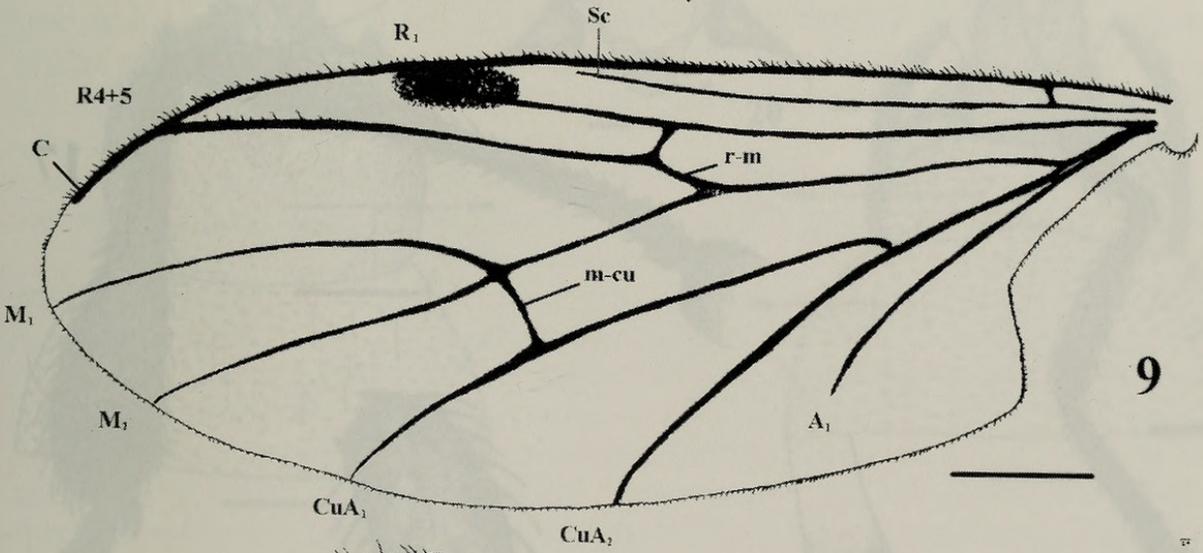
Figs. 3-7. *Bibionellus paulistensis* Lane & Forattini. 3, male antenna; 4, *B. tibialis* Edwards, male antenna; 5, *B. aczeli* Hardy, female head; 6, *B. barrettoii*, male head; 7, *B. barrettoii* female head. Scales, 0.1 mm

Material examined. BRAZIL, **Goiás**: Jataí, 1 ♂, I.1955, M. Carrera *et al.* (MZSP); Corumbá, 5 ♂ (holotype and 4 paratypes), 3 ♀ (paratypes), XI.1945, M.P. Barretto col. (MZSP). **São Paulo**: Ribeirão Preto, Campus USP, 3 ♀, XII.1985, L. Belinazio col. (DBRP); São Carlos, Campus UFSCar, 1 ♂, 1 ♀, 23.V.1991, Molfetta col. (DBRP); Boa Esperança do Sul (Fazenda Itaquerê), 1 ♀, 26.XI.1963, K. Lenko col. (MZSP); Tabatinga, 1 ♂, 1 ♀, 29.XI.1963 (MZSP); Pitangueiras, 1 ♂ paratype, X.1943, F. Lane col. (MZSP); Teodoro Sampaio, 1 ♂, 2 ♀, Malaise trap, XI.1977, M. Alvarenga col. (DBRP).

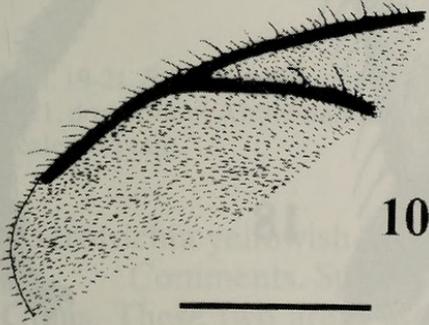
Redescription. Male (fig. 1): head reddish brown, ocelli shining jet black



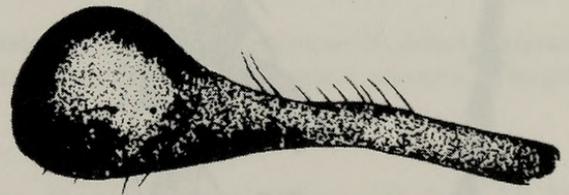
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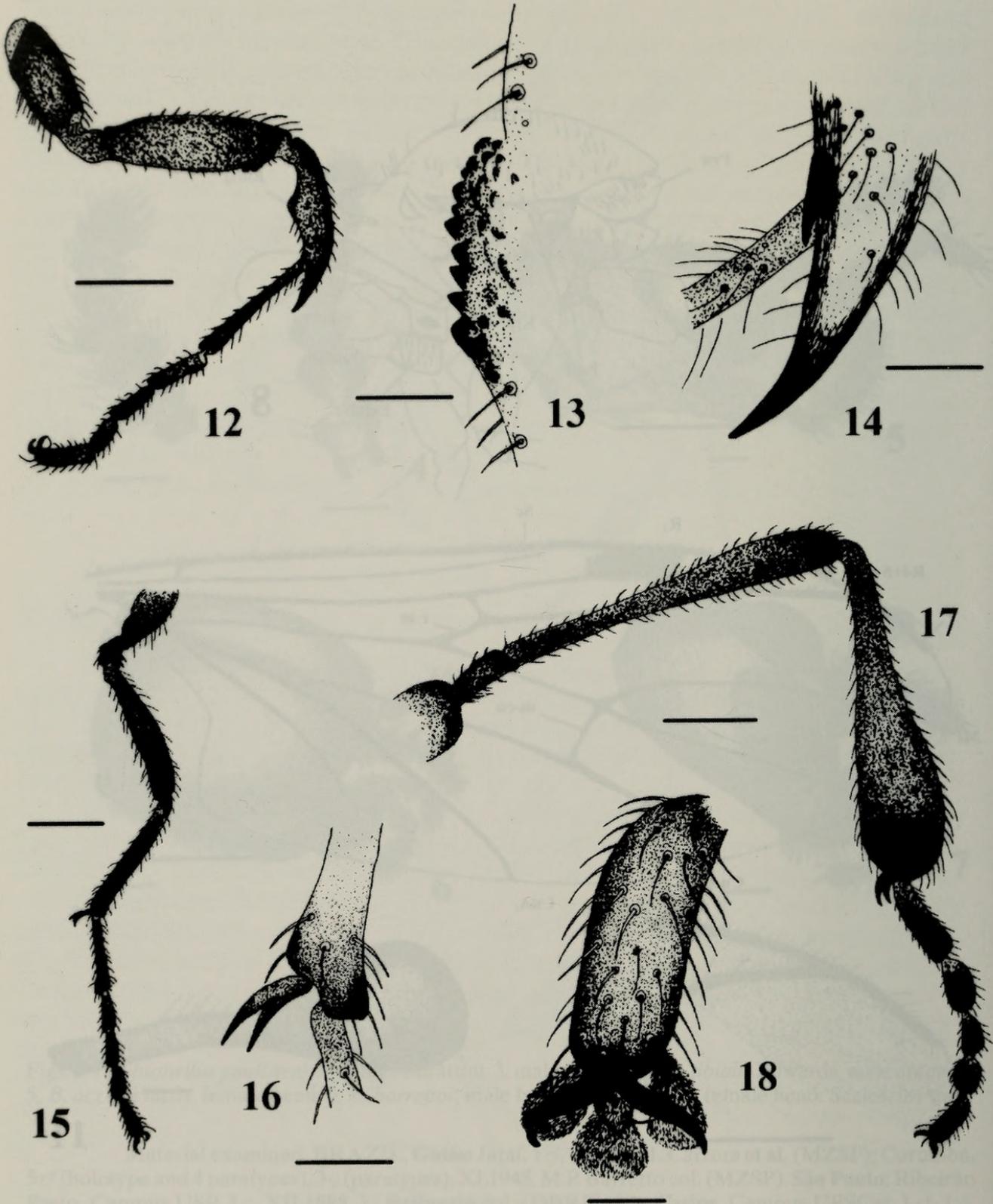


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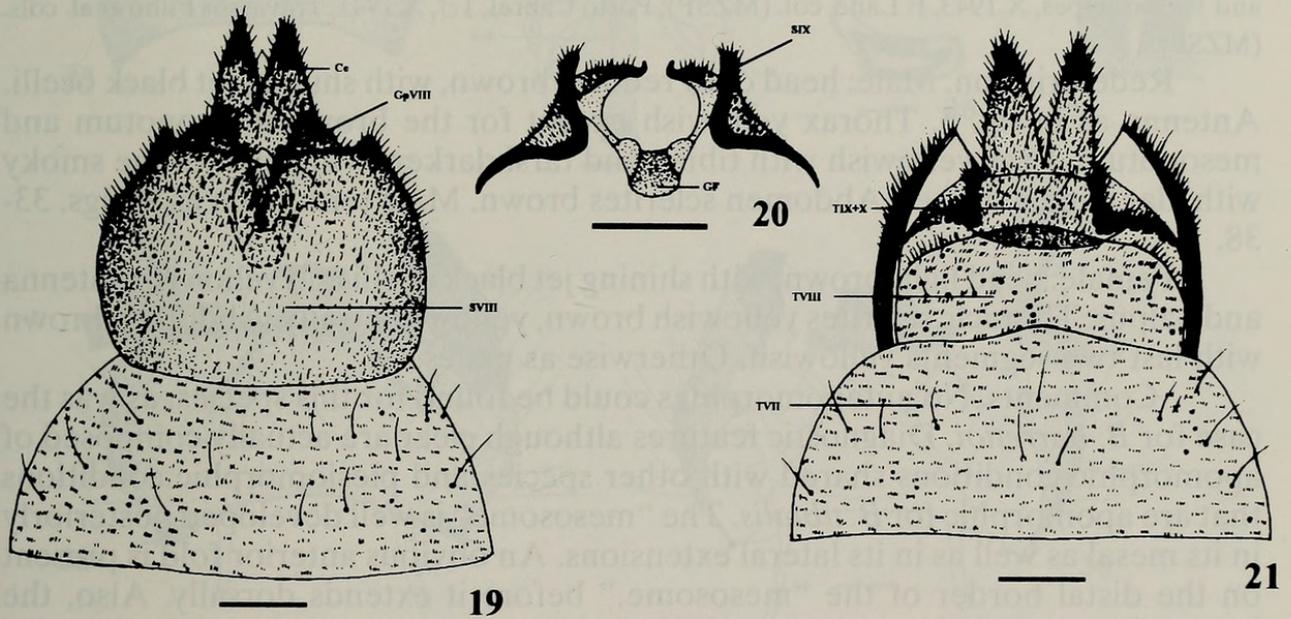
Figs. 8-11. *Bibionellus barrettoii* Lane & Forattini, female: 8, thorax, left view; 9, wing; 10, detail of wing apex; 11, *B. aczeli* Hardy, halter. Abbreviations: Anp, anepisternum; Em, epimeron; Es, espisternum; Ktp, katepisternum; Prn, pronotum. Scales: 0.5 mm, figs. 8-10; 0.1 mm, fig. 11.



Figs. 12-18. *Bibionellus aczeli* Hardy, male: 12, front leg; 13, detail of modified area of front femur; 14, detail of front tibial apex; 15, mid leg; 16, detail of mid tibial spurs; 17, hind leg; 18, hind last tarsomere. Scales: 0.5 mm, figs. 12, 15, 17; 0.125 mm, figs. 13, 14, 16, 18.

(fig. 6). Antennae brownish yellow with yellowish macrotrichia. Pleural thoracic sclerites and scutellum dark brown, scutum brownish yellow with yellowish setae. Fore tibia and tarsus lighter than the femur and coxa. Distal half of mid and hind tibia and tarsus darker than the coxae and femora. Wing (figs. 9-10). Abdomen sclerites brownish, the last two segments increasingly yellowish. Male terminalia as in figs. 28-32.

Female (fig. 2): head yellowish brown, with shining black ocelli (fig. 7). Antenna yellowish with the last article light brownish. Thorax (fig. 8) yellowish brown. Fore coxa and femur yellowish with tibia and tarsus brownish. Mid and hind coxae, femora, and basal half of tibiae yellowish, distal half of tibiae and tarsi brownish. Wing membrane smoky with stigma quite darker than in other species. Abdomen light brown with last two segments yellowish; abdominal



Figs. 19-21. *Bibionellus barrettoii* Lane & Forattini, female terminalia: 19, front view; 20, detail of sternite 9; 21, dorsal view. Abbreviations: Ce, cercus; GF, genital furca; Gp, gonapophysis; S, sternite; T, tergite. Scales, 0.1 mm.

macrotrichia yellowish. Otherwise as males. Female terminalia as in figs. 19-21.

Comments. Specimens were examined from the States of São Paulo and Goiás. These two areas are rather apart, separated by part of the Mantiqueira mountain chain and two important rivers, Rio Grande and Rio Parnaíba. Also, there are indications that the northeastern region of the State of São Paulo is historically connected to the areas of Atlantic Forest in the State of Rio de Janeiro (BRAVO & AMORIM, 1995), not to ciliary forests in Central Brazil. The differences detected among the populations of *B. barrettoii*, mainly the shape of the gonostylus, are insufficient to characterize them at this time as two separate species, although

still no autapomorphies could be found for *B. barrettoi*. *Rhynchosciara milleri* Pavan & Breuer (Sciaridae) presents a distribution similar to that of *B. barrettoi*, so the connection between these areas in the States of São Paulo and Goiás can be due to a rather recent modification of the distribution range of a species generating a biotic overlap. Diagnostic (even though archaeomorphic, i.e., a feature synapomorphic for a higher level of generality, see AMORIM, 1994) features for *B. barrettoi* are clear: the "mesosome" is long, mesally projected posteriorly, but the laterals are short, with a tuft of setae on its distal lobe.

### *Bibionellus paulistensis* Lane & Forattini

(Figs. 3, 33-38, 44,45)

*Bibionellus paulistensis* LANE & FORATTINI, 1948:571. Type locality: **BRAZIL**, State of São Paulo, Pitangueiras. Type: MZSP. HARDY, 1951:344.

Material examined Additional references: **BRAZIL, São Paulo**: Pitangueiras, ♂ holotype, 2 ♂ and 1 ♀ paratypes, X.1943, F. Lane, col. (MZSP); Porto Cabral, 1 ♂, X.1941, Travassos Filho et al. cols. (MZSP).

Redescription. Male: head dark reddish brown, with shining jet black ocelli. Antenna as in fig. 3. Thorax yellowish except for the brownish pronotum and mesonotum. Legs yellowish with tibiae and tarsi darker. Wing membrane smoky with alar stigma darker. Abdomen sclerites brown. Male terminalia as in figs. 33-38.

Female: head light brown, with shining jet black ocelli and yellowish antenna and palpus. Thoracic sclerites yellowish brown, yellow ventrally. Abdomen brown with last two segments yellowish. Otherwise as males.

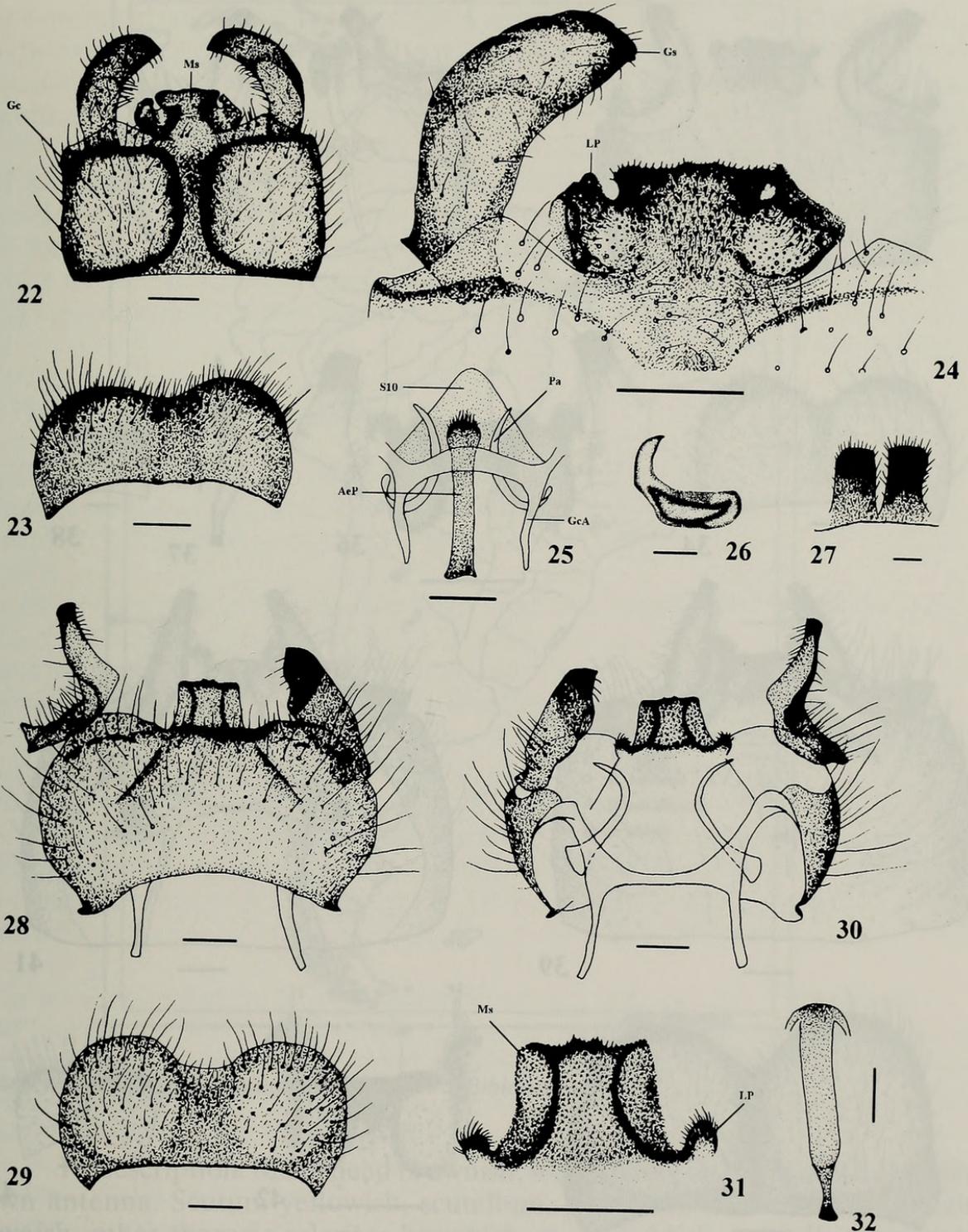
Comments. No autapomorphies could be found for this species, as was the case for *B. barrettoi*. Diagnostic features although clear are actually composed of apomorphic conditions shared with other species and plesiomorphic conditions that are apomorphic for *B. tibialis*. The "mesosome" is well developed posteriorly in its mesal as well as in its lateral extensions. An obvious anterior fold is present on the distal border of the "mesosome," before it extends dorsally. Also, the bases of the parameres are not particularly sclerotized. Populations that fit in this species are found in two areas of the State of São Paulo separated by the Rio Tietê, a very importante water system.

### *Bibionellus tibialis* Edwards

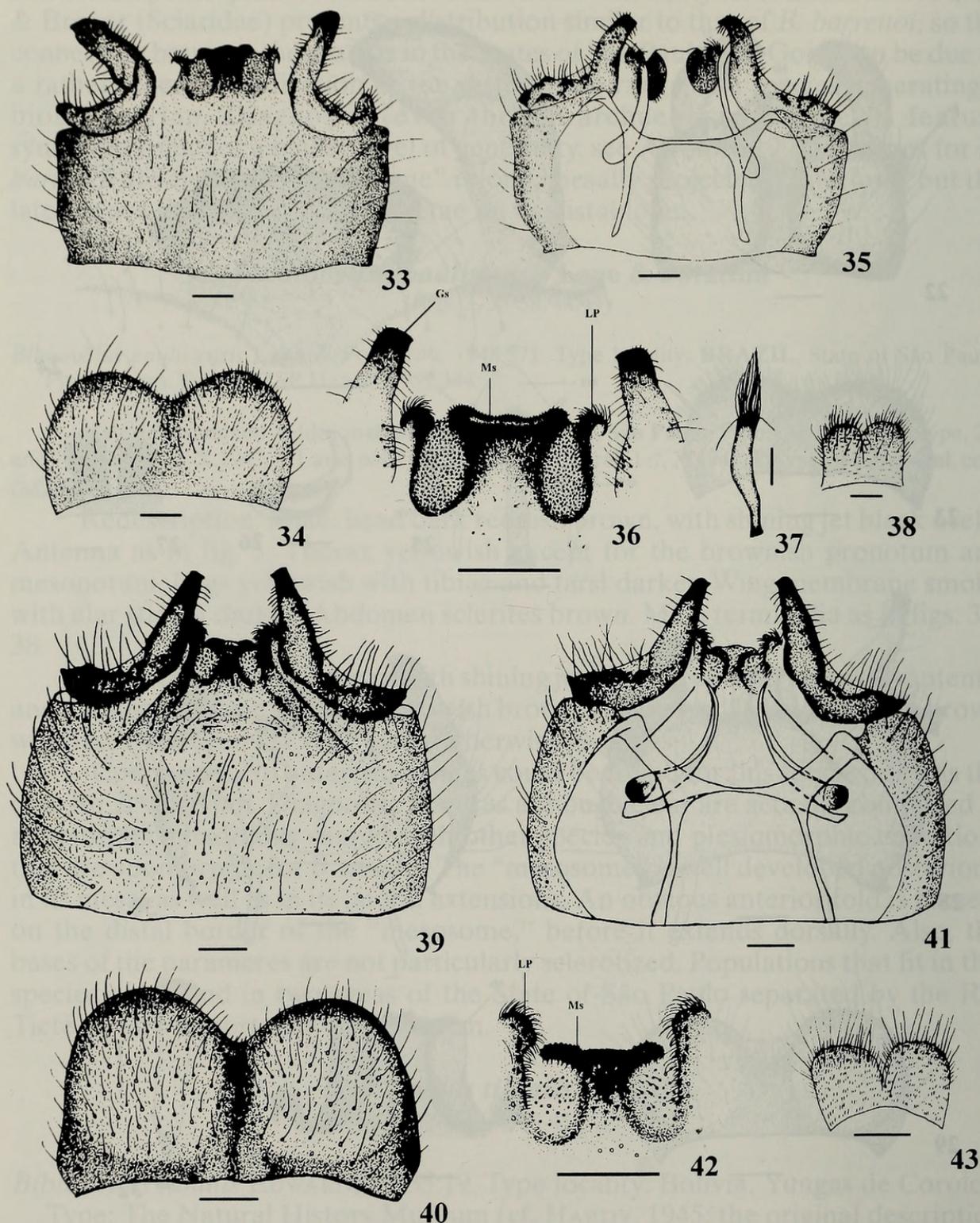
(Figs. 4, 39-45)

*Bibionellus tibialis* EDWARDS, 1935:19. Type locality: Bolivia, Yungas de Coroico. Type: The Natural History Museum (cf. HARDY, 1945; the original description indicated the Dresden Museum as the type depository). HARDY, 1945:497; LANE & FORATTINI, 1948:573.

Material examined Additional references: **ARGENTINA, Tucumán**: San Pedro de Calalao, 1 ♂, 1 ♀, I.1954, Duret col. (MZSP); 2 ♂, IX.1949, M. Arnau col. (IFML).



Figs. 22-32. Male terminalia. 22-27, *Bibionellus aczeli* Hardy: 22, ventral view; 23, tergite 9; 24, detail of gonostyle and "mesosome"; 25, detail of aedeagal plate, sternite 10 and parameres; 26, parameres; 27, cerci. 28-32. *Bibionellus barretto* Lane & Forattini: 28, ventral view; 29, tergite 9; 30, inner view of synsternogonocoxite, with parameres and gonostyles; 31, detail of "mesosome", ventral view; 32, aedeagal plate. Abbreviations: AeP, aedeagal plate; Gc, gonocoxite; GcA, gonocoxal apodeme; Gs, gonostyle; LP, lateral projection of mesosome; Ms, "mesosome"; Pa, paramere; S, sternite. Scales, 0.1 mm.



Figs. 33-43. Male terminalia. 33-38, *Bibionellus paulistensis* Lane & Forattini: 33, ventral view; 34, tergite 9; 35, inner view of synsternogonocoxite, with parameres and gonostyles; 36, detail of mesosome and gonostyles, ventral view; 37, aedeagal plate; 38, cerci. 39-43, *Bibionellus tibialis* Edwards, male terminalia: 39, ventral view; 40, tergite 9; 41, inner view of synsternogonocoxite, with parameres and gonostyle; 42, detail of "mesosome", ventral view; 43, cerci. Abbreviations: Gs, gonostyle; LP, lateral projection of mesosome; Ms, "mesosome". Scales, 0.1 mm.

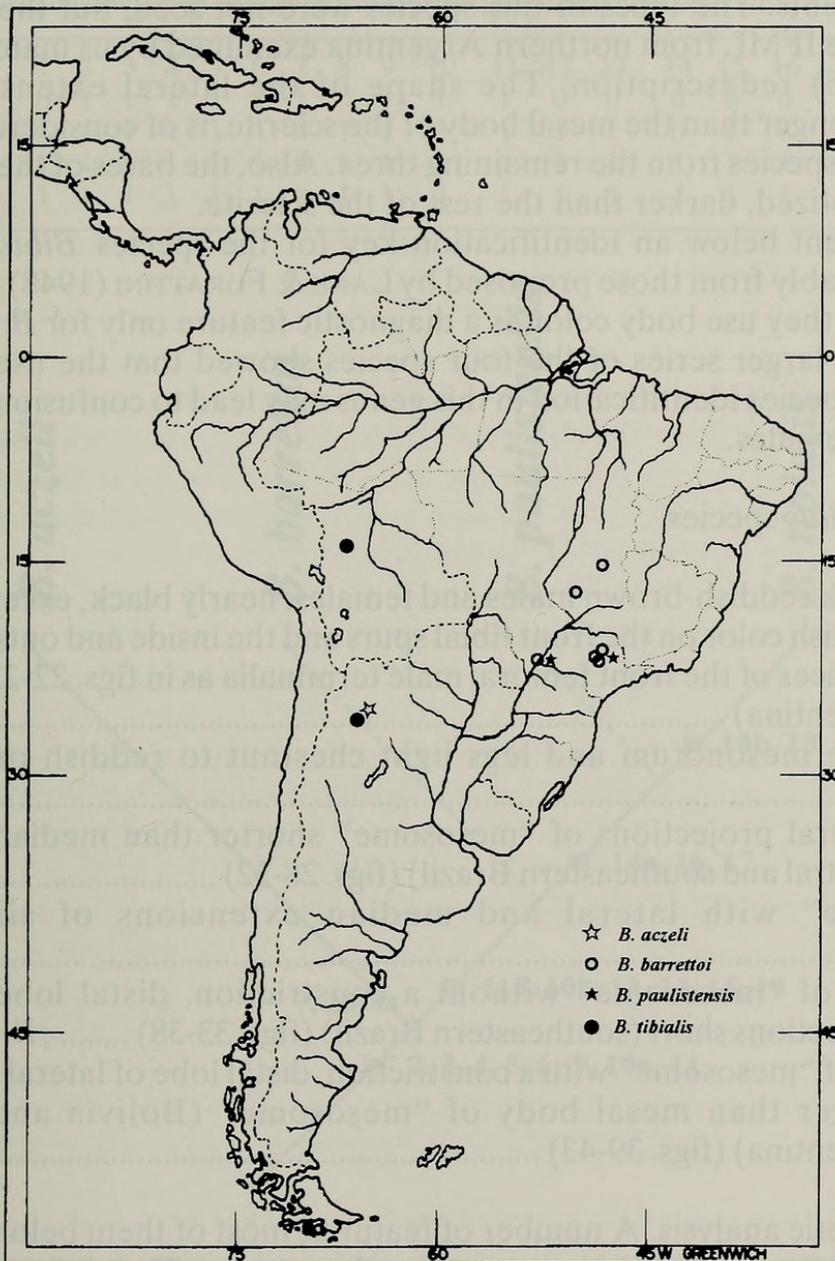


Fig. 44. Geographical distribution of the species of *Bibionellus*.

**Redescription.** Male: head brownish, with shining jet black ocelli and light brown antenna. Scutum yellowish, scutellum, pronotum and metanotum light brownish, other thoracic sclerites brownish, more reddish ventrally. Legs light brown, except for distal half of tibiae and tarsi, dark brown. Wing membrane smoky, with alar stigma darker. Abdominal sclerites brown with brownish macrotrichia. Terminalia as in figs. 39-43.

Female: head (fig. 4) light brownish, with shining jet black ocelli and yellow antenna. Thorax entirely yellow with light macrotrichia. Legs yellowish, except for brownish yellow tibiae and tarsi. Abdomen dark brown.

Comments. The types of this species were not seen, but the specimens deposited in the IFML from northern Argentina examined by us match very well HARDY'S (1945) redescription. The shape of the lateral extension of the "mesosome", longer than the mesal body of the sclerite, is of considerable help to distinguish this species from the remaining three. Also, the bases of the parameres are more sclerotized, darker than the rest of the sclerite.

We present below an identification key for the species *Bibionellus* that differs considerably from those proposed by LANE & FORATTINI (1948) and HARDY (1951) because they use body color as a diagnostic feature only for *B. aczeli*. The examination of larger series of the four species showed that the use of sclerite coloration for species identification in this genus may lead to confusion, especially regarding the females.

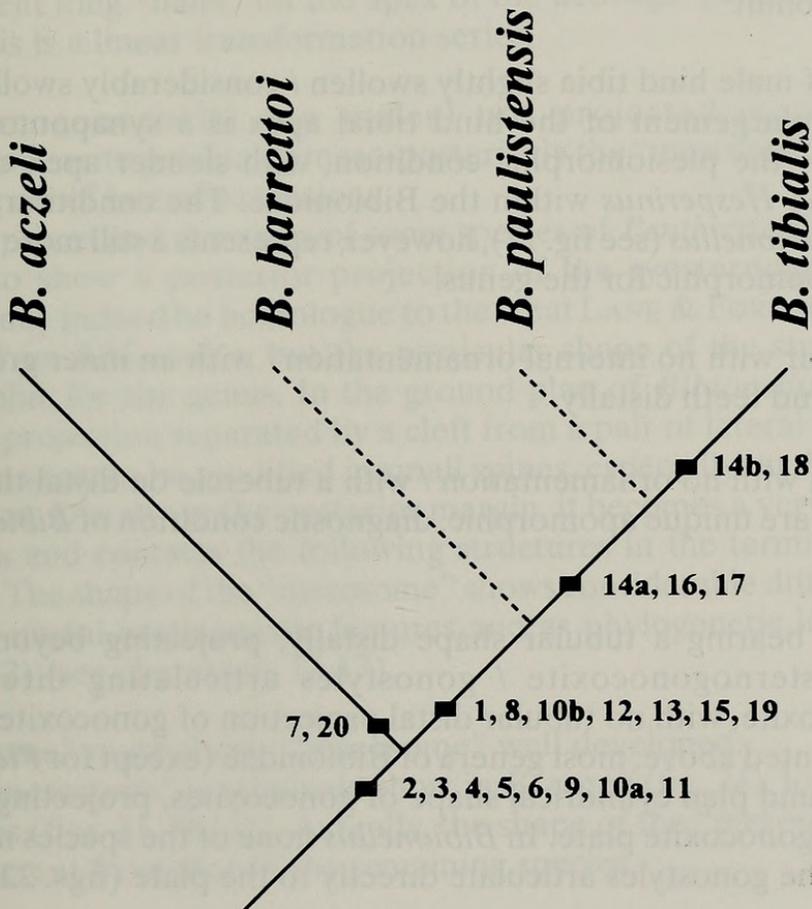
#### Key to *Bibionellus* species.

1. Entirely dark reddish-brown males and females, nearly black, except for slight reddish color on the front tibial spurs and the inside and outside median surfaces of the front femora; male terminalia as in figs. 22-23 (northern Argentina) ..... *B. aczeli*  
At least the mesonotum and legs light chestnut to reddish or yellowish ..... 2
2. (Males) lateral projections of "mesosome" shorter than median extension (central and southeastern Brazil) (figs. 28-32) ..... *B. barrettoi*  
"Mesosome" with lateral and median extensions of similar size ..... 3
3. Mesal part of "mesosome" without a constriction, distal lobe of lateral projections short (southeastern Brazil) (figs. 33-38) ..... *B. paulistensis*  
Mesal part of "mesosome" with a constriction, distal lobe of lateral projections longer than mesal body of "mesosome" (Bolivia and northern Argentina) (figs. 39-43) ..... *B. tibialis*

Phylogenetic analysis. A number of features, most of them belonging to the male terminalia, present differences among the species. These characters were interpreted phylogenetically and generated a cladogram for the four species of *Bibionellus*. The features are listed below, in each case with the plesiomorphic condition described first, followed by the apomorphic condition(s). Eventually, linear transformation series with more than two steps have the successive apomorphic conditions presented as "a," "b," etc. The condition of each character in each species is presented in the matrix on Table I. A discussion follows each transformation series, in which the character polarization is justified. The group+ artifact (AMORIM, 1982) was used to refer to unnamed monophyletic groups in sequenced phylogenetic classifications. *B. barrettoi*<sup>+</sup>, for example, corresponds to the monophyletic group composed of *B. barrettoi*+*B. paulistensis*+*B. tibialis*. The characters of the transformations series are the same appearing in the cladogram (fig. 45).

Table I. Matrix for characters in the list of transformation series of *Bibionellus*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>B. aczeli</i>	0	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1
<i>B. barretto</i>	1	1	1	1	1	1	0	1	1	2	1	1	1	0	1	0	0	0	1	0
<i>B. paulistensis</i>	1	1	1	1	1	1	0	1	1	2	1	1	1	1	1	1	1	0	1	0
<i>B. tibialis</i>	1	1	1	1	1	1	0	1	1	2	1	1	1	2	1	1	1	1	?	0

Fig. 45. Cladogram with the phylogenetic relationships proposed for the species of *Bibionellus*. Character numbers follow the transformation series referred to in the list of characters in the text.

1. Male entirely dark brown / at least some yellowish sclerites.

*B. aczeli* is the only species with entirely dark brownish males. *Bibio*, *Dilophus* and *Penthetria* include both species entirely black brownish and species with some or all sclerites yellowish. These latter species, however, seem to occupy more terminal positions on the evolution of each of the genera. *Hesperinus* and *Penthetria* are mainly blackish brown. Also, TOZONI (1989) accepts that the brown color is plesiomorphic for *Olbiogaster* Osten-Sacken (Anisopodidae). Dark color is accepted here as the ground plan condition for *Bibionellus*. This places *B. aczeli* outside of a monophyletic taxon composed of the remaining three species of the genus.

2. C ending at  $R_{4+5}$  or just beyond it / C extending considerably beyond  $R_{4+5}$ .

The extension of C beyond  $R_{4+5}$  in the wing is clearly a ground plan condition of Diptera. However, in the Bibionidae the reduction of C is a synapomorphy of the Bibionini (PINTO, 1992). C is nearly absent beyond  $R_{4+5}$  in *Bibio* and *Enicoscolus*, it is short in *Bibiodes*, but well developed in *Bibionellus* (figs. 9, 10), still longer than the condition seen in *Plecia*, *Penthetria* or *Hesperinus*. The condition in *Bibionellus* is considered a reversion of the reduction of  $R_{4+5}$  at the base of the Bibionini.

3. Distal third of male hind tibia slightly swollen / considerably swollen.

A slight enlargement of the hind tibial apex is a synapomorphy of the Penthetriinae<sup>+</sup> – the plesiomorphic condition, with slender apex of hind tibia – is found only in *Hesperinus* within the Bibionidae. The condition found in all four species of *Bibionellus* (see fig. 17), however, represents a still more apomorphic condition, synapomorphic for the genus.

4. Anterior femur with no internal ornamentation / with an inner group of small protuberances and teeth distally.

5. Anterior tibia with no ornamentation / with a tubercle on distal third.

These two are unique apomorphic, diagnostic condition of *Bibionellus* (figs. 12-13).

6. Gonocoxites bearing a tubular shape distally, projecting beyond posterior margin of synsternogonocoxite / gonostyles articulating directly to the synsternogonocoxite, with no tubular distal projection of gonocoxite.

As commented above, most genera of Bibionidae (except for *Plecia*) present the Diptera ground plan cylindrical shape of gonocoxites, projecting posteriorly to the synsternogonocoxite plate. In *Bibionellus* none of the species maintain this condition, and the gonostyles articulate directly to the plate (figs. 22, 28, 33, 39).

7. Synsternogonocoxite evenly convex / synsternogonocoxite with a mesal, longitudinal rift separating a pair of lobes.

The apomorphic condition of this character is seen only in *B. aczeli*. This is an important feature, since it indicates that this specific taxon is monophyletic and confirms the heterobathmy at this level (see character 1).

8. Gonostyle with a mesal fold / gonostyle with a sharp angle mesally.

The usual finger-like shape of the Diptera ground plan gonostyle is not present in any of the Bibionidae species, but rather the gonostyle has a mesal fold. *B. aczeli* (fig. 26), with a not very sharp fold, more clearly represents the condition found in other genera of the family. *B. barrettoi*, *B. paulistensis*, and *B. tibialis* (figs. 28, 33, 39) have the gonostyle strongly folded, another feature indicating that this group of species compose a monophyletic unity inside the genus.

9. Gonostyle apically smooth / apex of gonostyle with an inner tooth.

This is another synapomorphy for the genus.

10. Aedeagal plate smooth / a. with short pilosity / b. with long pilosity.

The aedeagal plate found in *Bibio* or *Dilophus* does not present the apical pilosity found in *Bibionellus* species, what represents a synapomorphy for the genus. Inside the genus *B. aczeli* has short pilosity (fig. 25), while the remaining species present long "hairs" on the apex of the aedeagal plate (fig. 37). It seems clear that this is a linear transformation series.

11. Synsternogonocoxite (on males) not projected meso-posteriorly / synsternogonocoxite producing meso-posteriorly the "mesosome", with a median body and a pair of lateral extensions.

Descriptions and drawings of some species of *Penthetria*, *Plecia*, and *Bibio* also seem to show a posterior projection of the synsternogonocoxite. That membrane may indeed be homologue to the what LANE & FORATTINI (1948) called "mesosome" in *Bibionellus*, but the particular shape of the structure is clearly synapomorphic for the genus. In the ground plan of *Bibionellus* it has a rather short mesal projection separated by a cleft from a pair of lateral projections. The macrotrichia seem to be modified in small spines, especially on the mesal body of the projection. Distally to the posterior margin, it becomes a very fine membrane that extends and contacts the following structures in the terminalia (aedeagus, sternite 10). The shape of the "mesosome" shows considerable differences between the species, useful as diagnostic features and as phylogenetic information (figs. 24, 31, 36, 42) (see characters 12-17).

12. "Mesosome" quite short / "mesosome" well developed.

The "mesosome" is relatively short in *B. aczeli* (fig. 24), longer in the other three species (figs. 31, 36, 42). Actually, the shape of the "mesosome" in *B. aczeli* is quite different from that of the remaining species.

13. Lateral projections of "mesosome" with short and sparse macrotrichia posteriorly / lateral projections of "mesosome" with a tuft of quite long macrotrichia.

The apomorphic condition (figs. 31, 36, 42) of this character is absent in *Bibionellus* only in *B. aczeli* (fig. 24).

14. Lateral projections of "mesosome" short / a. as long as mesal body of "mesosome" / b. longer than mesal body of "mesosome".

The laterals of the "mesosome" have different extensions in the genus. In *B. aczeli* (fig. 24) it is very short. In *B. barrettoi* the "mesosome" is long mesally (fig. 31), as *B. paulistensis* and *B. tibialis*, but has short laterals, more like *B. aczeli*. In *B. paulistensis* (fig. 36) the laterals are as long as the mesal body of the "mesosome". Finally, in *B. tibialis* (fig. 42) the laterals are longer than the remainder of the "mesosome".

15. "Mesosome" posterior margin straight, spines limited to ventral face of the sclerite / posterior margin of the "mesosome" curved dorsally, spines continuing more dorsally.

The apomorphic condition of this transformation series is absent only in *B. aczeli*.

16. Posterior margin of "mesosome" straight / a fold present on the distal margin of the mesosome.

The apomorphic condition of this structure is limited to *B. paulistensis* and *B. tibialis*.

17. Mesal body of "mesosome" rectangular / mesal body of "mesosome" strangulated, base slender than apex.

This is an autapomorphy of *B. tibialis*. Some specimens of this species also have modified macrotrichia on the mesosome, but we are not sure if this can be taken as an autapomorphy for the entire species.

18. Base of parameres as sclerotized as the rest of sclerite / base of parameres darker, clearly more sclerotized than sclerite distally.

Another autapomorphy of *B. tibialis*.

19. Base of aedeagal plate large than rest of sclerite / aedeagal plate slender and more sclerotized basally.

This is another synapomorphy of the group composed by *B. barrettoi*, *B. paulistensis* and *B. tibialis*.

20. Posterior margin of synsternogonocoxite not projected / a posterior blade projected on synsternogonocoxite posterior margin.

The posterior margin of *B. aczeli* is the only to have a posterior extension, an autapomorphy for the species.

Discussion. Different apomorphies (characters 1, 8, 10b, 12, 13, 15, and 19) indicate quite clearly that a monophyletic group within *Bibionellus* is composed of *B. barrettoi*, *B. paulistensis* and *B. tibialis*. Also, at least two autapomorphies (characters 7, 20) show that *B. aczeli* is not a merophyletic set of populations, hence establishing the heterobathmy at the base of the evolution of the genus. Within the monophyletic group composed by the remaining three species, it seems reasonable to accept that *B. paulistensis*+*B. tibialis* compose a monophyletic unity, as indicate characters 14a, 16, and 17. Characters 14b and 18, on the other hand, indicate that *B. tibialis* is monophyletic. Characters 2, 3, 4, 5, 6, 9, 10a and 11 are synapomorphies for the genus. There are no homoplasies in the cladogram and the consistency index is 1.00.

The set of features listed above is still insufficient to establish two of the species, *B. paulistensis* and *B. barrettoi*, as historical entities. As seen above, *B. paulistensis* is known from two localities quite close together in the State of São Paulo and the specific name *B. paulistensis* may eventually apply to

phylogenetically related populations (i.e., the species may be monophyletic), nevertheless autapomorphies must yet be found on a still more detailed analysis. The name *B. barrettoi*, on the other hand, applies to populations quite apart from each other, found in the states of São Paulo and Goiás. These populations may not correspond to sister populations of a monophyletic unity. Phylogenetic information from external morphology seems possibly exhausted and only other sources of phylogenetic information, as cytology or molecular data, may demonstrate whether the name *B. barrettoi* applies or not to a historical entity. Although unable to solve these two particular points, however, this morphological study, seems to corroborate quite substantially the phylogenetic relationships in the remaining levels of the evolution of the genus.

Biogeographical conclusions inferred from the cladogram should be considered very carefully. The sister group of *Bibionellus* is the pair of genera [*Bibiodes*+*Enicoscolus*], respectively with Nearctic/Nearctic+Australian distribution (PINTO, 1992). *Bibio* is considered a group with Pangaeic origin (PINTO, 1992), so its sister group – (*Bibionellus* (*Bibiodes* + *Enicoscolus*)) – should have the same age. If this interpretation is correct, the presence of *Bibionellus* in the Neotropical region is as old as the detachment of South America from other tropical Gondwanic areas, Late Jurassic or Early Cretaceous. The existence of only four recent Neotropical species in the such monophyletic group probably indicates the occurrence of considerable extinction along the Tertiary: other Neotropical, monophyletic groups with Gondwanic origin use to have large number of species, usually with a number of subgroups, each of which with large distribution in Central America and tropical South America. Each of the species of *Bibionellus*, consequently, may correspond to a remnant of an older group in the continent, with relatives in other Neotropical areas extinct or not collected. Biogeographic information obtained from a cladogram with so few terminal species, consequently, could correspond to false components generated by biogeographically paralogous groups. This is particularly true for a hypothesized relationship between northern State of São Paulo (*B. paulistensis*) and Bolivia and northern Argentina (*B. tibialis*). Maybe the only useful information for historical biogeography here would be the distribution of *B. tibialis* itself, connecting northern Argentina to Bolivia, delimiting a historical unity.

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