

THE NEOTROPICAL BITING MIDGES RELATED TO *CULICOIDES PARAENSIS* (DIPTERA: CERATOPOGONIDAE)

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Culicoides paraensis (Goeldi), a common and widespread American bloodsucking midge that has been incriminated in the transmission of Mansonellosis and Oropouche Fever of humans in South America, is redescribed and figured. All published records are listed and new distribution is based on examination of extensive collections from throughout its range. Three closely related species of the subgenus *Haematomyidium* that have been confused with *C. paraensis* are briefly redescribed and figured, and a key is presented for their identification.

Key words: *Culicoides paraensis* – human disease transmission – larval habitats – related species

Culicoides paraensis (Goeldi) is one of the commonest and widespread ceratopogonid midges in the Western Hemisphere, especially in the tropics. Its range extends from northern Argentina in the south to Pennsylvania and Wisconsin, U. S. A., in the north, but it is unrecorded from the Greater Antilles. The females are common daytime bloodsuckers of man and have been involved in the transmission of two human diseases. The larvae breed in collections of wet debris in tree-rot cavities and in rotting vegetable material such as banana stumps, cacao pods, and tropical fruits.

A survey of the literature yielded more than 70 references to this species, but most were distribution records and until recently little was known of its biology and disease vector potential. Its recent incrimination as the most important vector of Oropouche virus disease of humans in Brazil has focused interest in its biology and control. Several closely related and very similar species have recently been described from northern South America. This has required a closer look at the species that has been reported as *Culicoides paraensis*, to ensure the proper identification of the disease vector. The present study was undertaken to facilitate these identifications, giving a detailed description and figures for *Culicoides paraensis*, the most important species in this group, and shorter diagnoses of the related species.

The methods used in our study and the terminology used in our descriptions follow

that explained in the comprehensive revisions by Wirth & Blanton for Panama (1959), the Amazon Basin (1973), and the West Indies (1974).

DISEASE TRANSMISSION

Oropouche Virus – Oropouche virus is a major cause of human febrile illness in the Amazon Region of Brazil and has also been reported from Trinidad. Symptoms are fever, chills, headache, myalgia, arthralgia, and dizziness persisting for 2-7 days; some persons are severely ill but no deaths have been reported. Pinheiro et al. (1976) isolated the virus from about 15,000 *Culicoides* midges inoculated into mice. Over 95% of the midges were *Culicoides paraensis* (Goeldi). Roberts et al. (1981) showed epidemiological data correlating high populations of *C. paraensis* with urban outbreaks of Oropouche fever in three municipalities in Pará, Brazil, and LeDuc et al. (1981) reported similar correlation of *C. paraensis* with an epidemic in a rural community in Pará. According to Pinheiro et al. (1981) the virus probably occurs in nature in two distinct cycles: a sylvatic cycle which is responsible for maintenance of the virus in nature, with primates, sloths, and possibly some species of wild birds as vertebrate hosts, but the sylvatic vector still unknown; and an urban cycle during which man may be infected, and once infected, probably serves as an amplifying host among anthropophagous insects. Experiments reported by Pinheiro et al. (1981, 1982) proved that the

virus could be transmitted experimentally from hamsters to hamsters and from man to hamsters using *C. paraensis* midges. This observation represents the first definitive evidence of transmission of an arbovirus pathogenic to humans by a vector of the family Ceratopogonidae.

Linley et al. (1983) summarized previous epidemiological studies and emphasized the key role *C. paraensis* plays as an urban vector because of its association with urban plantings of cacao and banana, where it breeds in large numbers of cacao husks and in rotting banana stumps. Although a mosquito, *Culex quinquefasciatus* Say, was found to harbor Oropouche virus in urban situation, and forest mosquitoes [*Aedes serratus* (Theobald), *Coquillettidia venezuelensis* (Theobald)] in forest situations, *C. paraensis* was found to transmit Oropouche virus from a blood meal of a much lower virus titre than the mosquitoes and thus was thought to be a much more important vector. The biology of *C. paraensis* in forest situations is very incompletely known, but Roberts et al. (1981) investigated its habits in villages where Oropouche outbreaks has occurred and found a remarkable correlation between high population of *C. paraensis* and duration of human habitations long enough to establish permanent plantings of banana and cacao. Rotting banana stems and cacao pods in close association with habitations produced remarkably high populations of the midge. Reduction or removal of these extremely productive sources would seem to promise effective control of Oropouche epidemics.

Mansonellosis – *Mansonella ozzardi* (Manson) is a non-pathogenic human filarial work widespread in the American tropics. Buckley (1934) searched for possible vectors in St. Vincent, West Indies, and obtained development in feeding experiments with *Culicoides furens* (Poey). Likewise Romaña & Wygodzinsky (1950) found developmental stages of *M. ozzardi* in *C. paraensis* near Tucuman, Argentina, for as much as 12 days (as long as they could get the midges to live in captivity) after they fed on an infected person. Thirty-five of the midges which fed became infected. The parasite was found in Argentina only in a wooded region where *C. paraensis* bred in tree holes and was not found on the treeless plains.

According to Bruijning (1957) *ozzardi*-filariasis in Surinam was endemic to the Amerindians living in the sand savannahs or in the sandy area along the rivers, which would indicate a possible association with *C. paraensis*. The filaria was not endemic in the bush negroes nor in the population of the coastal areas but was prevalent in the Carib and Arawak Indians, indicating that the disease originated in the neotropics. Rozendaal & Slootweg (1984), however, reported a decrease in the prevalence of *ozzardi*-filariasis to zero in the Surinam savannahs, and a concurrent decrease but continued presence of *Mansonella perstans* (Manson). A village with 8 percent of the examined population positive for *M. perstans* showed large numbers of *Culicoides travassosi* Forattini present; very few midges of any species were found in a village without filaria infections, although several species of mosquitoes were prevalent. It was concluded that *C. travassosi* was the most likely vector of *perstans*-filariasis in the Surinam savannahs.

Cerqueira (1959) and Tidwell et al. (1980) reported the transmission of *M. ozzardi* by species of *Simulium* (Diptera, family Simuliidae) in the Amazon Basin, and evidence indicating involvement of *Culicoides* vectors was lacking. Ripert et al. (1977) however, reported that in Haiti the geographic distribution of the human cases of *Mansonella*-filariasis coincided exactly with the coastal distribution of the presumed *C. furens* vector. Raccurt and Lowrie (1981) and Lowrie & Raccurt (1981, 1984) demonstrated that *C. furens* was an effective vector in Haiti and that *C. barbosai* Wirth and Blanton was also a natural vector. Nathan (1978) stated that in coastal north Trinidad, *M. ozzardi* is transmitted by *Culicoides phlebotomus* (Williston). Lowrie et al. (1983) were able to show complete development of *M. ozzardi* in *Leptoconops bequaerti* (Kieffer) in Haiti but were of the opinion that this midge was not as significant a vector as *C. furens* and *C. barbosai*.

The difference in vector competence in disease geographic areas led investigators to consider the possibility that the Amazonian strain of *M. ozzardi* might be a distinct species from the Caribbean strain. However, to date no other evidence has been found to support this hypothesis. Mellor (1976) reported that he was able to obtain infective stages of the Caribbean strain of *M. ozzardi* experimentally

in *Culicoides nubeculosus* (Meigen) and *C. variipennis* (Coquillett) using midges from laboratory colonies. Lowrie et al. (1982) showed that laboratory-bred *C. variipennis* could serve as competent laboratory hosts for the Amazon strain of *M. ozzardi*. Thus, both strains of this filaria do not require a specific insect host. The Amazonian strain is commonly transmitted by simuliid flies and it is possible that certain Amazonian *Culicoides* species, including *C. paraensis*, may also play a role in the transmission cycle.

LARVAL HABITATS

The larval biology of Neotropical *Culicoides*, while receiving considerable study, remains for the most part unknown. Wirth & Blanton (1959) described known breeding sites for only 15 of the 88 reported Panamanian species of *Culicoides*, some of which have a biology closely associated with the local flora, in which the immature stages are found in plants, plant products, or the rainwater associated with them. Williams (1964) made a significant contribution to the biology of Neotropical *Culicoides*, reporting the larval habitats for 24 species in Trinidad, of which 15 species were found associated with plant materials, including *C. paraensis* with rotting cocoa pods. Clastrier (1971) reared *C. quasiparaensis* Clastrier from moss growing on a palm trunk and from moist material accumulated in the axils of palm fronds in French Guiana. Vitale et al. (1981) reported results of an extensive study of *Culicoides* reared from arboreal habitats in Panama, with more than 200 collections. These yielded significant numbers of *Culicoides*, but only five species of the subgenus *Haematomyidium* Brèthes, two of which belong to the *C. paraensis* Group. Bromeliads yielded *C. paraensis* and *C. bayano* Wirth; tree holes yielded *C. annuliductus* Wirth, *bayano*, *filiductus* Wirth, *paraensis*, and *lahillei* (Iches); moist soil and leaf debris yielded *C. bayano*; and rotting palm stumps yielded *C. bayano* and *filiductus*. Hoch et al. (1987) captured *C. paraensis* using emergence traps in rotting banana stumps and cacao pods.

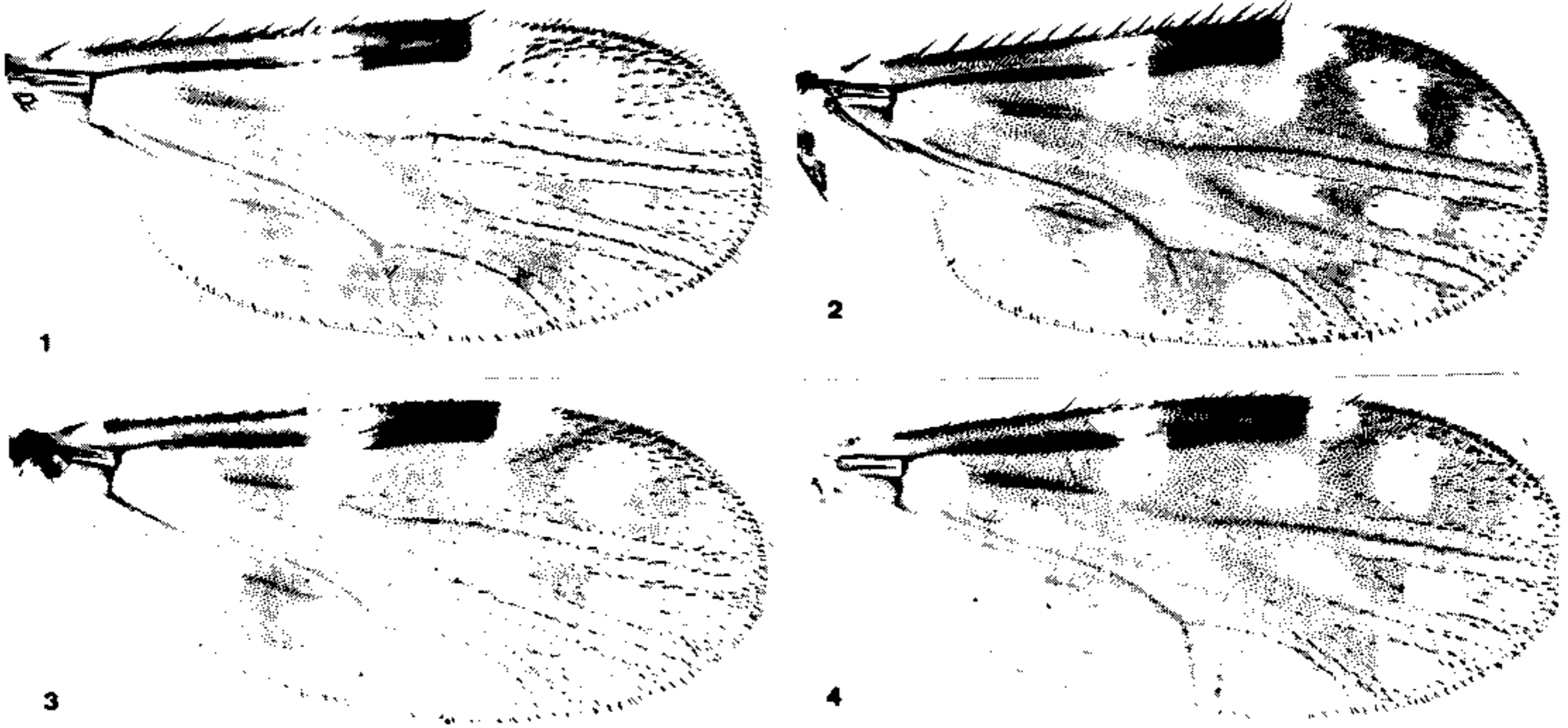
- sometimes fused; subapical pale spot in cell R5 usually transverse, rarely attaining wing margin; cell M2 with only one pale spot distal to level of mediocubital fork; two functional spermathecae present; antennal sensillar pattern 3,8-10, sometimes also on some of segments 4-7 (Subgenus *Haematomyidium*). 2
- Without the above combination of characters other subgenera of *Culicoides*.
- 2. Cell M1 with three pale spots (*paraensis* Group) 3
- Cell M1 with one or two pale spots *lahillei* (= *debilipalpis*) Group
- 3. Small pale spot present lying anterior to mediocubital stem near base; smaller spermatheca with long threadlike duct, sclerotized ring of duct short and cylindrical; eyes narrowly separated; wing with marginal pale spots large and distinct *filiductus* Wirth
- No pale spot anterior to mediocubital stem near base; smaller spermatheca with duct stouter, not threadlike; sclerotized ring, eye separation, and wing spots various 4
- 4. Third palpal segment broad (PR 1.7) with pit broad and shallow, rarely deep and opening by a smaller pore; spermathecae very unequal; eyes narrowly separated above, contiguous below, the interocular space wedge-shaped; male 9th tergum with short, angulate apicolateral processes; parameres sinuate without ventral lobe; aedeagus with low basal arch *quasiparaensis* Clastrier
- Third palpal segment slender to broad with pit deep and narrow, opening by a smaller pore; spermathecae slightly unequal to equal (variable); eyes broadly separated; male 9th tergum with slender apicolateral processes; parameres with or without ventral lobe; aedeagus with high basal arch 5
- 5. Third palpal segment short and stout, PR 1.7; paramere with definitive broad ventral swelling, without elongate lobe *neoparaensis* Tavares & Souza
- Third palpal segment longer and more slender PR 2.1-2.8; male paramere uniformly slender in midportion, with elongate lobe *paraensis* (Goeldi)

KEY TO SPECIES OF THE *CULICOIDES* *PARAENSIS* GROUP

- 1. Second radial cell included in a very dark spot; cell R5 with three or four small pale spots, the two poststigmatic pale spots

Culicoides paraensis (Goeldi)

Haematomyidium paraense Goeldi, 1905: 137 (female; Pará, Brazil; fig. wing); Kieffer, 1906:66 (catalog).



Photographs of wings of female of *Culicoides* of the *paraensis* group. Fig. 1: *paraensis*. Fig. 2: *filiductus*. Fig. 3: *neoparaensis*. Fig. 4: *quasiparaensis*.

TABLE

Mean values of numerical characters of females of the *Culicoides paraensis* group

Species	Wing length (mm)	Costal ratio	Antennal ratio	Antennal sensillar pattern	Palpal ratio	P/H ratio
<i>filiductus</i>	0.87	0.60	0.72	3,8-10	2.8	0.73
<i>neoparaensis</i>	0.90	0.62	0.86	3,(7),8-10	1.7	0.71
<i>paraensis</i>	0.78	0.59	0.77	3,8-10	2.1	0.82
<i>quasiparaensis</i>	0.83	0.61	0.80	3,8-10	1.7	0.75

Culicoides paraensis (Goeldi); Lutz, 1913: 55 (male, female; Brazil; fig. wing; combination); Neiva & Penna, 1916:96 (Brazil); Lutz & Nunez Tovar, 1928:13 (Venezuela); Wille, 1925:415 (southern Brazil); Macfie, 1932:486 (redescribed; Trinidad); Dunn, 1934:178 (Panama, biting man); Buckley, 1934:99 (St. Vincent; not common; negative for *Mansonella ozzardi* infection); Costa Lima, 1937:414 (in key;? synonym *undecimpunctatus* Kieffer); Macfie, 1938:164 (Grenada); Macfie, 1939:200 (Santa Catarina, Brazil); Martorell, 1939:210 (Venezuela; common name "jején"); Floch & Abonnenc, 1942:2 (French Guiana; fig. wing); Iriarte, 1943:192 (Venezuela); Fairchild, 1943:572 (Panama); Barretto, 1944:92 (male described; fig. wing, genitalia; Brazil); Briceño-Iragorry, 1946:398 (Venezuela); Fox, 1946:255 (in key; notes; distribution); Andusee et al., 1947:11 (Venezuela); Barbosa, 1947:23 (Brazil, Peru,

Panama, Venezuela); Macfie, 1948:72 (in key); Ortiz & Pena Garcia, 1948:7 (Venezuela); Briceño-Iragorry, 1949:318 (Venezuela); Ortiz, 1949:326 (Venezuela); Floch & Abonnenc, 1949a:1343 (common in French Guiana; likely vector of *Mansonella*); Floch & Abonnenc, 1949b:71 (Venezuela); Iriarte, 1950:363 (Venezuela); Romaña & Wygodzinsky, 1950:31 (habits, transmission of *Mansonella ozzardi*; Argentina); Ortiz, 1951a:10 (in key); Ortiz, 1951b:574 (male, female redescribed; figs.; Venezuela); Mirsa et al., 1952:161 (Venezuela); Tucker, 1952:349 (Barbados); Barbosa, 1952:19 (Argentina, Brazil); Gibson & Ascoli, 1952:317 (Guatemala; biting habits; negative host for *Onchocerca volvulus*); Woke, 1954:71 (Taboga Id., Panama; biting man); Snow, 1955:515 (Tennessee; biting habits); Fox, 1955:250 (extensive bibliography; summary of distribution); Ortiz & Leon, 1955:570 (Ecuador);

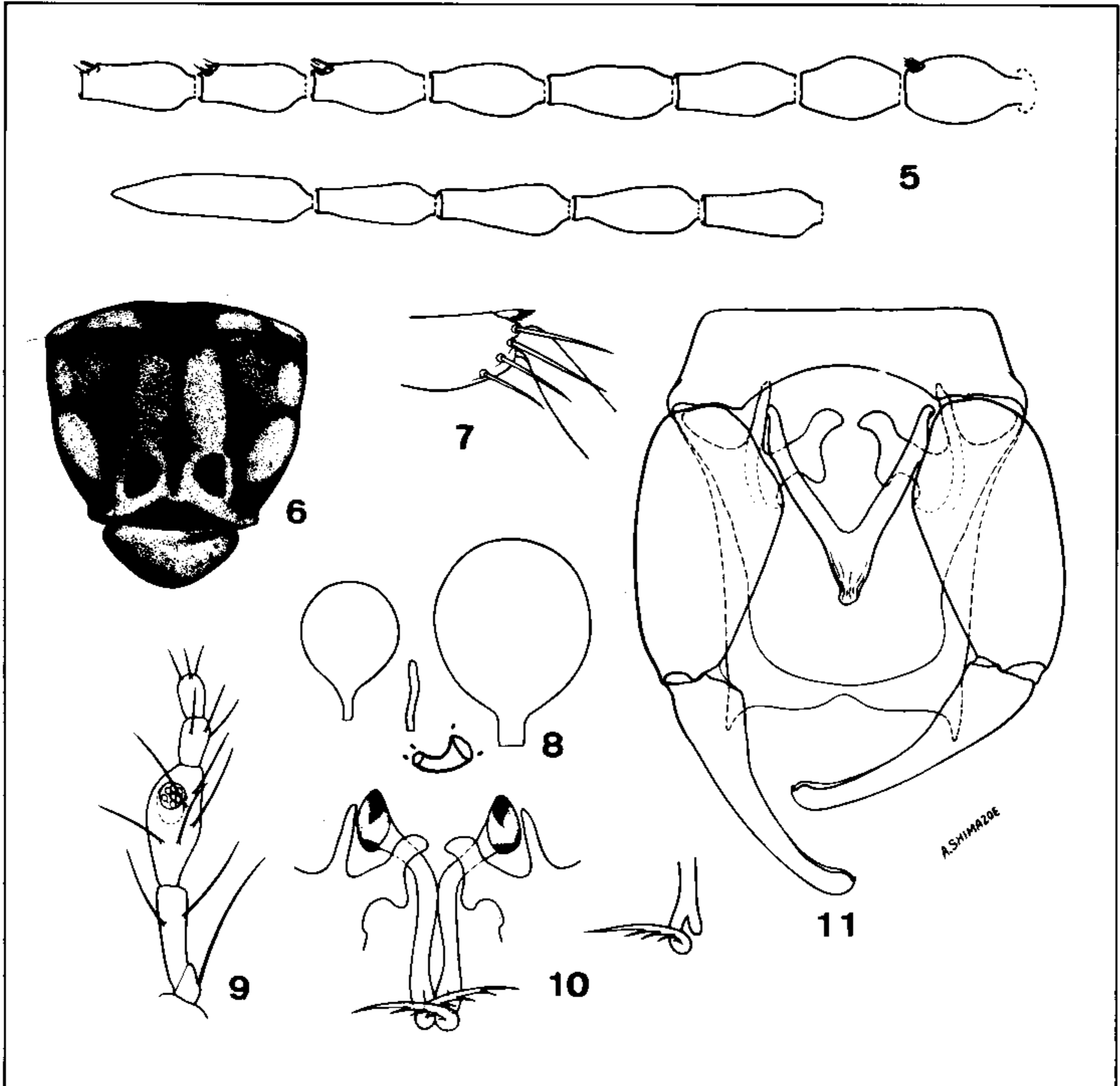
Wirth, 1955:109 (Guatemala); Snow et al., 1957:27 (Alabama, Tennessee; biting habits; reared tree hole); Forattini, 1957:426 (re-described; figs; distribution; extensive bibliography); Snow & Pickard, 1958:4 (Mississippi, Alabama; habitat); Snow et al., 1958:19 (South Carolina; feeding habits); Wirth & Blanton, 1959:440 (re-described; figs.; Panama; synonym *undecimpunctatus*); Breeland, 1960:165 (Panama; reared tree hole); Williams, 1964:463 (Trinidad; larval habitat in rotting cocoa pods); Messersmith, 1965:322 (Virginia; in poultry houses); Smith, 1965:65 (Florida; tree holes); Cavalieri and Chiossone, 1966:149 (Argentina); Khalaf, 1966a:227 (Louisiana; re-described); Khalaf, 1966b:882 (Louisiana; seasonal incidence); Khalaf, 1967:54 (Louisiana, rare species); Smith & Varnell, 1967:520 (Florida; tree holes); Hair & Turner, 1968:106 (Virginia, biting man); Childers & Wingo, 1968:16 (Missouri; fig. wing; reared cottonwood sap flows); Khalaf, 1969:1156 (Louisiana, Mississippi; rare species); Gazeau & Messersmith, 1970a:32 (Maryland; biting man); Gazeau & Messersmith, 1970b:36 (Maryland); Battle & Turner, 1971:68 (Virginia; re-described; figs.); Wirth & Blanton, 1971:36 (notes comparing *debilipalpis*); Winder & Silva, 1972:652 (Brazil; reared cacao plantation); Humphreys & Turner, 1973:82 (Virginia; feeding preference); Wirth & Blanton, 1973:443 (Amazon Basin records); Wirth & Blanton, 1974:71 (re-described; figs.; West Indies distribution); Tanner & Turner, 1974:66 (Virginia; feeding habits); Aitken et al., 1975:135 (Trinidad); Winder, 1977:59 (Brazil, in cacao flowers; reared from jack-fruit); Scholl et al., 1979:288 (Wisconsin; biting habits); Blanton & Wirth, 1979:131 (re-described; figs.; Florida; review of biology and distribution); Vitale et al., 1981:155 (in key; Panama; reared tree holes, bromeliad); Pinheiro et al., 1981:172 (Brazil; transmission Oropouche virus; biology); Foil et al., 1984:205 (Louisiana; negative for infection with *Onchocerca cervicalis*); Hayes et al., 1984:370 (Alabama, feeding on dairy cattle); Mullen et al., 1985:203 (Alabama; feeding on dairy cattle); Wirth et al., 1985:28 (wing photo; Nearctic distribution); Hoch et al., 1986:284 (Brazil; breeding sites and control); Gerhardt, 1986:192 (Tennessee; feeding on deer, cattle); Spinelli & Wirth, 1987:55 (in key); Wirth et al., 1988:50 (wing photo; Neotropical distribution).

Culicoides undecimpunctatus Kieffer, 1917: 307 (female; Argentina).

Female: Wing length 0.78 mm; breadth 0.38 mm.

Head: Eyes broadly separated, with short interfacetal pubescence. Antenna (Fig. 5) with lengths of flagellar segments in proportion of 15-11-12-14-14-14-15-15-16-16-16-25; antennal ratio 0.77; sensilla coeloconica on segments 3,8-10. Palpal segments (Fig. 9) with lengths in proportion of 8-17-20-7-10; third segment slightly swollen with small, deep, sensory pit; palpal ratio 2.1. Proboscis moderately long, P/H Ratio 0.82; mandible with 14 teeth. *Thorax*: Dark brown; mesonotum (Fig. 6) with dark grayish pollinosity, three more or less prominent longitudinal setae anteriorly, the lateral ones widening at sutural level. Legs dark brown, fore and mid femora with subapical, all tibiae with subbasal, and hind tibia with apical, narrow pale rings; hind tibial comb (Fig. 7) with four spines, the second from the spur longest. *Wing* (Fig. 1): Pattern as figured; second radial cell dark; pale spot over r-m crossvein narrow, extending to costal margin; cell R5 with four small round pale spots, the two poststigmatic pale spots well separated, the posterior one located slightly proximad of the other, the third spot larger and located subapically in cell, the fourth small and located at extreme apex; cell M1 with three small pale spots; cell M2 with pale spot at basal arculus, a pale spot lying behind medial fork and one in front of mediocubital fork, and one spot in distal part of cell lying at wing margin; cell M4 with small round pale spot near wing margin; anal cell with one pale spot in distal portion; apices of veins M1, M2, M3 + 4, and Cul dark. Macrotrichia sparse on distal half of wing, a few in base of cell M2 and in anal cell; second radial cell with distinct lumen; costal ratio 0.59. Halter pale, base of knob brownish. *Abdomen*: Dark brown. Spermathecae (Fig. 8) two with rudimentary third and sclerotized ring; functional spermathecae ovoid with long slender necks; unequal, measuring 0.057 by 0.037 mm and 0.048 by 0.029 mm.

Male genitalia (Fig. 11): Ninth sternum with broad, shallow, caudomedian excavation, ventral membrane not spiculate; ninth tergum long and tapering with short, pointed, widely separated apicolateral processes. Basistyle with ventral root foot-shaped, "ankle" slender and posterior "heel" well developed, dorsal root slender; dististyle slender and curved with bent tip. Aedeagus V-shaped, basal arch extending



Culicoides paraensis (Goeldi). Fig. 5: ♀ antenna. Fig. 6: mesonotum. Fig. 7: hind tibial comb. Fig. 8: spermathecae. Fig. 9: ♀ palpus. Fig. 10: parameres. Fig. 11: ♂ genitalia, parameres omitted. (modifications of the original plate by Felipe-Bauer).

to two-thirds total length, basal arms nearly straight; distal portion with simple rounded tip. Parameres (Fig. 10) separate; each with large basal knob; stem slender, bent at some distance from base, midportion straight with a well-developed ventral lobe; distal portion abruptly bent and tapered to a fine point with lateral fringe of fine spines.

Immature stages: Unknown.

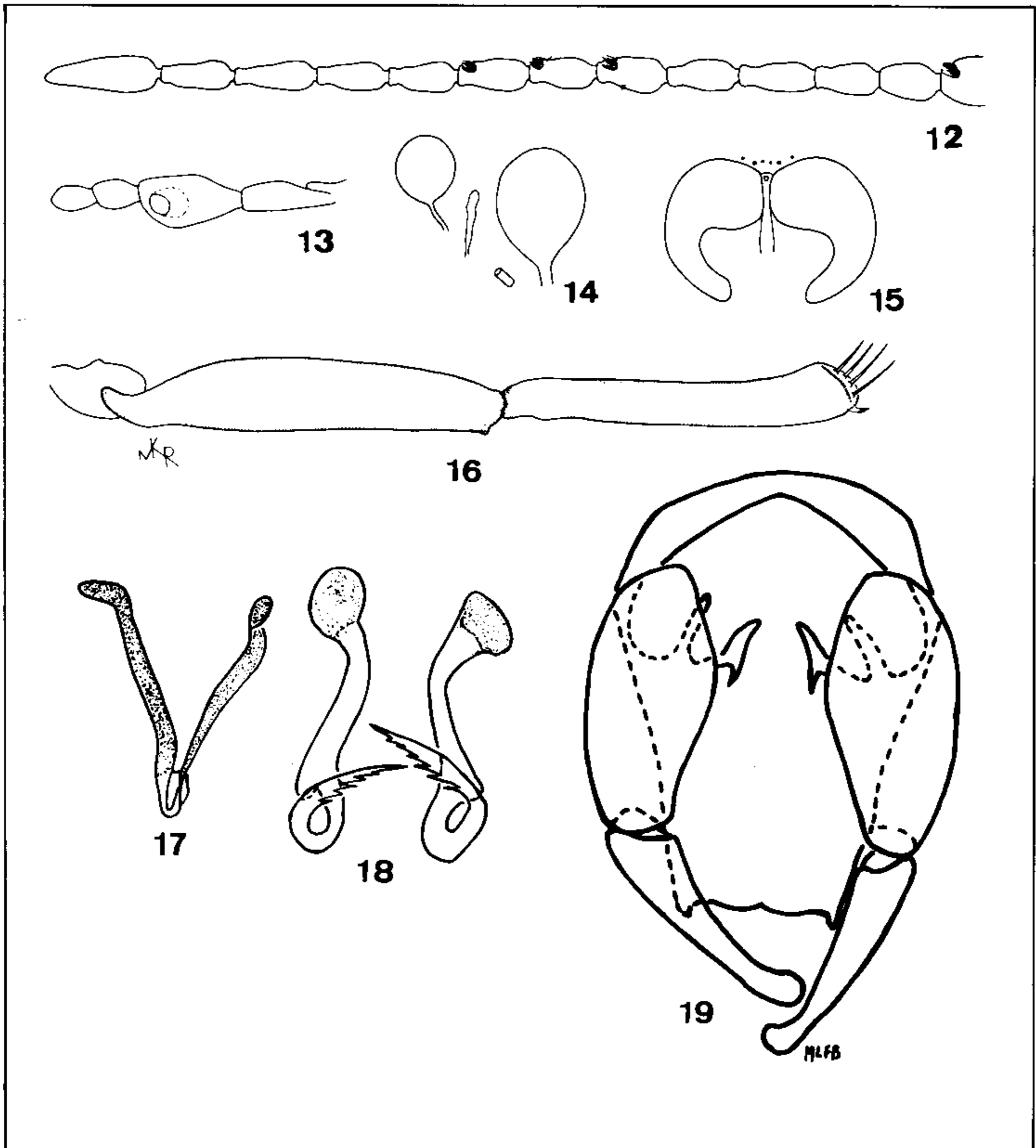
Types: Syntypes, Belém, Pará, Brazil, E. Goeldi (according to Goeldi (according to Goeldi, 1905:139, syntypes were deposited in the British Museum (Nat. Hist.) in London).

We have been unable to locate syntype material in the BMNH or in the Museum Goeldi in Belém. Therefore, we designated a female specimen from the type locality of *C. paraensis* as Neotype, which is deposited in the Collection of the Instituto Oswaldo Cruz, Rio de Janeiro, Brazil (No. 197).

Neotype: Belém, Brazil, EMBRAPA, 11.xi.1986, A. L. Hoch, biting man 1800 hrs, female.

Distribution: Eastern U. S. A., Mexico, Central and South America to Argentina; Barbados, Grenada and Trinidad in the West Indies.

Specimens examined: ARGENTINA: Salta, 44 km Aguaray, 9.vi.1987, Estevez, Ronderos & Spinelli, biting man, 7 females. Rio Carapari, 8 km Pocitos, Feb., R. Woodruff, 2 females. BARBADOS: Dover Beach, 10-19.xi.1982, 16-20.vii.1984, E. C. Greiner, some biting man, 3 males, 15 females. St. Thomas, 2.viii.1988, E. C. Greiner, 1 male, 7 females. BOLIVIA: Cochabamba, Chpiiriri, ii.1967, F. O. Teran, biting man, 4 females. La Paz, 24 km Coripata, 2.v.1969, P. & P. Spangler, 1 female. BRAZIL: Acre, Bela Vista, 13 km W Rio Branco, 24.ii.1980, L. A. L. coll., biting man, 3 females (KRAMER). Bahia, Corte de Pedra, no date, A. L. Hoch, biting man, 10 females; km 22, Estrada Ilheus-Itabuna, 1973, S. Soria, suction trap, 4 males, 2 females; Itabuna, 20.v.1970, J. A. Winder, light trap, 1 male, 5 females. Amazonas, km 50 BR-174, Manaus, 22.ii.1979, J. Arias, light trap, 2 females; Rio Tootobi, 11.viii.1976, R. R. Pinger, biting man, 3 females. Pará, Armadilha de Cruz, 24.i.1976, no collector, 1 female; Belém, APEG Forest, 18.xi.1970, T. H. G. Aitken, biting man, 1700 hrs, 20 m tree platform, 1 female; Belém, APEG Forest, xi.1969, T. H. G. Aitken, light trap, 2 males; Belém, EMBRAPA, 11.xi.1986, A. L. Hoch, biting, 1800 hrs, 9 females; Mujui dos Campos, 3.iii.1975, D. R. Roberts, biting man, 3 females; Benevidas, Canutana, Faz. Saboro, BR-316, km 24, A. L. Hoch, 1987, 10 females. Pernambuco, Recife, no date, F. S. Barbosa, 10 females. Rio de Janeiro, Itaguaí, 13.vi.1984, Baptista coll., biting man, 1 female; same, 22.v.1984, M. L. Felipe-Bauer, 1 female; same, 11.iv.1984, Rodrigues coll., biting man, 2 females; same, 9.v.1984, no collector, biting man, 2 females; Itaguaí, Faz. da Barrinha, 17.x.1974, Aragão & Tavares, light trap, 3 females. São Paulo, Mun. S. Anastácio, Fazenda São Sebastião, ii.1953, O. P. Forattini, 4 females; Mun. Pres. Venceslau, Córrego Agua Azul, x.1952, O. P. Forattini, 2 females. Santa Catarina, Mun. Florianópolis, Ponte Grossa, 31.i.1956, SAIM coll., 1 female; Nova Teutonia, ii.1971, F. Plaumann, 4 females. COLOMBIA: Amazonas, Leticia, 15.ii.1987, Itoma, 2 females (BOGOTÁ); Arara Vic. Leticia, 15.vi.1978, M. A. Tidwell, biting, 1 female. Antioquia, Rio Anori Valley, Buenos Aires, 690 m, 10.x.1970, biting man, ground, mature forest, 1 female; Providencia, 618 m, 7.vii.1971, biting man in forest canopy, 1 female; Tiroteos, 590 m, 12.i.1971, reared from larvae in bamboo pot in forest canopy, 2 females (all coll. C. H. Porter). Meta, Villvicencio, El Buque, 18.iv.1978, E. Chery, 1 female (BOGOTA). Tolima, Mariqueta, Florazul, no date, 1 female; Vereda La Guardia, Finca Belgica, xii.1983, 2 females (all M. Rodriguez coll.); Melgar, El Aguila, 29.i.1980, E. Martinez, 1 female (BOGOTA). Valle, Buchitolo, 24.vii.1973, J. E. Browne, ex human, 1 male, 1 female; Navarro, 5.ii.1964, V. H. Lee, light trap, 1 male, 1 female (wing photo). Vaupes, San Jose de Inambu, 14.vii.1977, E. Sabogal, 1 female; Los Angeles, 16.vii.1977, E. Sabogal, 1 female; San Pablo, 11.vii.1977, E. Sabogal, 1 female. Ortega, 10.xi.1971, R. A. Alvarez, biting man, 1 female. COSTA RICA: Limon, Finca La Lola, vic. Guapiles, 23.vi.1980, A. M. Young, 1 female. Puntarenas, Palmar Sur, 5.viii.1964, F. S. Blanton, light trap, 14 males, 13 females. Guapiles, 27.ii.1989, E. C. Greiner, 1 female. Alajuela, Atenas, 23.xii.1988, E. C. Greiner, 4 females. ECUADOR: Bolivar, Columa, no date, L. A. Leon, 1 female. Guayas, Barranco Chico, 29.viii.1956, R. Levi Castillo, 5 females; Chilcales, 21.viii.1955, R. Levi Castillo, 2 females; Manglar Alto, 6.ii.1955, R. Levi Castillo, 2 females; Milagro, San Miguel, v.1955, R. Levi Castillo, 1 male, 2 females. Los Rios, Guare, viii.1955, R. Levi Castillo, 3 females; Quevedo, Pichilingue, INIAP, iv.1978, J. Mendoza, 3 females; El Oro, El Passaje, 1.xi.1954, R. Levi Castillo, 1 female. Napo, Limoncocha, 11.vii.1977, W. E. Steiner, 1 female. Pichincha, Manabi, viii.1955, R. Levi Castillo, 2 females; Santo Domingo de los Colorados, 1 female. Zamora-Chinchipe, Zumba, vi.1956, L. A. Leon, 2 females. EL SALVADOR: Cuscutlan, San Pedro Perulapan, 600 m, 15-28.iii.1956, J. F. Matta, 5 males, 5 females. San Salvador, Santa Tecla, Finca La Pena, 7.iv.1961, F. S. Blanton, 1 female. San Vicente, Santo Domingo, 20.xi.1966, F. S. Blanton, 1 female. GRENADA: Boulogne Estate, 8.xii.1968, P. Bacon, biting, cocoa estate, 2 females. GUATEMALA: Chimaltenango, Yepocapa, Finca San Rafael, 22.ii, 26.vii.1951, C. Gibson & W. Ascoli, 6 males, 3 females. Suchitepequez, San Antonio Suchitepequez, 6.vii.1965, P. J. Spangler, malaise trap, 1 female. San Julian, 6.vi.1988, E. C. Greiner, 1 female. HONDURAS: Atlantida, Lancetilla, ix-xii.1953, F. S. Blanton, 2 males, 1 female. Cortes, La Lima, 30.vi.1964, F. S. Blanton, 2 males, 6 females. MEXICO: Tabasco, Villhermosa, 6.viii.1964, P. J. Spangler, light trap, 1 male. Veracruz, Cuitlahuac, 3.vii.1965, P. J. Spangler, 1 male; Fortin, 30.viii.1964, F. S. Blanton, 1 female.



Culicoides filiductus Wirth. Fig. 12: ♀ antenna. Fig. 13: ♀ palpus. Fig. 14: spermathecae. Fig. 15: eye separation. Fig. 16: hind leg. Fig. 17: aedeagus. Fig. 18: parameres. Fig. 19: ♂ genitalia, aedeagus and parameres removed. (modifications of the original plate by Felipe-Bauer).

PANAMA: Bocas del Toro, Almirante, 14.xii.1952, F. S. Blanton, 2 females. Canal Zone, Barro Colorado Island, vii.1967, W. W. Wirth, light trap, 3 males, 10 females; Fort San Lorenzo, 5.viii.1952, F. S. Blanton, 1 female; Huile Sia Clara, 13.v.1952, F. S. Blanton, 1 female; Loma Boracho, 29.x.1951, F. S. Blanton, 1 female; Mojinga Swamp, Fort Sherman, xi.1951, ii.1952, ix.1957, F. S. Blanton, light trap, 5 males, 5 females; Gatun, *Sterculia* tree canopy

in rain forest, 2.vii.1979, E. Broadhead, 1 female. Panama Prov., Bayano Field Station, vi.1976, G. C. Vitale, reared from tree hole, 3 males, 13 females. PERU: Loreto, San Antonio, 22.viii.1965, J. C. Hitchcock, biting man, 1 female. SURINAM: Marowijne, Tapanahoni River, Godoholo (4° 00' N, 54° 49' W), 11.v.1980, H. J. Emanuels, biting man, 1 female. TOBAGO: Blenheim, 12.xi.1985, E. L. Treiner, 1 female. TRINIDAD: Macqueripe Naval

Station, 3.i.1958, T. H. G. Aitken, light trap, 1 female. Rio Grande Forest, Sangre Grande, biting man 28 m tree station, 28.iii.1956, 28.vi.1958, T. H. G. Aitken, 3 females. St. Pats Estate, 3.xii.1953, W. Downes, light trap, 1 female; 24.xii.1954, T. H. G. Aitken, tree station, 2 females. Simla, ii.1966, W. D. Duckworth, 1 male. Vega de Oropouche, 22.iv.1966, E. S. Tikasingh, 1 female. No locality, viii-ix. 1963, R. W. Williams, reared cocoa pods, 3 males, 3 females. U. S. A: Alabama, Cypress Creek, 20.iii.1952, W. E. Snow, ex tree hole, 1 male, 1 female; Greenbrier, 26.v.1958, W. E. Snow, 1 female; Red Bay, 12.xii.1957, W. E. Snow, reared tree hole, 1 male. Florida, Alachua Co., Gainesville, Chantilly Acres, ix.1967, F. S. Blanton, light trap, 2 females; Gainesville, iii.1965, G. B. Quinn, 2 females; San Felasco Hammock, i.1965, A. Boike, ex tree hole, 4 females. Leon Co.; Tallahassee, iii.1960, M. A. Kohn, at light, 2 females; 5 km n Tallahassee, v.1970, F. S. Blanton, light trap, 3 females; Liberty Co., Torreya State Park, 30.vi.1957, F. S. Blanton, light trap, 1 female; Putnam CN., Lon's Lake, ix.1971, F. S. Blanton, light trap, 2 females. Louisiana, Carlisle, 3.viii.1964, 1 male, 1 female; Covington, 20.x.1965, 4 females; Lafitte, 25.vii.1964, 3 males, 4 females; Maplewood, 30.x.1964, 1 female (all K. T. Khalaf coll.); W. Feliciana Parish, Lake Rosemound, 9.v.1972, M. A. Tidwell, light trap, 1 female. Maryland, Montgomery C 1/4., Cxlesville, 24.viii.1958, A. A. Hubert, biting man, 8 females; Forest Glen, 29.viii.1966, W. W. Wirth, light trap, 1 male, 1 female. Missouri, Boone Co., 2 km s Easley, 8.viii.1966; C. C. Childers, reared tree hole, 2 females. North Carolina, South Mills, 2.ix.1962, A. B. Gurney, biting man, 1 female; Jackson Co., Dulaney Bog, 7 mi s Cachiers, 9.vii.1987, W. W. Wirth, malaise trap, 1 female; Macon Co., Highlands, 16.vi.1986, W. W. Wirth, biting man 5 PM, 1 female; Transylvania Co., Lake Toxaway, 9-20. vii.1989, W. W. Wirth, light trap, 3 females. Oklahoma, Leflore Co., Page, 23.vi.1937, Standish & Kaiser, 5 females. Pennsylvania, Conewago Creek, 20 km w York, 20.vi.1959, A. A. Hubert, light trap, 2 females; Davidsburg, 16.vii.1960, P. J. Spangler, biting man, 1 female. Texas, Kenedy Co., King Ranch vic. Armstrong, 25.v.1933, C. B. Philip, 1 female. Virginia, Fairfax Co., Falls Church, 18.viii.1958, 1.ix. 1961, W. W. Wirth, light trap, 2 females; 18.vi.1961, W. W. Wirth, biting man, 1 female; Franklin Co., Ferrum, 15.vii.1959, D. H. Messersmith, 1 female; Giles Co., Newport,

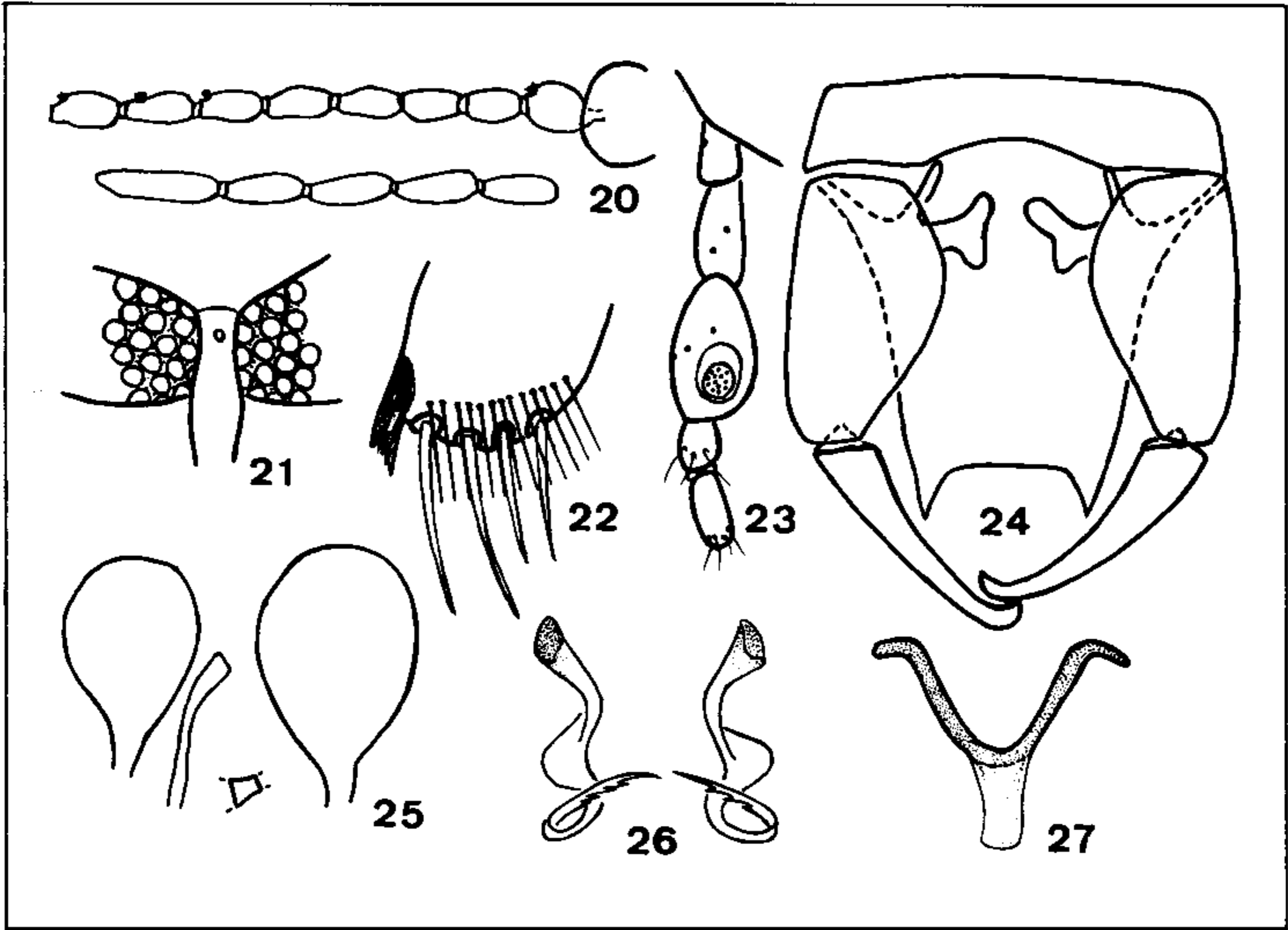
28.v.1965, J. A. Hair, reared tree hole, 3 females; Madison Co., Rose River, 435 m, Shanandoah Nat. Park, J. F. & D. Burger, biting man 1200-1300 hr, 3 females. West Virginia, Capon Springs, 29.viii.1956, E. J. Gerberg, 2 females. Wisconsin, Iowa Co., Hanson's Farm, 14.vii.1978, P. Scholl, biting man, 2 females.

Culicoides filiductus Wirth
(Figs. 12-19)

Culicoides filiductus Wirth, in Vitale et al., 1981:155 (female; pupa; figs.; Panama); Wirth et al., 1988:48 (wing photo; distribution).

Diagnostic characters: Moderately large for the *paraensis* Group, wing length 0.87 mm. The eyes are narrowly separated, with sparse interocular pubescence, and the third palpal segment is broad (PR 2.8) with a deep pit opening by a smaller pore. As outlined in the key, *C. filiductus* can be distinguished from the other four known species of the *paraensis* Group by the presence of a small pale spot in the base of cell M2 at about the midlength of the vein forming the stem of the mediocubital fork. It shares with *C. quasiparaensis* the small size of the smaller spermatheca, about half the diameter of the larger, but in *filiductus* the duct of the smaller spermatheca is much more slender, threadlike. In *filiductus* the pale wing spots are large and distinct, the subapical pale spot in cell R5 is distinctly notched on its distal side, and the distal pale spot in cell R5 broadly meets the wing margin. The male genitalia (see below) are nearly identical with those of *C. paraensis*, but are shorter and broader, and the ventral lobe of the parameres is not so prominent, somewhat angulate distally, but not drawn out distally in an elongate process rounded distally.

Male genitalia (Fig. 19): Ninth sternum with a broad, deep caudomedian excavation, ventral membrane bare; 9th tergum moderately long and tapering with short, tapered, pointed apicolateral processes, the caudal margin between them with distinct mesal cleft. Basistyle about twice as long as basal breadth, ventral root moderately broad and foot-shaped, the "heel" well developed, dorsal root slender; dististyle moderately long and broad, slightly curved. Aedeagus (Fig. 17) V-shaped, the basal arms slender and curved, basal arch reaching 0.6 total length; distal process slender, poorly



Culicoides neoparaensis Tavares & Souza. Fig. 20: ♀ antenna. Fig. 21: eye separation. Fig. 22: hind tibial comb. Fig. 23: ♀ palpus. Fig. 24: ♂ genitalia, aedeagus and parameres removed. Fig. 25: spermathecae. Fig. 26: parameres. Fig. 27: aedeagus.

sclerotized with simple rounded tip, the ventral side appearing channel-like. Parameres (Fig. 18) each with a stout basal knob; stem moderately slender and curved at some distance from knob, distally with moderately developed ventral lobe; apical portion tapered to fine point, laterally fringed.

Distribution: Belize, El Salvador, Honduras, Panama.

Specimens examined: BELIZE: Cayo Dist., Central Farm, xi.1961, R. H. L. Disney, trap baited with *Ototymys*, 1♀. EL SALVADOR: Cuscutlan, San Pedro Perulapan, 600 m, 19.vii.1966, J. F. Matta, 4 females. La Libertad, Sta. Tecla, 8.ix.1961, F. S. Blanton, 1 female. HONDURAS: Comayagua, Signatepeque, 20.vi.1966, J. F. Matta, 1 female. PANAMA: Mojinga Swamp, Canal Zone, 4.xii.1951, F. S. Blanton, light trap, 2 males, 3 females.

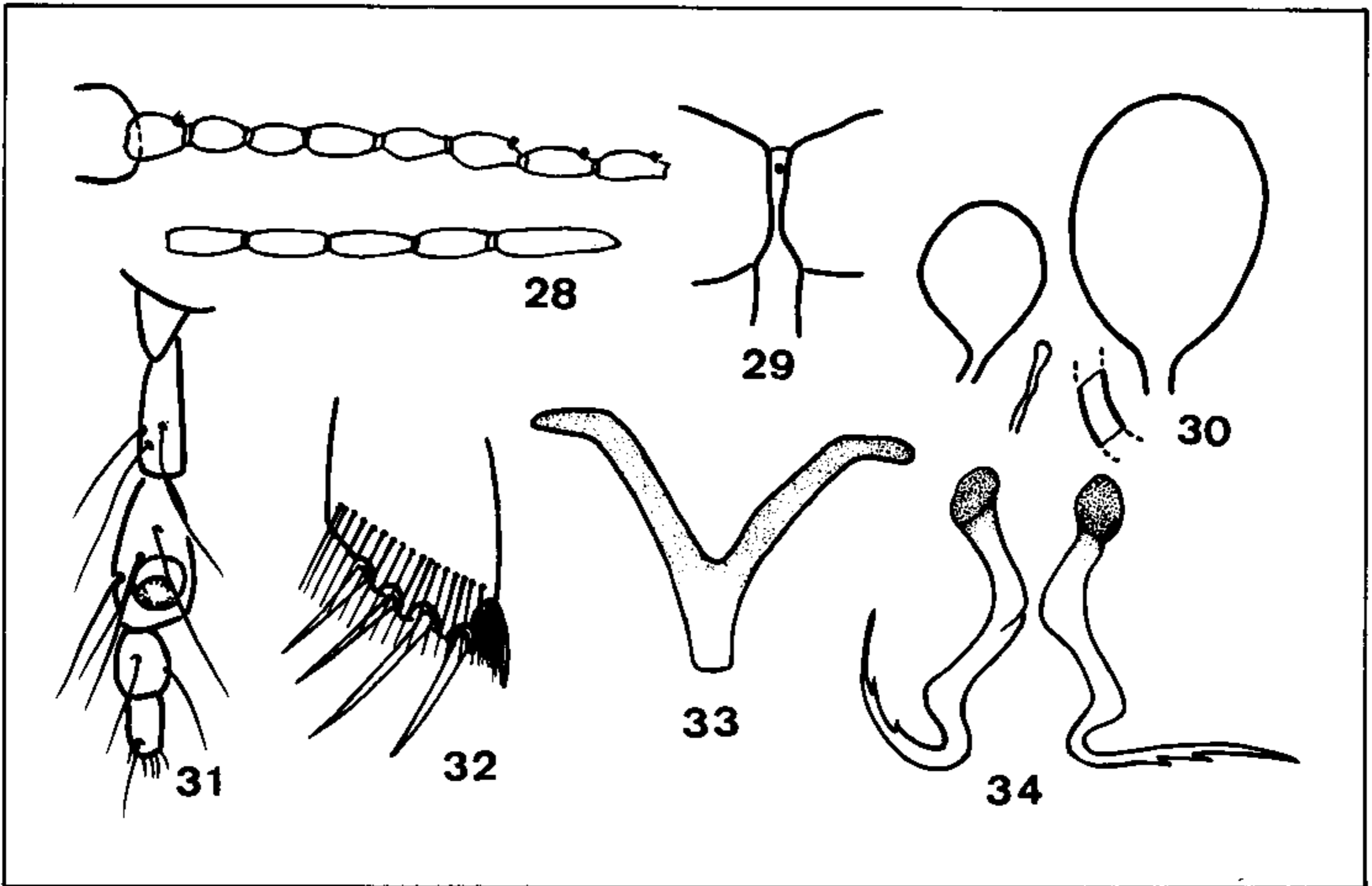
Culicoides neoparaensis Tavares & Souza
(Figs 20-27)

Culicoides neoparaensis Tavares & Souza, 1978:621 (male, female; Brazil, figs.); Wirth et al., 1988:50 (wing photo; distribution).

Diagnostic characters: Moderately large for the *Culicoides paraensis* Group, wing length 0.90 mm. Eyes broadly separated, pubescent. Resembling *C. undecimpunctatus* in its moderately large size and subequal to slightly unequal spermathecae with stout necks. The third palpal segment is much stouter (PR 1.7) than in *undecimpunctatus* (PR 2.8). The sclerotized ring associated with the spermathecae is short, and the 3rd. rudimentary spermatheca is greatly elongated. Male parameres with broad ventral swelling, and male aedeagus with shorter basal arch and longer distomedian process are quite distinctive.

Distribution: Brazil, Ecuador.

Specimens examined: BRAZIL: Amazonas, km 50 BR-174 n. of Manaus, 22.ii.1979, J. Arias, light trap, 1 female. Rio de Janeiro,



Culicoides quasiparaensis Clastrier. Fig. 28: ♀ antenna. Fig. 29: eye separation. Fig. 30: spermathecae. Fig. 31: ♀ palpus. Fig. 32: hind tibial comb. Fig. 33: aedeagus. Fig. 34: parameres.

Jacarepagua, Pau da Fome, ix.1975, Tavares & Ruiz, 2 females (photo), 1 male (paratypes); same, xi.1975, 1 female (paratype); same, x.1975, 2 females (alotype, paratype), 1 male (paratype); same, iii.1979, 1 male (paratype); same, viii.1976, Tavares coll., 3 females, 1 male; same, i.1977, vii.1977, Tavares coll., 2 females, 1 male; Represa dos Ciganos, Estr. Grajaú-Jacarepagua, 9.x.1984, Felipe-Bauer coll., biting man, 2 females. Santa Catarina, Nova Teutonia, i.1971, F. Plaumann, 1 female. ECUADOR: Guayas, Barranco Chico, 28.viii.1955, R. Levi Castillo, 1 female.

Discussion: Although Tavares & Souza (1978) give the antennal sensillar pattern as 3,7-10, examination of female paratypes shows sensilla on segments 3,8-10 as typical of the *C. paraensis* Group, and this pattern holds true in the specimens examined that we list above.

Tavares & Souza (1978) described the pattern of the eyes as narrowly separated. All the here examined specimens showed broadly separated eyes, similar to *C. paraensis*. The reexamination of the female paratypes revealed that the eye separation pattern of the original description is due to an artifact of mounting on the slide.

Culicoides quasiparaensis Clastrier
(Figs 28-34)

Culicoides quasiparaensis Clastrier, 1971:286 (male, female; French Guiana; figs.); Wirth et al., 1988:50 (wing, photo; distribution).

Diagnostic characters: A small species of the *paraensis* Group, wing length 0.83 mm. Eyes microscopically pubescent, narrowly separated by a wedge-shaped space above, contiguous below. *C. quasiparaensis* resembles *C. filiductus* in its very unequal spermathecae and small size, but lacks the small pale spot just in front of the midportion of the mediocubital stem, the duct of the small spermatheca is slender but more tapering and not filiform, and the sclerotized ring is quite short. The third palpal segment of *quasiparaensis* is quite distinctive, short and broad (PR 1.7), and bearing a broad, shallow, sensory pit. Clastrier figured a deeper pit opening by a smaller pore in his types, but in our series the pit is usually as described above, but occasionally specimens were observed with the pit variably deeper with a smaller pore. Antennal segment 11 is about the same as segment 10. The male genitalia of *C. quasiparaensis* are quite distinctive. The parameres are slender and sinuate and lack any trace of a

ventral lobe, and the ninth tergum is broad distally, with a very slight, angulate distomesal indentation, and the apicolateral processes are reduced to blunt, angulate structures. The aedeagus has a very low basal arch, broad, tapering main body, and the distal process tapers gradually to a rather broad, truncate tip.

Distribution: Brazil, Colombia, El Salvador, French Guiana, Honduras, Panama.

Specimens examined: BRAZIL: Amazonas, km 50, BR-174, n of Manaus, 22.ii.1979, J. Arias, CDC light trap, 2 males. Rondônia, Ji-Paraná, km 354, BR-354, 12.iii.1980, J. Arias, light trap, 1 male. COLOMBIA: Antioquia, Rio Anori Valley, Buenos Aires, 610 m, 16.ix.1970, C. H. Porter, light trap in forest, 1 female; La Tirana, 320 m, 7.iii.1971, C. H. Porter, light trap, 2 males; Rio Anori, ix.1970, D. G. Young, UV light trap in tropic rain forest, 3 males, 2 females. Putamayo, Pto. Leguizamo, Sta. Cecilia, 10.viii.1977, M. F. Suarez, 1 male. EL SALVADOR: Cuscutlan, San Pedro Perulapan, 600 m, 15-27.viii.1966, J. F. Matta, 3 females. San Miguel, San Jorge, viii.1966, F. S. Blanton, light trap, 1 female. HONDURAS: Lancetilla, Atlantida, xii.1953, F. S. Blanton, light trap, 1 male, 9 females. PANAMA: Canal Zone, Barro Colorado Id., vii.1967, W. W. Wirth, light trap, 1 male, 15 females; Mojinga Swamp, 4.xii.1951, F. S. Blanton, light trap, 12 females; San Lorenzo, 15.viii.1952, F. S. Blanton, light trap, 1 male.

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