

Revision and cladistic analysis of the Neotropical spider genus *Phoneutria* Perty, 1833 (Araneae, Ctenidae), with notes on related Cteninae

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Summary

The genus *Phoneutria* is revised, including five current species: *P. boliviensis* (F. O. Pickard-Cambridge), *P. fera* Perty, *P. reidyi* (F. O. Pickard-Cambridge), *P. nigriventer* (Keyserling), and *P. bahiensis* sp. n. from north-eastern Brazil. A new diagnosis for the genus is presented. The following new synonymies are established: *P. keyserlingi* (F. O. Pickard-Cambridge) and *P. pertyi* (F. O. Pickard-Cambridge) with *P. nigriventer*; *P. depilata* (Strand), *P. nigriventroides* (Strand), *Ctenus chilesicus* Strand, “*C. peregrinoides*” Strand, *C. valdehirsutus* Strand and *C. signativenter* Strand with *P. boliviensis*; and *C. forcipatus* Mello-Leitão with *P. reidyi*. *P. unilineata* (Simon) and *P. decora* Gerstäcker are transferred to *Ctenus*. *Phoneutria rufibarbis* Perty and *P. ochracea* C. L. Koch are considered *species inquirenda*. A key to species is provided. A cladistic analysis of *Phoneutria* is presented, using comparative morphological data. The monophyly of Cteninae and the interrelationships of the genera are discussed. The subfamily Phoneutriinae Bücherl is synonymised with Cteninae.

Introduction

The family Ctenidae was proposed by Keyserling (1877) to include *Ctenus* Walckenaer, 1805, *Microctenus* Keyserling, 1877, *Acanthoctenus* Keyserling, 1877 and *Caloctenus* Keyserling, 1877. The study of this family has been made difficult by the loss of the type specimen of the type species *Ctenus dubius* Walckenaer, 1805. Several species were included in this genus and furthermore the limits of the family were unclear. Simon (1897) regarded the ctenids as a subfamily (Cteninae) of the Clubionidae, while F. O. Pickard-Cambridge (1897) recognised a lineage of genera that he identified as “cteniform” and in 1900 he restored the family Ctenidae.

Mello-Leitão (1936) divided the family into four subfamilies which differ in the distribution of spines on tibiae I and II and the labial ratio. Lehtinen (1967) considered the ocular disposition 2-4-2 and the oval anterior lateral eyes as characters of the family. He revised the subfamilies based on the cribellate and ecribellate lineages using genital and non-genital characters. Further contributions regarding the evolutionary relationships of ctenids have been made in recent years. Hüber *et al.* (1993) studied some genera with molecular data and proposed the polyphyly of Ctenidae. Griswold (1993) analysed the phylogenetic relationships of lycosoid genera, and established that Ctenidae are not

monophyletic and assumed that the limits of this family are not clear. Moreover, this author indicated the monophyly of *Ctenus* and *Phoneutria*, and included them in the ctenoid complex of Lycosoidea with *Machadonia* and *Phanotea* as the most closely related genera. Recently Silva (1998) presented a preliminary cladistic analysis of Ctenidae as an attempt to understand the monophyly of ctenids and their phylogenetic relationships.

The genus *Phoneutria* was described by Perty (1833) based on two species: *P. rufibarbis* and *P. fera*, based on two females from Rio Negro, Brazil, collected by the Martius and Spix expeditions. In the original description, Perty did not indicate the type species. Walckenaer (1837) placed these species in *Ctenus* Walckenaer, 1805. F. O. Pickard-Cambridge (1897) revised the cteniform species of South America and proposed *P. fera* as the type species of *Phoneutria* because the figure given by Perty allowed him to recognise the recurved median ocular row. He considered *P. rufibarbis* as “*forma ignota*” because of the incomplete description of this species. He also established two new names for specimens determined earlier by Keyserling: *Ctenus pertyi* for *P. rufibarbis* and *C. keyserlingi* for *C. ferus*. He placed in *Ctenus* all the South American species with a procurved or straight median ocular row. He established also that cteniform species with a recurved median ocular row belong to *Phoneutria*, which explains the inclusion of some African cteniform species in *Phoneutria*.

Simon (1897) synonymised *Phoneutria* with *Ctenus*, but later Mello-Leitão (1936) restored the genus *Phoneutria* based on the presence of dense scopulae on the prolateral and ventral surfaces of the palpal tibiae and tarsi. Mello-Leitão (1940) suggested the need for a systematic revision of *Ctenus*. Bücherl *et al.* (1964) found that the ocular rows were very variable, so they based their redescription of *Ctenus* and *Phoneutria* on genital morphology and the presence or absence of palpal scopulae. Lehtinen (1967) placed *Phoneutria* and *Ctenus* in Cteninae, with *Ctenus* as the type genus. He also included *Corinoctenus*, *Ctenopsis*, *Isoctenus*, *Oligoctenus* and *Tuticanus*, and based the monophyly of this subfamily on the presence of teeth on the epigynal lateral lobes, elevated epigynal middle field, wide embolus, divided claw tufts, and dense ventral scopulae on the tarsi and metatarsi. Bücherl (1969a) proposed the subfamily Phoneutriinae considering morphological, ethological and geographical data. Contributions on the systematics of *Phoneutria* species have been made by Bücherl *et al.* (1964, 1969), Schiapelli & Gerschman de Pikelin (1966, 1973), Eickstedt (1969, 1979, 1983), Eickstedt & Bücherl (1969), Eickstedt & Lucas (1969) and Eickstedt *et al.* (1969). A preliminary notice of the revision of this genus and an analysis of the systematic significance of the copulatory organs in Neotropical Ctenidae was presented by Simó (1996). Because of the high toxicity of the venom of the *Phoneutria* species, several studies have been made concerning the venom and phoneutricism, e.g. Brazil & Vellard (1925, 1926), Bücherl (1953a, b, 1956, 1968), Schenberg & Pereira

Lima (1971), Trejos *et al.* (1971) and Simó (1983). The development and reproductive biology were studied by Tretzel (1957), Bücherl (1969b), Lucas (1969) and Simó & Bardier (1989). The accidental introduction of these species into different regions of the world, transported with imported bananas, has been cited by Grisolia & Bianchini (1976), Schmidt (1954, 1956, 1970, 1971), Simó (1983, 1984) and Simó *et al.* (1988).

The relationships of ctenine genera are poorly known, owing to the scarcity of cladistic studies in the family and the lack of a revision of many Neotropical and Asian genera. Moreover, other problems occur: the type species of some genera were based on immatures, e.g. *Isoctenus* Bertkau, 1880, and the loss of the holotype and an incomplete original description, e.g. *Itatiaya* Mello-Leitão, 1915.

Studies of comparative morphology and new character systems are relevant to advances in the knowledge of phylogeny (Griswold, 1993). Furthermore, Shultz (1998) stated that different character systems may provide complementary information and lead to a more objective and empirical concept of phylogeny. The status of Ctenidae and the phylogenetic relationships of the genera will be clarified by studies at different taxonomic levels.

Material and methods

Drawings were made with a camera lucida. The epigyna were cleared with sodium hypochlorite and immersed in Hoyer's medium. The SEM photographs were obtained with a scanning microscope Jeol JSM T100 from the Facultad de Ciencias y Museo, La Plata (MLP), Argentina. The terminology of the features for the copulatory organs follows Sierwald (1989, 1990). All the measurements are in mm.

Abbreviations: Institutions: BMNH=Natural History Museum, London; FCE=Sección de Entomología, Facultad de Ciencias, Montevideo; IBSP=Laboratório de Artrópodes, Instituto Butantan, São Paulo;

MACN=Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires; MLP=Facultad de Ciencias y Museo de La Plata, La Plata; MNHN-M=Museo Nacional de Historia Natural, Montevideo; MNHN=Muséum National d'Histoire Naturelle, Paris; MNRJ=Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; MPEG=Museu Goeldi do Pará, Belém; MZSP=Museo de Zoologia, Universidade de São Paulo, São Paulo; SMF=Zoologisches Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt; UFBA=Departamento de Zoologia, Universidade Federal de Bahia, Salvador; ZMB=Museum für Naturkunde der Humboldt Universität, Berlin; ZMH=Zoologisches Institut und Zoologisches Museum, Universität Hamburg. Epigynal features: ap=anterior process, bs=base of spermatheca, cd=copulatory duct, ef=epigastric furrow, fd=fertilisation duct, lf=lateral field, lt=lateral teeth, mf=middle field, ol=oval lobe, pa=porose area of head of spermatheca, tl=transverse lobe. Bulb features: co=conductor, cy=cymbium, dtp=distal tegular projection, e=embolus, mta=median tegular apophysis, rta=retrolateral tibial apophysis, sd=spermatic duct, st=subtegulum, t=tegulum, ti=tibia.

Phylogenetic analysis: A data matrix of seventeen taxa as terminals belonging to five genera and twenty-seven characters (Table 1) was analysed with PeeWee 2.00 (Goloboff, 1993). To find the fittest tree, the command "mult* 15" was used to randomise the order of the taxa. Up to 20 trees were retained in the initial stage of the search. The process was repeated up to 15 times. The concavity index used was K=6, considering that the mildest weighting functions produced the most predictive hierarchical patterns (Ramirez, 1998).

Because the relationships of Cteninae are poorly known, other species outside *Phoneutria* were included as a preliminary approach to the phylogeny of this subfamily. Since *Ctenus* is a diverse and complex genus, different morphospecies were chosen for this analysis *Viracucha andicola* (Acanthocteninae) was considered an outgroup for Cteninae.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26		
Va	0	0	0	0	0	0	0	0	?	0	?	0	?	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	
Cx	0	0	1	1	1	1	0	1	0	1	2	1	0	1	1	1	0	2	1	1	0	1	1	0	1	0	1	0	1
Ct	0	0	1	1	1	1	0	1	0	1	2	1	0	1	0	1	0	2	1	1	0	1	1	0	1	0	1	0	1
Cl	0	0	1	1	1	1	0	1	0	1	2	1	0	1	0	1	0	2	1	0	1	1	1	0	1	0	1	0	1
Oo	0	0	1	1	1	1	0	1	0	1	1	1	0	1	0	1	0	1	1	0	1	2	1	0	0	0	0	0	0
Cc	0	0	1	1	1	1	0	1	0	1	0	1	0	1	0	1	0	1	1	1	1	2	1	1	0	0	0	0	0
Cv	0	0	1	1	1	1	0	1	0	1	0	1	0	1	1	1	0	1	1	0	0	2	1	0	0	0	0	0	0
Ci	0	0	1	1	0	1	0	1	0	1	0	1	0	1	2	1	1	1	1	1	1	2	1	1	0	0	0	0	0
Cm	0	0	1	1	1	1	0	1	0	1	2	1	0	1	2	1	1	0	1	1	0	1	2	0	0	0	0	0	0
Ca	0	0	1	1	1	1	0	1	0	1	0	1	0	1	0	1	0	1	1	1	1	2	1	1	0	0	0	0	0
Cu	0	0	1	1	1	1	0	1	0	1	0	1	0	1	0	1	0	2	1	1	0	1	1	0	0	0	1	0	0
Co	0	0	1	1	1	1	1	1	0	0	?	1	0	1	2	1	0	1	1	1	0	1	1	0	0	0	1	0	0
Pn	1	1	1	1	0	2	0	1	0	1	0	1	1	1	0	1	1	1	1	0	0	2	1	0	0	0	0	0	0
Pf	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	1	2	1	0	0	0	0	0	0
Pr	1	1	1	1	0	1	1	1	0	1	0	1	1	1	0	1	1	1	1	0	1	2	1	0	0	0	0	0	0
Ps	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	0	2	1	0	0	0	0	0	0
Pb	1	1	1	1	1	2	0	1	0	1	0	1	1	1	0	1	1	1	1	0	0	2	1	0	0	0	0	0	0

Table 1: Data matrix. See text for details of species and characters.

Taxa: Species included in the phylogenetic analysis: *Viracucha andicola* (Simon, 1906) (Va); types, 1♂ 1♀, Espírito Santo, San Mateo, Bolivia (Gaslepp, MNHN-15719). *Ctenus coxalis* F. O. Pickard-Cambridge, 1902 (Cx); 1♂ 1♀, São Paulo, Brazil (R. A. Oliveira, 27 May 1996, IBSP 8510). *Ctenus taeniatus* Keyserling, 1891 (Ct); 1♂ 1♀, Arequita, Lavalleja, Uruguay (Eq. Sec. Ent., 17 May 1998, FCE). *Ctenus longipes* Keyserling, 1891 (Cl); Quebrada de los Cuervos, Treinta y Tres, Uruguay, 1♂ (Simó, 25 August 1990, FCE), 1♀ (Simó, 29 May 1990, FCE). *Oligoctenus ornatus* (Keyserling, 1877) (Oo); 1♂ 1♀, Jacaré, São Paulo, Brazil (S. Kamall, September 1961, IBSP 1705). *Ctenus crulsi* Mello-Leitão, 1930 (Cc); 1♂, Balbina, Amazonas, Brazil (Eq. Inst. Butantan, April 1988, IBSP 5668), 1♀, Reserva Ducke, Manaus, Amazonas, Brazil (T. Gasnier, IBSP 14514). *Ctenus villasboasi* Mello-Leitão, 1949 (Cv); 2♂ 2♀, Usina Hidrelétrica de Samuel, Rio Jamari, Rondônia (Eq. Inst. Butantan, December 1980, IBSP 7173 and IBSP 7167). *Ctenus inaja* Höfer, Brescovit & Gasnier, 1994 (Ci); 1♂ 1♀, Reserva Florestal Adolfo Ducke, Manaus, Amazonas, Brazil (described by Höfer *et al.*, 1994). *Ctenus maculisternis* Strand, 1910 (Cm); 1♂, Tucuruí, Pará, Brazil (Eq. Inst. Butantan, August 1989, IBSP 5585), 1♀, Usina Hidrelétrica de Samuel, Rio Jamari, Rondônia, Brazil (Eq. Inst. Butantan, February 1989, IBSP-5689). *Ctenus amphora* Mello-Leitão, 1930 (Ca); 1♂ 1♀, Reserva Florestal Adolfo Ducke, Manaus, Amazonas, Brazil (described by Höfer *et al.*, 1994). *Centroctenus auberti* (Caporiacco, 1954) (Cu); 1♂, Fazenda Esteio, Manaus, Amazonas (T. Gasnier, 12 January 1994, IBSP 8166), 1♀, Reserva Florestal Adolfo Ducke, Manaus, Amazonas, Brazil (described by Höfer *et al.*, 1994). *Centroctenus ocelliventer* (Strand, 1910) (Co); 1♂ 1♀, Alter do Chão, Pará, Brazil (described by Brescovit, 1996). *Phoneutria nigriventer* (Pn), *P. fera* (Pf), *P. reidyi* (Pr), *P. bahiensis* (Ps) and *P. boliviensis* (Pb).

Characters: Multistate characters were categorised as non-additive.

0. Tarsal and tibial pedipalpal scopulae: absent (0); present (1).
1. Defensive behaviour with erect position of body, anterior legs elevated and with lateral movements: absent (0); present (1).
2. Ventral spination of tibiae I: 2-2-2-2-2-2 (0); 2-2-2-2-2 (1).
3. Cribellum: present (0); absent (1).

Females:

4. Female tibiae I, lateral spines: present (0); absent (1).
5. Median field of epigynum: septum (0); quadrangular lobe (1); triangular lobe (2).
6. Anterior lobe of epigynum: absent (0); present (1).
7. Transverse lobes on median field of epigynum: absent (0); present (1).
8. Number of transverse lobes on median field of epigynum: one lobe (0); two lobes (1).
9. Oval anterior lobes on median field of epigynum: absent (0); present (1).

10. Morphology of oval anterior lobes of epigynum: convex lobes emerging at anterior middle field (0); sclerotised lobes at anterior middle field (1); elongated lobes extending through epigynal folds (2).
11. Copulatory opening: placed in broad atria (0); placed in longitudinal concavities or pockets (1).
12. Position of pockets in epigynum: anterior (0); median (1). Taxa (Va) with no pockets scored as unknown (?).
13. Teeth on lateral lobes of epigynum: absent (0); present (1).
14. Position of teeth on lateral lobes of epigynum: median (0); anterior (1), basal (2).
15. Copulatory duct: long, describing a loop (0); simple, straight or slightly sinuous (1).
16. Simple copulatory duct: longer than spermatheca (0); equal to or shorter than spermatheca (1). Taxa (Va) with no simple copulatory duct scored as unknown (?).
17. External shape of spermatheca: elongated, with a head, constriction and basal area (0); spherical, head and base areas undifferentiated (1); spherical to subspherical, with head and base areas clearly differentiated (2).
18. Emergence point of fertilisation duct from base of spermatheca: internal (0); basal (1).

Males:

19. Metatarsus I, apical and lateral spines: present (0); absent (1).
20. Distal tegular projection: absent (0); present (1).
21. Median tegular apophysis shape: not cup-shaped (0); cup-shaped, simple dorsal concavity (1); cup-shaped, dorsal concavity with narrow groove, projecting prolaterally (2).
22. Embolus shape: conical with laminar projection (0); curved conical with broad base (1); curved spine (2).
23. Basal embolar projection (for this feature see Höfer *et al.* (1994) and Brescovit (1996)): absent (0); present (1).
24. Cymbium, basal projection: absent (0); present (1).
25. Male pedipalpal tibia length: equal to or slightly longer than cymbium (0); twice as long as cymbium (1).
26. Male pedipalpal tibia length and width proportion: length greater than width, ventral apophysis absent or poorly developed (0); as long as wide, apically wider, with retrolateral and ventral apophyses well developed (1).

Taxonomy

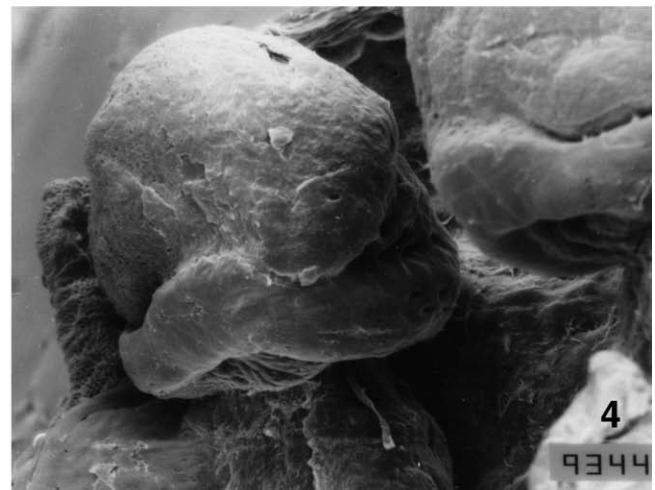
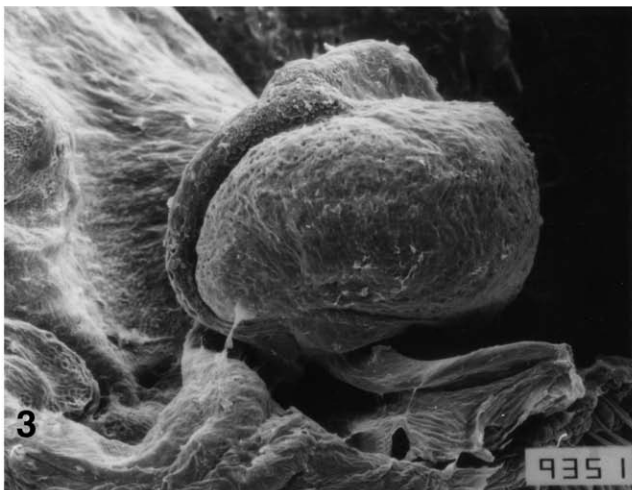
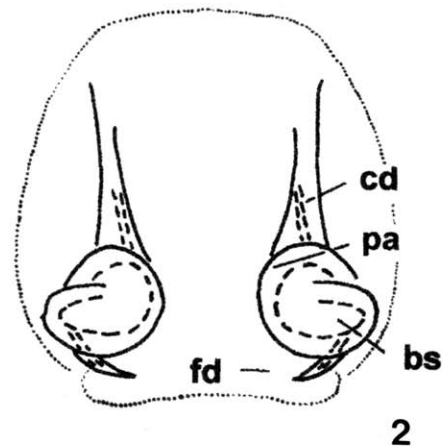
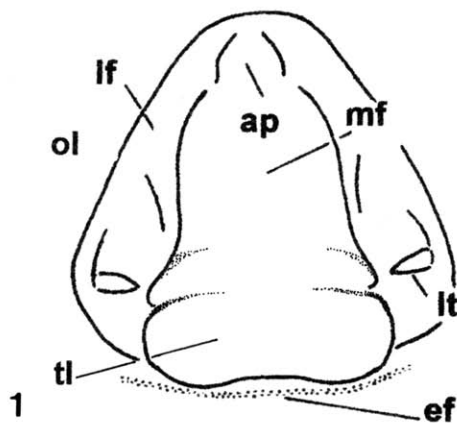
Genus *Phoneutria* Perty, 1833 (Figs. 1–2, 5)

Phoneutria Perty, 1833: 196, 197 (type species *Phoneutria fera* Perty, 1833, designated by F. O. Pickard-Cambridge, 1897: 56, 57, 65, 72); Bonnet, 1958: 3619–3620; Mello-Leitão, 1936: 2, 14; 1940: 104, 105; Neave, 1939: 725; Bücherl *et al.*, 1964: 96–97, 100; Bücherl, 1969a: 47–48; Brignoli, 1983: 588; Platnick, 1989: 503; 1993: 677; 1998: 615.

Diagnosis: Differs from *Ctenus* and other ctenids by the presence of dense scopulae on the palpal promargin and ventral faces, and by the defensive display: erect position and lateral movements of the body with elevated forelegs.

Description: Ecribellate ctenids. Total length 17.0–48.0. Carapace oval in dorsal view, brown, anteriorly rounded, posteriorly truncated, longer than wide; widest between coxae II and III, narrowed at coxae I; lateral margins with black line. Thoracic groove longitudinal, black with dark radially divergent lines. Eyes: elevated ocular tubercle swollen and projecting forward. From front, ocular disposition 2-4-2; both eye rows recurved. AME, PME and PLE circular, larger than oval ALE. Interdistances: AME separated by slightly more than half their diameter, PME-PLE by diameter of PLE, ALE-PLE by radius of AME, AME-PME by slightly less than AME diameter, AME-ALE by diameter of PME or slightly more; MOQ as long as wide. Clypeal height equal to AME diameter. Chelicerae with 3 promarginal and 5 retromarginal teeth. Endites: twice labium length, distally truncated, slightly convergent, with anterior, lateral serrula and anterior, median scopulae. Labium slightly longer than wide, articulated to sternum and with truncated apex. Sternum with sinuous edges, anteriorly truncated, posteriorly pointed.

Palp with dense promarginal and ventral tibial and tarsal scopulae. Leg formula I, IV, II, III. Leg spination usually: I tibia v2-2-2-2-2, p0, r0, metatarsus v2-2-2, p0, r0; II tibia v2-2-2-2-2, p1, r0, metatarsus v2-2-2, p0, r0; III tibia v2-2-2, p1-1, r1-1, metatarsus v2-2-2, p1-1-2, r1-1-2; IV tibia v2-2-2, p1-1, r1-1, metatarsus v2-2-2, p1-1-1-2, r1-1-1-2. Tibiae, metatarsi and tarsi of legs I–IV with dense scopulae; trochanters notched. Trichobothria bases with many transverse ridges; tarsal organ with central, narrowed opening. Legs brown, tarsi with two pectinate claws and claw tufts. Tarsi and metatarsi with two rows of dorsal trichobothria. Abdomen: dorsally light brown with two longitudinal lines of light spots; ventrally dark brown to yellowish; behind epigastric furrow there are radial bands with white spots which diverge from spinnerets. Colulus triangular. Females larger than males. Male palp with retrolateral tibial apophysis; embolus swollen, curved, without basal projection; membranous conductor and cup-shaped median tegular apophysis. Epigynum: middle field elevated, triangular or quadrangular shape, convex anterior lobes and posterior transverse lobe; lateral fields with teeth; copulatory opening pocket-like; copulatory duct slightly sinuous; spermathecae spherical with undifferentiated head and base; fertilisation duct emerging basally.



Figs. 1–4: Morphological features of the female copulatory organs of *Phoneutria*. **1** Epigynum; **2** Vulva; **3–4** Spermatheca of *P. nigriventer*: **3** Ventral view; **4** Lateral view, showing porose area. Scale lines=1 mm. For abbreviations see text.

Composition: Five species.

Distribution: Four groups are recognised:

1. Amazonian: represented by *P. fera* and *P. reidyi*.
2. Central America, Colombia, Ecuador, Perú, Bolivia and north-western Brazil, represented by *P. boliviensis*.
3. Central and south-eastern Brazil, Paraguay, northern Argentina and Uruguay, represented by *P. nigriventer*.
4. South of Bahia state, Brazil, represented by *P. bahiensis* (endemic).

Natural history: *Phoneutria* species live on trees under natural conditions and hunt among the vegetation; secondarily they occur in banana plantations. The transport of this fruit has carried these species to various cities and they have adapted to live in suburban areas of Central and South America.

***Phoneutria fera* Perty, 1833** (Figs. 8–9, 14, 25)

Phoneutria fera Perty, 1833: 197, pl. 39, fig. 3 (female holotype from Río Negro, Amazonas, Brazil, not examined, presumed lost);

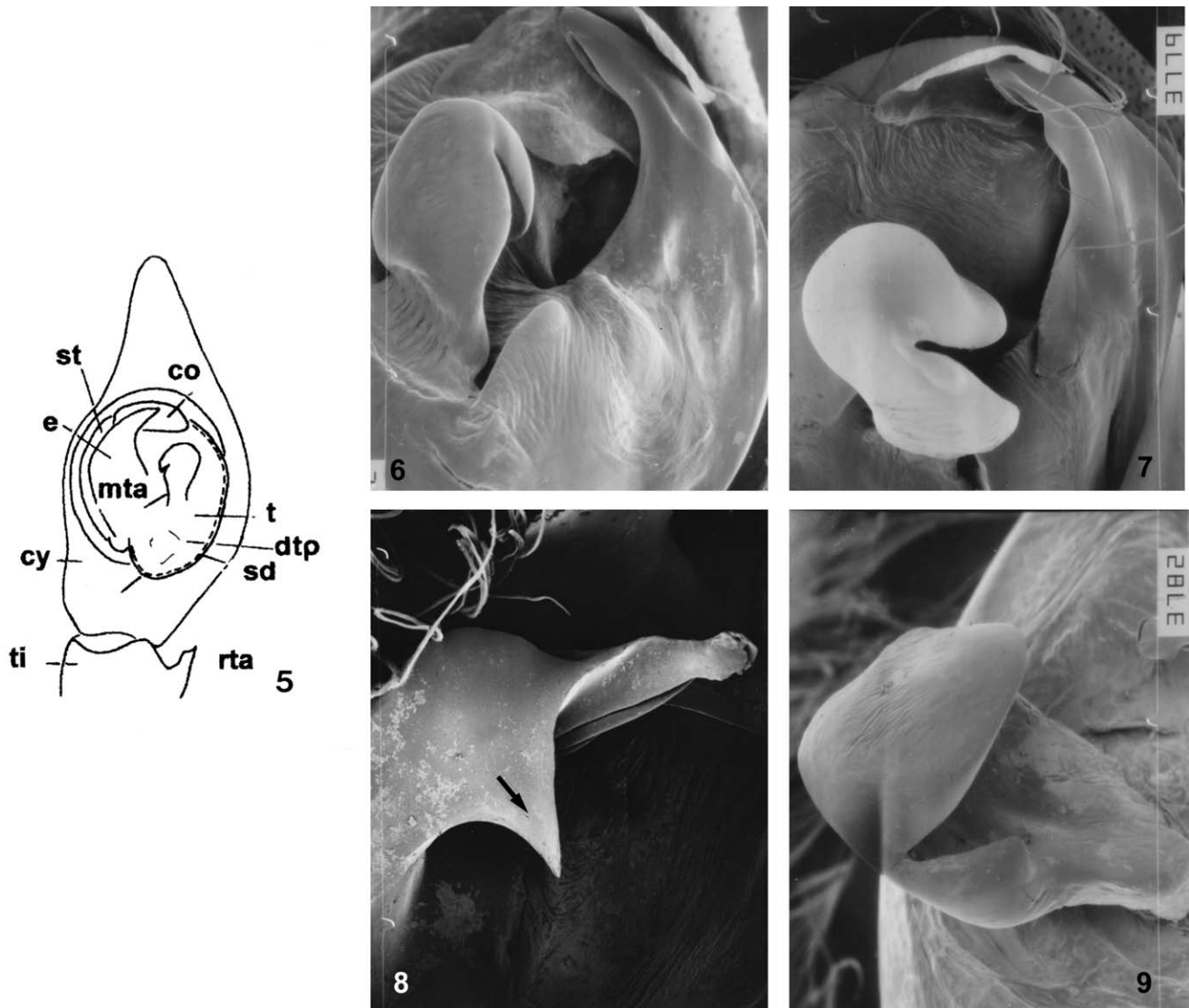
Gervais, 1840: 307; F. O. Pickard-Cambridge, 1897: 53, 57, 59, 64, 66 (designated as type species of genus); Bonnet, 1958: 3620; Bücherl *et al.*, 1969: 47, 52; Eickstedt *et al.*, 1969: 68 (redescription ♀); Bücherl, 1971: 223; Eickstedt, 1979: 96–98, 100; 1983: 183–188 (redescription ♂); Platnick, 1989: 503; 1993: 677; 1998: 615.

Ctenus sus Strand, 1910: 300 (male holotype from Surinam, Michaelis leg., in ZMB 19905, examined); Petrunkevitch, 1911: 478; Caporiacco, 1948: 681; Roewer, 1955: 656; Bonnet, 1956: 1290; Eickstedt, 1983: 184 (syn.).

Phoneutria sus: Bücherl, 1968: 188 (new combination); Eickstedt, 1983: 184; Platnick, 1989: 503; 1993: 677.

Note: For a complement of the synonymic list see Eickstedt (1983: 183).

Diagnosis: This species resembles *P. reidyi* and *P. bahiensis*, but differs from other species of *Phoneutria* by its larger size and the morphology of the copulatory organs. Females can be recognised by the presence of an anterior lobe and two transverse lobes on the epigynal middle field (Eickstedt, 1983: fig. 5). Males can be distinguished by the morphology of the retrolateral tibial apophysis and by the embolus, with a laminar prolongation at the apex (Fig. 8: arrow).



Figs. 5–9: Morphological features of the male copulatory organs of *Phoneutria*. **5** Palpal bulb, ventral view; **6** Right bulb of *P. boliviensis*, ventral view, showing embolus, conductor, and tegular median apophysis with apical groove; **7** Right bulb of *P. nigriventer*, ventral view; **8** Embolus of *P. fera*, laminar projection indicated by arrow; **9** Median tegular apophysis of *P. fera*. Scale lines=1 mm. For abbreviations see text.

Description: Male and female were described by Eickstedt (1983: 183, figs. 1, 3, 5, 7–8).

Other material examined: BRAZIL: *Acre*: Taboquinha, Parque Nacional de Serra do Divisor: 17 November 1996 (R. S. Vieira, IBSP 9216), 1♀ 1 immature; 5–25 September 1996 (R. S. Vieira, IBSP 9277), 1♂; 14 March 1997 (J. Resende & R. S. Vieira, IBSP 12325), 1♀. Xapuri, Pimenteira, 5–7 April 1996 (IBSP/SMNK team, IBSP 16111), 1♂ 1 immature. *Amazonas*: Aracá river, Fazenda Branco, 16 May 1982 (B. Mascarenhas, IBSP 6187), 1♀ 1 immature ♂. Rio Mapiá, Borba, 22 April 1996 (IBSP/SMNK team, IBSP 15984), 1♂. Usina Hidrelétrica de Balbina, Presidente Figueiredo, 1987–1988 (without collector, IBSP 14289, 14293, 14666, 14667, 14670, 14671), 3♂ 4♀. Campus UA, 1994–1995 (M. E. Oliveira, IBSP 15196), 1♀. Reserva Ducke, 22 March 1985 (W. E. Magnusson, IBSP 14311), 1♀ 1 immature. Iauarete: January 1971 (Hoge, IBSP 2518), 1♀; (IBSP 2846), 1♀; (IBSP 2517), 3 immatures, 1 immature ♂. Barcelos, Igarapé Urumutum: 17 August 1980 (B. Mascarenhas, IBSP 2983), 1♂; (IBSP 3285), 1♂; (IBSP 2984), 1♂. Japuriquara, 1964 (Pereira, MZSP 3945), 1♂. *Mato Grosso*: Cuiabá, 16 December 1987 (D. M. de P. Moreira, IBSP 14292), 1♂. 70 km de Alta Floresta, Fazenda Campana, Rio Cristalino, June 1996 (G. Brisola, IBSP 8517, 8598), 1♂ 1♀. Alta Floresta, May 1993 (G. Brisola, IBSP 5814), 1♀. *Mato Grosso do Sul*: Bonito, May 1983 (M. Soma, IBSP 4910), 1♂. *Pará*: Belém, Mocambo, 25 April 1978 (collected with Malaise trap, MPEG), 1♂. *Roraima*: Ilha de Maracá, 11 December 1994 (G. Skuk, IBSP 5758), 1♂. *São Paulo*: São Paulo, 14 January 1998 (M. Matsubara, IBSP 14665, 14666), 1♂ 1♀. ECUADOR: Los Tayos: 10 July 1976 (Ashmole, IBSP 4299), 1♂; 20 July 1976 (Ashmole, IBSP 2982), 1♂. PERÚ: Panguana, Yuyapichis river, 6 September 1977 (Meede, IBSP 2903), 1♂. *Loreto*: Iquitos, without date (G. Resch, IBSP 14304), 3♀. GUYANA: Upper Mazaruni, Pipilipai: 30 July 1971 (M. Lyes, IBSP 2619), 1♂; (IBSP 2620), 1 immature.

Distribution: Amazonian region of Brazil, Ecuador, Perú, Surinam and Guyana. Specimens from São Paulo (Brazil) were probably introduced with transported wood.

***Phoneutria nigriventer* (Keyserling, 1891)** (Figs. 3–4, 7, 10–13, 15, 24)

Ctenus nigriventer Keyserling, 1891: 144, pl. 4, fig. 98 (female holotype from Rio Grande do Sul, Brazil, von Ihering leg., in BMNH 1890-7-1-2914, examined); Strand, 1910: 296–298 (description ♂); Petrunkevitch, 1911: 475 (except citation of Strand, 1907); Platnick, 1993: 674.

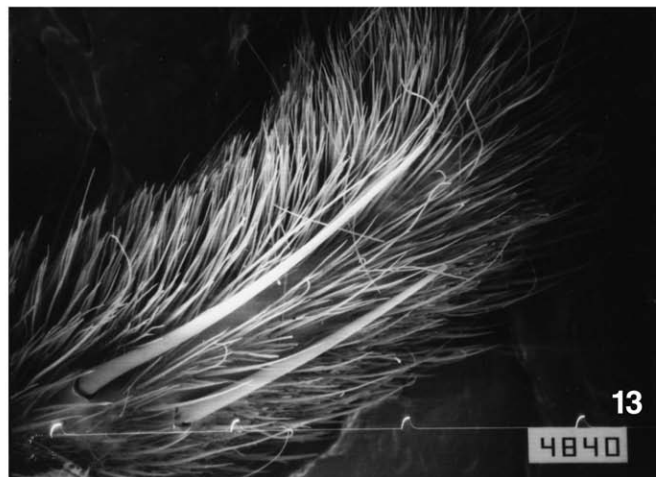
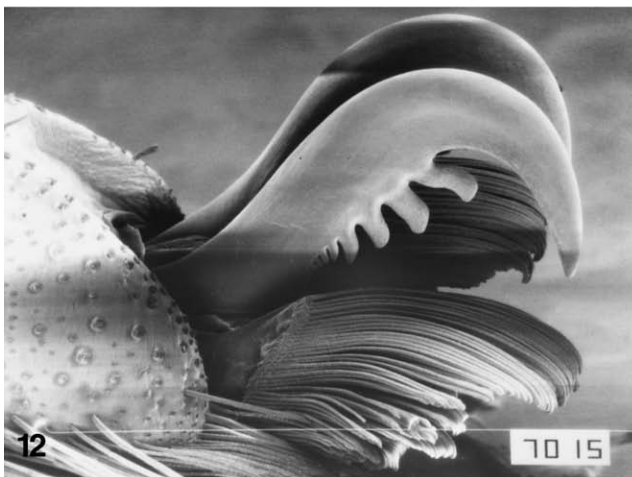
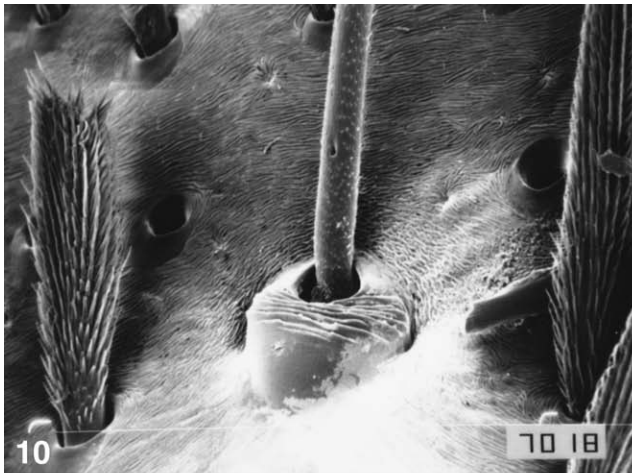
Ctenus ferus: Keyserling, 1891: 145 (misidentification).

Ctenus keyserlingi F. O. Pickard-Cambridge, 1897: 53, 55, 59, 64, 76, 81 (new name for specimens misidentified as *Ctenus ferus* by Keyserling, female holotype from Rio de Janeiro, Brazil, Goeldi leg., in BMNH, Keyserling coll., examined). **New synonymy.**

Ctenus rufibarbis: Keyserling, 1881: 576 (misidentification).

Ctenus pertyi F. O. Pickard-Cambridge, 1897: 80 (new name for specimens misidentified as *Ctenus rufibarbis* by Keyserling, female holotype from Nova Friburgo, Rio de Janeiro, Brazil, in BMNH no. 2067, examined); F. O. Pickard-Cambridge, 1902: 409, 412; Mello-Leitão, 1933: 47; 1936: 18 (listed under *P. rufibarbis*); Eickstedt, 1979: 99. **New synonymy.**

Ctenus nigriventroides: Strand, 1915: 129, 130 (misidentification, two females from Joinville, Santa Catarina, Brazil), W. Ehrhardt leg., 1906, in SMF 5003, examined; Roewer, 1955: 653 (in part, only material from Brazil); Mello-Leitão, 1936: 16.



Figs. 10–13: *P. nigriventer*. **10** Sensillum and trichobothrium, left tarsus IV; **11** Tarsal organ, left tarsus I; **12** Claw, left tarsus I; **13** Pedipalp scopula, female tarsus. Scale lines=0.01 mm (11), 0.1 mm (10), 1.0 mm (12, 13).

Ctenus rufichelis Mello-Leitão, 1917: 97, figs. 15, 16 (male holotype from São João del Rey, Minas Gerais, Brazil, presumed lost); Bücherl, 1968: 190 (syn.); Eickstedt, 1979: 106–109.

Ctenus paca Mello-Leitão, 1922: 41 (immature female holotype from São Paulo, São Paulo, Brazil, Garbe leg., 1921, in MZSP 11053, examined); Bücherl, 1968: 190 (syn.); Eickstedt & Lucas, 1969: 75; Platnick, 1993: 674.

Ctenus luederwaldti Mello-Leitão, 1927: 397, 403 (immature female holotype from Blumenau, Santa Catarina, Brazil, Luederwaldt leg., November 1924, in MZSP 940, examined); Bücherl, 1968: 189 (syn.); Eickstedt & Lucas, 1969: 76; Eickstedt, 1979: 118; Platnick, 1993: 674.

Phoneutria nigriventer: Mello-Leitão, 1936: 15, 17, 599, pl. 1: fig. 36, pl. 3: figs. 34, 35; Eickstedt, 1979: 106–117, figs. 1, 3, 5, 7–10 (redescription ♂♀); Platnick, 1989: 503; 1993: 677; 1998: 615.

Phoneutria nigriventroides: Mello-Leitão, 1936: 599; Bonnet, 1958: 3621 (in part, only material from Brazil); Eickstedt, 1979: 111 (only specimens from Brazil).

Phoneutria paca: Mello-Leitão, 1936: 15, 18; Eickstedt & Lucas, 1969: 75–77; Eickstedt, 1979: 106, 109–110; Platnick, 1993: 677.

Phoneutria rufichelis: Mello-Leitão, 1936: 15 (new combination); Bücherl *et al.*, 1969: 64, 66; Eickstedt, 1979: 106, 109; Platnick, 1993: 678.

Phoneutria ochracea: Mello-Leitão, 1936: 17, fig. 37 (misidentification).

Phoneutria luederwaldti: Mello-Leitão, 1936: 15, 18; Eickstedt, 1979: 118 (syn. with *P. keyserlingi*); Platnick, 1989: 503; 1993: 677.

Phoneutria pertyi: Eickstedt, 1979: 97, 99, 100.

Phoneutria keyserlingi: Bücherl, 1969b: 157; Bücherl, 1972: 123; Schiapelli & Gerschman de Pikelin, 1973: 32 (syn. with *P. fera*); Eickstedt, 1979: 118, figs. 2, 4, 6, 8–10 (revalidation and redescription); Platnick, 1989: 503; 1993: 677; 1998: 615.

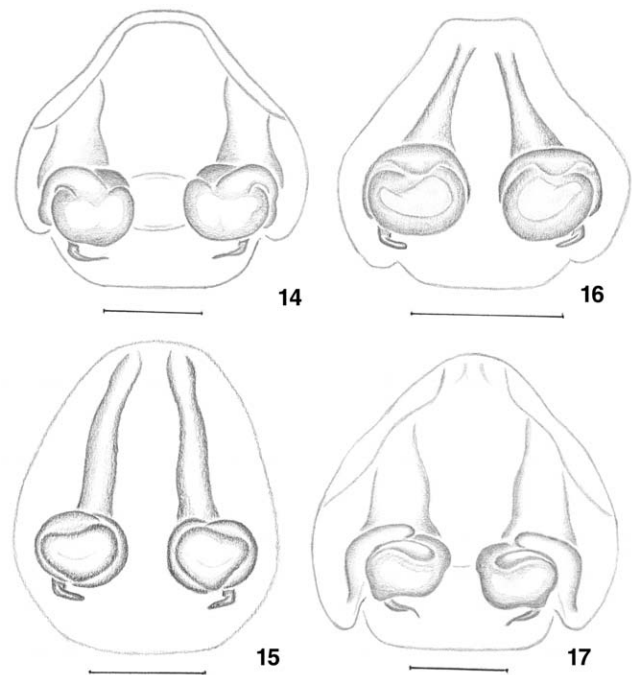
Note: For a complement of the synonymic list see Eickstedt (1979: 106, 118).

Synonyms: The morphology of the edges of the middle field is highly variable; the lateral guides can be continuous or very sinuous. Eickstedt (1979) distinguished *P. nigriventer* from *P. keyserlingi* by the larger epigynal lateral guides and the less curved embolus of the latter species. These differences only represent intraspecific variability. The use of the lateral guides of the epigynum as a diagnostic character has not been recommended in other ctenids such as *Asthenoctenus* (Simó & Eickstedt, 1994).

Phoneutria pertyi (F. O. Pickard-Cambridge, 1897) was distinguished on the basis of the equal length of legs I and IV and by the epigynum not being truncated anteriorly. Eickstedt (1979) considered this species as valid until more material from the type locality could be studied and compared with the holotype. We examined other specimens and considered that the characters indicated by Pickard-Cambridge are not diagnostic and that the morphology of the epigynum of the holotype of this species corresponds with *P. nigriventer*.

Diagnosis: Females can be distinguished by the triangular middle epigynal field with truncated apex and by the reduction of the teeth on the lateral lobes (Eickstedt, 1979: figs. 1, 2). Males can be recognised by the morphology of the retrolateral tibial apophysis and the tegular median apophysis (Figs. 7, 24).

Description: Male and female described by Eickstedt, 1979: 106, figs. 1, 3, 5, 7–10, table 1 and 118, figs. 2, 4, 6, 8–10, table 2. Additional data presented here: elongate sensillum, and trichobothrial base bearing many transverse ridges (Fig. 10); tarsal organ with central narrowed opening (Fig. 11); claws of leg I pectinate with five teeth



Figs. 14–17: Vulvae. **14** *P. fera*; **15** *P. nigriventer*; **16** *P. boliviensis*; **17** *P. reidyi*. Scale lines=1.0 mm.

(Fig. 12); scopulae of female pedipalp well developed (Fig. 13). Palp as in Figs. 7 and 24. Epigynum as in Fig. 15.

Other material examined: BRAZIL: (MNHN 19299), 2♀. *Bahia*: Jussari, 1967–1971 (Ceplac, MNRJ 13289), 1♂. *Distrito Federal*: Brasília, 1974 (Mattei, IBSP 2764), 1♀ 1♂. *Espírito Santo*: Reserva Florestal Vale do Rio Doce, 19–25 July 1997 (Brescovit *et al.*, IBSP 12651, 12692, 12867, 12919, 16521), 3♂ 2♀. Domingos Martins, 27 April 1989 (Nickel, IBSP 14119, 14297), 2♂. *Goiás* (IBSP 1927), 1♀. Parque Nacional de Emas, Minas, 3 May 1997 (Girardi, IBSP 9529), 1♂. *Mato Grosso*: Barra do Garças, December 1994 (Baugarten, IBSP 6033), 1♂. Ilha do Padre, 8 June 1981 (IBSP 554), 1♀. *Mato Grosso do Sul*: Bonito, May 1983 (Soma, IBSP 4910), 1♂. Corumbá, 19 February 1981 (Mix, IBSP 11856), 1♂. Usina Hidrelétrica Sérgio Motta, 15 November–23 December 1998 (IBSP team, IBSP 23441, 23484), 1♂ 1♀. Paranaíba, 19 January 1984 (da Silva, IBSP 6809, 6810, 6813, 14112, 14298), 3♂ 2♀. *Minas Gerais*: Arceburgo, March 1998 (Batistella, IBSP 4754), 1♂. Belo Horizonte, May 1981 (Neves, IBSP 1181, 6813), 2♂. Bocaina de Minas, April–June 1988 (Cruzeta, IBSP 4749, 14066), 1♂ 1♀. Cambuí, October 1994 (Gregorio, IBSP 1766), 1♀ 2♂. Juiz de Fora, April 1972 (Vieira, IBSP 2574), 1♀. *Rio de Janeiro*: Barra Mansa, May 1995 (Folly & Almeida, IBSP 11860, 11888), 1♂ 1♀. Nova Friburgo, September 1981 (Mix, IBSP 2957, 3157, 3142, 3027, 3154, 2957), 5♀ 3♂. Petrópolis (Assunção, IBSP 2703), 1♀. Rio de Janeiro (Bachmann, MACN-5882), 1♀. Serra das Araras, 21 December 1996 (Lunetta, IBSP 14114), 1♀. Serra dos Orgãos, 25 March 1996 (Cotrim, IBSP 11890), 1♀. *Santa Catarina*: Balneário Barra do Sul, 12 December 1997 (Rzeppa, IBSP 15362), 1♂. Joinville, October 1948 (Goffergé, MZSP 6895), 2♀. Florianópolis: January 1982 (Senice, IBSP 4913), 1♀; 13 May 1997 (Giraldi, IBSP 9991), 1♂. *Rio Grande do Sul*: Porto Alegre (IBSP 2575), 1♀ 1♂. *São Paulo*: Cananéia, 2 July 1971 (IBSP 2494), 1♂ 1♀. Guarani do Oeste, 20 July 1978 (Peronto, IBSP 14106), 2♀. Iguape, 24 July 1979 (Yokoda, IBSP 11582), 1♂. Ilha dos Búzios, April 1997 (Zanetti, IBSP 10282), 1♀. Santana do Parnaíba, 15 June 1998 (Pref. Municipal, IBSP 20473), 1♂. Santos (Birabén, MACN-5878), 1♀. Santos-Piassaguera, February 1913 (Luederwaldt, MZSP-8935), 1♂. Ilha São Sebastião, 12 November 1960 (Urban, MZSP-6572), 1♀. São Paulo, 8 October 1967 (Simões, MZSP 6889), 2♀. Ilha de Alcatrazes, October 1920 (Luederwaldt & Fonseca, MZSP 8941), 1♀. Paranaipacaba, 31 May 1954 (IBSP 947), 1♀ 1♂. *Paraná*: Boa Vista da Aparecida, 7–14 October 1998 (IBSP team, IBSP 21366, 21368, 21392), 3♀. Candói/Mangueirinha, 2 May 1996 (Bertani *et al.*, IBSP 11533, 11588, 11590, 11597, 11608, 11627, 11628, 11631, 11703),

11♂ 22♀. Cruzeiro do Iguaçu, 8–15 October 1998 (IBSP team, IBSP 21365), 1♀. Curitiba, 1994/1995 (IBSP 440, 489), 2♂. Rio Azul (Koas, IBSP 2446), 3♀. Laranjeiras, Salto Santiago, 19 October 1979 (I. Knyzak, IBSP 14294, 14306), 12♀. Serra dos Dourados, Usina Hidrelétrica do Foz do Areia, 23 April 1980 (IBSP 10027, 10028, 10029, 10500, 10533, 10561, 10562), 6♂ 19♀. URUGUAY: *Montevideo*: Mercado Agrícola, 9 October 1971 (Mowszcowicz, MNHN-M 267), 2♀. Mercado Modelo (in bananas imported from Brazil): 21 May 1970 (Montero, MNHN-M 717), 1♀; May–August 1983 (Simó, MNHN-M 958, 980, 1006), 7♀ 1♂; 10 March 1984 (Simó, MNHN-M 1054), 1♀ 2♂; July 1986 (Blengini, MNHN-M), 3♀ 1♂; 4 March 1986 (Simó, FCE), 1♀. ARGENTINA: *Misiones*: Santa Ana, May 1975 (Tosh, MACN-6836), 1♀. Pueblo Libertad, August 1963 (Assaia-Fornes, MACN-6454), 2♀. *Buenos Aires*: Capital: May 1966 (Prosen, MACN-5879), 1♀ 1♂; March 1974 (Grisolia, MACN), 15♀ 7♂. San Luis (Greslebin, MACN-5876), 1♀. Hospital Muniz, 24 May 1963 (Stern, MACN), 1♀. La Paternal, 26 March 1965 (Arin, MACN), 1♀. PARAGUAY: (MNHN 8581), 1♀ 1♂ 3 immatures. (See also material cited in Eickstedt (1979) for *P. nigriventer* and *P. keyserlingi*.)

Distribution: Northern Argentina, Uruguay, Paraguay, central and south-eastern Brazil. Specimens from Montevideo (Uruguay) and Buenos Aires (Argentina) were probably introduced with imported bananas.

***Phoneutria boliviensis* (F. O. Pickard-Cambridge, 1897)**
(Figs. 6, 16, 22)

Ctenus boliviensis F. O. Pickard-Cambridge, 1897: 80 (female holotype from Madre de Dios, Bolivia, not found, see Schiapelli & Gerschman de Pikelin, 1973: 36); F. O. Pickard-Cambridge, 1902: 407, 409, 412; Strand, 1907: 426; Petrunkevitch, 1911: 471; Vellard, 1936: 173; Roewer, 1955: 648; Bonnet, 1956: 1276; Platnick, 1993: 674.

Ctenus nigriventroides Strand, 1907 (female holotype from Bolivia, not found, presumed lost); Petrunkevitch, 1911: 735 (syn. with *C. nigriventer*); Roewer, 1955: 653 (in part, only material from Bolivia; Bücherl *et al.*, 1969: 60; Platnick, 1993: 674. **New synonymy.**

Ctenus signativenter Strand, 1910: 305 (male and two female syntypes, all immatures, from Paramba, Ecuador, 3500 ft, 28 April 1898, Rosenberg leg., in ZMB 30660, examined); Petrunkevitch, 1911: 477, Roewer, 1955: 655; Bonnet, 1956: 1289. **New synonymy.**

Ctenus depilatus Strand, 1910: 413, 414 (male holotype from Colombia, Dana leg., in ZMB 30615, examined); Petrunkevitch, 1911: 472; Roewer, 1955: 649; Bonnet, 1956: 1279. **New synonymy.**

Ctenus valdehirsutulus Strand, 1910: 318 (syntypes: female from Sara, W. Bolivia, 60 m, 14 March 1907, J. Steinbach leg., in ZMB 30615, examined; female from Sara, Dpto. Sta. Cruz de la Sierra, Bolivia, 500 m, Steinbach, in ZMB 30616, examined); Petrunkevitch, 1911: 478; Roewer, 1955: 656; Bonnet, 1956: 1291. **New synonymy.**

Ctenus peregrinus: Strand, 1910: 318 (as *peregrinoides*) (syntypes: two females from Guatemala, in ZMB 30717, examined); Strand, 1927: 24. **New synonymy.**

Ctenus nigriventer: Petrunkevitch, 1911: 475 (only citation of Strand, 1907), 735.

Ctenus peregrinus: Petrunkevitch, 1911: 476 (only Strand citation); Roewer, 1955: 654 (only Strand citation); Bonnet, 1956: 1287 (only Strand citation).

Ctenus chilesicus Strand, 1915: 128 (female holotype from Chile, 1902, O. Hohenomser S. leg., in SMF-4557, examined); Roewer, 1955: 648; Bonnet, 1956: 1278. **New synonymy.**

Phoneutria depilata: Schmidt, 1954: 417, 418; 1971: 424.

Phoneutria boliviensis: Schmidt, 1954: 414; 1956: 28; Bücherl, 1968: 188; 1969a: 49; Schiapelli & Gerschman de Pikelin, 1973: 31, 33–38 (redescription ♂♀); Valerio, 1983: 101, 102; Platnick, 1989: 503; 1993: 677; 1998: 615.

Phoneutria colombiana Schmidt, 1954: 418; 1956: 28 (female holotype from Colombia, in SMF, examined); Schiapelli & Gerschman

de Pikelin, 1973: 34 (syn.); Brignoli, 1983: 588; Platnick, 1993: 677.

Phoneutria nigriventroides: Bonnet, 1958: 3621 (in part, only material from Bolivia); Eickstedt, 1979: 111; Platnick, 1993: 678.

Comments: Schiapelli & Gerschman de Pikelin (1973) indicated that the vial with the holotype, deposited in the Natural History Museum, London, contained a female of *P. nigriventer* and an immature *Phoneutria* sp. We did not find these specimens among other material examined in the BMNH, so we consider the holotype to be lost.

Variability: Brazilian and Bolivian material has the epigynal middle field convex at the apex. Specimens from Central America and Colombia have the lateral edges of the middle field separated at the apex and gradually diverging posteriorly.

Synonyms: The morphology of the epigynal middle field is variable. In specimens from Central America to Colombia it is triangular, with a wide base and a narrow apex, but in specimens from Ecuador to Bolivia the apex is more rounded.

Strand (1910) distinguished *Ctenus depilatus* from *C. boliviensis* by the thinner apex of the embolus, by the prominence on the median tegular apophysis in lateral view and by the smaller retrolateral tibial apophysis. These differences represent only intraspecific variation.

Ctenus valdehirsutulus Strand, 1910 and *C. chilesicus* Strand, 1915. The epigynal morphology is like that described for specimens from Ecuador to Bolivia. For this reason, these species are considered as junior synonyms of *P. boliviensis*.

Ctenus nigriventroides Strand, 1907. Strand (1907) described under *C. nigriventer* a female from Bolivia with different coloration (not found, probably lost; see Eickstedt, 1979: 111), for which he suggested the name *C. nigriventroides*. Strand considered that the epigynal morphology of this species was similar to that of *P. nigriventer* but with the middle field edges gradually divergent. Although the holotype is lost, the presence of a triangular epigynal lobe and the study of other specimens from Bolivia indicate that this species is a junior synonym of *P. boliviensis*.

Ctenus peregrinus: Strand, 1910. Under this species described by F. O. Pickard-Cambridge (1900), Strand included two females from Guatemala. This author found some differences in epigynal morphology between his specimens and the holotype and he suggested that, if they represented a new species, it might be designated as *C. peregrinoides*. Study of the specimens cited by Strand shows that they are two females of *P. boliviensis*.

Ctenus signativenter Strand, 1910. Study of the sub-adult specimens described by Strand indicates that by colour and distribution they correspond to specimens of *P. boliviensis* from Ecuador.

Diagnosis: Females of *P. boliviensis* differ from *P. nigriventer* by the larger lateral field teeth and by having the epigynal middle field edges less sclerotised and closer at the apex (see Schiapelli & Gerschman de Pikelin, 1973: fig. 4). Males can be distinguished from other species by the morphology of the retrolateral tibial

apophysis (see Schiapelli & Gerschman de Pikelin, 1973: figs. 7–8).

Description: Male and female described by Schiapelli & Gerschman de Pikelin, 1973: 34, figs. 4–8. Palp as in Figs. 6, 22. Epigynum as in Fig. 16.

Other material examined: BOLIVIA: Charuplaga (Simons, BMNH 03-7-1-145-148), 1♂. Sara, San Ignacio, 9 April 1961 (Lourenço, IBSP 2148), 1♀ immature. PERU: Panguana, near Yuyapichis river, 24 August 1977 (U. Meede, IBSP 2905), 2♀. Tournavista, left margin of Pachitea river, November 1968 (O. Meneses, IBSP 3148), 1♀. Marcapata Valley (BMNH 03-4-1-149-153), 3♂ 1♀. Rio Jopano, 1903 (BMNH 03-7-1-164), 1♂. Sulidero, 1903 (BMNH 03-7-1-162-163), 1♀ 1♂. Paramba, 1898 (BMNH 1898-12-17-5-7), 2♀ 1♂. Pavoruba, 1903 (BMNH 03-7-1-165-166), 2♀. Loreto: Puerto Recreo: January 1969 (V. Revera, IBSP 2174), 1♀; April 1969 (O. Meneses, IBSP 3147), 1♀. Lima: Pachitea river, Bosque Leoncio Prado (O. Meneses, IBSP 2558), 2♀. Cuzco: La Convención, 9 July 1976 (Kiteri, FCE), 1♀. ECUADOR: (BMNH 03-7-1-165-166), 1♀. 1903 (Rosenberg, BMNH 1903-7-1-165-166), 2♀. March 1960 (Schmidt, ZMH), 1♀. 1972 (Schmidt, SMF 25858/6), 3♀. 20 July 1965 (R. Brandt, IBSP 2496), 1♀, and 21 August 1970 (R. Brandt, IBSP 2496), 1♀ (Santiago, Chile, in bananas imported from Ecuador). Los Tayos: 21 July 1976 (P. Ashmole, IBSP 4300), 1♀; (P. Ashmole, IBSP 4302), 1♀; 30 July 1976 (P. Ashmole, IBSP 4301), 1♀. Pambilar, 1886 (Ex. Boel., MNHN 19094), 4♂. Andes, 1874 (Ex. Boel., MNHN 21948), 5♀ 3♂. *Esmeraldas*: Carondelet, 1903 (Rosenberg, BMNH 1903-7-1-154-157), 2♀ 2♂. COLOMBIA: 19 May 1954 (Schmidt, ZMH), 1♀; (Schmidt, SMF 25854/1), 1♀. Antioquia: March 1983 (R. Velez, IBSP 14118), 1♀. Medellín, 1993 (without collector, IBSP 11861), 1♀. Magdalena: Santa Martha (BMNH 02-11-2-11-14), 3♀ 2 immatures. COSTA RICA: 18 December 1990 (D. Pinz, IBSP 10495), 1♀. Guapiles, July 1971 (R. Zeledon, IBSP 2471), 1♀. BRAZIL: Acre: Xapurí, Pimenteira, 5–7 April 1986 (IBSP/SMNK team, IBSP 16112), 1♀. Rio Branco, Reserva Extrativista Humaitá, 12 April 1966 (IBSP/SMNK team, IBSP 15806), 1♂ 1♀. Parque Nacional da Serra do Divisor, Pedernal, 13 November 1996 (R. S. Vieira, IBSP 9155), 1♂. Morro Queimado, 8 November 1996 (R. S. Vieira, IBSP 9107), 1♀. Anil, 12 November 1996 (R. S. Vieira, IBSP 9283), 1♂ 1 immature. Amazonas: Humaitá, 15 November 1986 (Moretti, IBSP 4285), 1♂. São Paulo, Campus do Instituto de Biociências, 8 May 1991 (G. C. dos Santos, IBSP 14068), 1♀. PARAGUAY: (MNHN 8581), 1♂ 1♀, 1 immature ♂, 2 immatures. CHILE: Santiago: Santiago, 1966 (R. Brandt, IBSP 1977), 1♀.

Distribution: Bolivia, Paraguay, Peru, Ecuador, north-western Brazil, Colombia and Central America. Specimens from Santiago (Chile) and São Paulo (Brazil) were probably introduced with imported bananas.

Phoneutria reidyi (F. O. Pickard-Cambridge, 1897) (Figs. 17, 23)

Ctenus reidyi F. O. Pickard-Cambridge, 1897: 54, 76, 78 (female holotype from Santarém, Pará, Brazil, 1896, in BMNH 1896-12-13-95, examined); F. O. Pickard-Cambridge, 1902: 409, 412; Petrunkevitch, 1911: 476; Vellard, 1936: 173; Roewer, 1955: 654; Bücherl, 1968: 188 (syn. with *C. rufibarbis* Perty); Platnick, 1993: 674.

Ctenus andrewsi F. O. Pickard-Cambridge, 1897: 34, 76, 79, pl. 3: fig. 2b (female holotype from Santarém, Pará, Brazil, 1896, American Exped., 1896 coll., in BMNH 1896-12-13-92-94, examined; Bücherl, 1968: 188 (syn. with *C. rufibarbis* Perty); Platnick, 1993: 674.

Ctenus forcipatus Mello-Leitão, 1922: 39 (female holotype from Mariana, Minas Gerais, Brazil, 1919, Pinto Fonseca leg., in MZSP 8930, examined); 1936: 5, 7; Roewer, 1955: 650; Bonnet, 1956: 1281. **New synonymy.**

Phoneutria reidyi: Mello-Leitão, 1936: 15, 18; Vellard, 1936: 179; Caporiacco, 1948: 681; Bonnet, 1958: 3621; Bücherl, 1968: 188; Bücherl *et al.*, 1969: 61; Eickstedt *et al.*, 1969: 67 (redescription ♀); Bücherl, 1971: 223; Schiapelli & Gerschman de Pikelin,

1973: 31 (redescription of holotype); Eickstedt, 1983: 188 (revalidation); Platnick, 1989: 503; 1993: 678.

Phoneutria andrewsi: Mello-Leitão, 1936: 15, 16, fig. 31; Bonnet, 1958: 3620; Bücherl, 1968: 188; Bücherl *et al.*, 1969: 48; Eickstedt *et al.*, 1969: 67, 70 (syn. with *P. reidyi*); Bücherl, 1971: 223; Schiapelli & Gerschman de Pikelin, 1973: 32; Platnick, 1993: 677.

Phoneutria fera: Eickstedt, 1969: 33 (misidentification).

Note: For a complement of the synonymic list and description of this species see Schiapelli & Gerschman de Pikelin (1973: 32, figs. 1–3) and Eickstedt (1983: 188, figs. 2, 4, 6).

Synonym: *Ctenus forcipatus* Mello-Leitão, 1922. Examination of the epigynum of the female described by Mello-Leitão from Minas Gerais, Brazil, indicated that it corresponds to a female epigynum of *P. reidyi*.

Diagnosis: *P. reidyi* resembles *P. fera* and *P. bahiensis*, but differs by the smaller anterior epigynal lobe and by having the anterior edge of the epigynal middle field internally curved (Fig. 17) and by the morphology of the retrolateral tibial apophysis and the embolus (more curved and thinner at its base) of the male palp (Fig. 23 and Eickstedt, 1979: fig. 2).

Other material examined: BRAZIL: Amapá: Macapá, June 1966 (Barros, IBSP 2002), 1♀. Amazonas: Negro river, 20 April 1967 (Col. Exp. Dept. Zool., MZSP 6328), 1♀. Barreira do Matupiri, 18 April 1996 (IBSP/SMNK team, IBSP 15451), 1♂. Boca do Purus river, 1 April 1967 (Vanzolini, MZSP 6313), 1♀. Presidente Figueiredo, 4 October 1991 (Pontes, IBSP 14216), 1♀. Pará: Tucuruí, April 1984 (IBSP team, IBSP 5336), 1♀. Inajá, Boca do Pocuruí river, December 1984, March 1985 (Butantan team, IBSP 5630, 5631, 6829), 33♀ 9♂. Left margin of Tocantins river, 21 June 1984 (Overal *et al.*, MPEG), 1♀ 2♂. Canoal, 28 March 1984 (Bandeira & Torres, MPEG), 1♂. Bujaru (km 26), 12 May 1978 (Neto, MPEG), 1♀. Benavides, 9 December 1979 (Helio, MPEG), 1♀. Ananindeua, 10 November 1972 (Da Silva, MPEG), 1♂. Uriboca, BR316, km 7, 18 July 1975 (Da Silva, MPEG), 2♂. Belém, July 1971 (Galiano, MACN 6457), 1♀. Icoaraci, 2 August 1977 (Da Silva, MPEG), 1♂. Fazenda Velha, June 1968 (Kano, IBSP 2169), 1♀. Rodovia, km 93, 20 October 1959 (MZSP 6305), 1♀. Rondônia: Porto Velho, Barreira do Matupiri, 9 October 1973 (Inaluy, IBSP 2714), 2♀. Usina Hidrelétrica de Samuel, January–February 1989 (Butantan team, IBSP 6213, 6214, 6215, 6216, 14290, 14303, 14690, 14681, 14676, 14689, 14694, 14704, 14680, 14711, 14687, 14705, 14683, 14725, 14673, 14682, 14726, 14703, 14691, 14723, 14702, 14724, 14675, 14707, 14692, 14696, 14678, 14708, 14709, 14712), 14♂ 19♀. Mato Grosso: Apicás, 30 January–27 February 1997 (Calleffo & Skuk, IBSP 8555, 8556), 3♂ 1♀. São José do Rio Claro, 12–27 June 1997 (Calleffo, IBSP 11004), 1♀. Distrito Federal: Brasília, February 1971 (Lourenço, IBSP 2805), 1♀. Minas Gerais: Mariana, 1919, Fonseca leg. (MZSP 8930, holotype of *C. forcipatus*). VENEZUELA: Divisa (IBSP 1183), 1♂. PERU: Chauchamayo, 1907 (BMNH 07-5-4-5-8), 1♀. Marcapeta Valley (BMNH 03-7-1-149-153), 3♂ 1♀. Junin: Galera (MNHN 21951), 1♂. GUYANA: 1939 (Hudson, BMNH 1939-3-24-57), 1♀.

Distribution: Amazonian region of Brazil, Peru, Venezuela and Guyana. This species was probably introduced into Minas Gerais, Brazil, by human transport.

Phoneutria bahiensis, new species (Figs. 18–21, 26)

Types: Male holotype from Ceplac, Reserve Forest, Ilhéus, Bahia, Brazil, 12 April 1998, A.D. Brescovit *et al.* leg., IBSP 19027; 1♀ paratype, same data as holotype, IBSP 19040; 1♂ paratype, same locality, 11 April 1998, A.D. Brescovit leg., IBSP 19344.

Etymology: The specific name refers to its occurrence in the state of Bahia, Brazil.

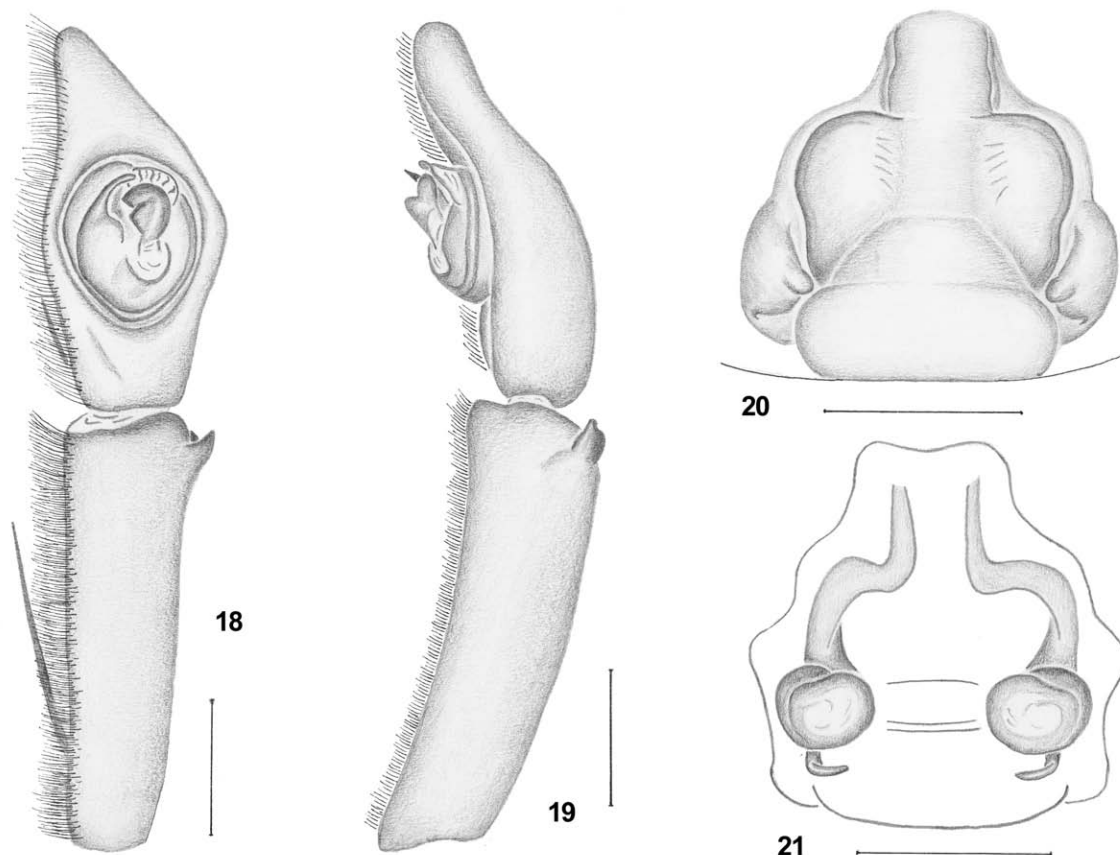
Diagnosis: *P. bahiensis* resembles *P. fera* and *P. reidyi*, but the females differ from *P. fera* by the smaller anterior epigynal lobe and differ from *P. reidyi* by the presence of two posterior epigynal transverse lobes. Males can be distinguished by the longer pedipalpal tibiae and the morphology of the retrolateral tibial apophysis.

Description: *Male* (UFBA, LAP-A no. 173): Total length 24.0. Carapace length 14.0 width 10.5. Abdomen length 9.5. Carapace orange, with black line on margin. Black thoracic groove with dark radial divergent lines. Clypeus height equal to AME diameter. Eye diameters and interdistances: AME 0.6, PME 0.7, ALE 0.4, PLE 0.6; AME-AME 0.3, AME-ALE 0.7, PME-PME 0.4, PME-PLE 0.6, ALE-PLE 0.2, MOQ: length 1.7, anterior width 1.7, posterior width 1.5. Median ocular row straight, PME describe a recurved line with PLE. Sternum with lateral band of dense hairs. Endites distally truncated, slightly convergent, with anterior and lateral serrula and anterior and median scopulae. Labium slightly longer than wide, articulated to sternum, and with truncated apex. Chelicerae with 3 promarginal and 5 retromarginal teeth. Leg formula I, IV, II, III. Leg measurements (femur+patella+tibiae+metatarsus+tarsus: total length): I: 16.6, 6.5, 17.5, 17.6, 4.7: 62.9; II: 15.8, 6.3, 15.5, 15.4, 4.0: 57.0; III: 13.2, 5.3, 11.5, 12.2, 3.4: 45.6; IV: 16.4, 5.7, 15.0, 20.4, 4.4: 61.9. Leg spination: I-II: tibiae v2-2-2-2-2, pl-1, d1-1-1, r1-1;

metatarsi v2-2-2, p1, r1, d0. Tibiae, metatarsi and tarsi of legs I-IV with dense scopula. Tarsi with two claws and claw tufts. Abdomen: light brown dorsally, dark brown ventrally; behind epigastric furrow, four radial bands with white spots which diverge from spinnerets. Colulus triangular. Pedipalp with dense tibial and tarsal promarginal scopula. Retrolateral tibial apophysis pointed at apex. Swollen curved embolus, membranous conductor and cup-shaped median tegular apophysis.

Female (UFBA, LAP-A no. 172): As in male except: Total length 36.0. Carapace length 18.5, width 14.6. Abdomen length 16.8. Eye diameters and interdistances: AME 0.6, PME 0.7, ALE 0.5, PLE 0.7; AME-AME 0.6, AME-ALE 1.1, PME-PME 0.5, PME-PLE 1.1, ALE-PLE 0.5. MOQ: length 2.0, anterior width 1.9, posterior width 1.8. Leg formula IV, I, II, III. Leg measurements (femur+patella+tibia+metatarsus+ tarsus: total length): I: 15.5, 7.9, 15.7, 13.5, 3.8: 56.4; II: 14.8, 7.5, 13.3, 12.5, 3.5: 51.6; III: 12.8, 6.5, 9.3, 9.9, 3.1: 41.6; IV: 16.0, 6.6, 13.6, 17.0, 3.7: 56.9. Leg spination: I-II: tibiae v2-2-2-2-2, p0, d0, r0; metatarsi v2-2-2, p0, d0, r0. Pedipalpal tibia and tarsus with longitudinal lines of dark hairs. Abdomen: venter yellowish behind epigastric furrow. Epigynum with anterior lobular process and two posterior transverse lobes in middle field.

Variation: Male length ($n=3$): total 20.0-24.8; carapace 9.5-14.0; femur I 11.8-16.6. Female length ($n=6$): total 22.5-37.5; carapace 11.5-18.0; femur I 12.4-15.6.



Figs. 18-21: Copulatory organs of *P. bahiensis*, sp. n. **18** Palpal bulb, ventral view; **19** Bulb, retrolateral view; **20** Epigynum; **21** Vulva. Scale lines=1.0 mm.

Other material examined: BRAZIL: *Bahía*: Fazenda José Lomanto Junior, 6 March 1969 (A. Timotheo da Costa, IBSP 2427), 1♂. Salvador: Parque Zoobotânico, June 1986 (UFBA, LAP-A 1098), 1♀; Parque Metropolitano de Lagoa de Abaeté-Itapoã, 10 April 1991 (UFBA, LAP-A 872), 1♀. Ilhéus: 5 July 1988 (UFBA, LAP-A 173), 1♂; 12 December 1988 (UFBA, LAP-A 172), 1♀; (UFBA, LAP-A 1317), 1♀; Ceplac, 12 April 1998 (A. D. Brescovit *et al.*, IBSP 22076), 2 immatures. Porto Seguro (A. C. Soares, IBSP 9516), 1♀.

Distribution: Known only from *Bahía*, Brazil.

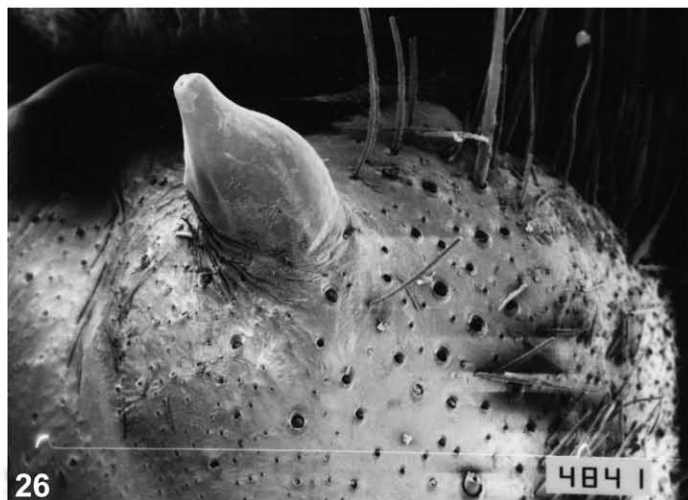
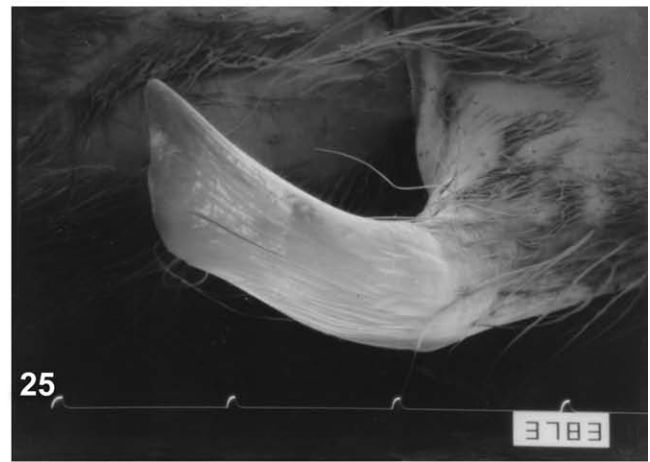
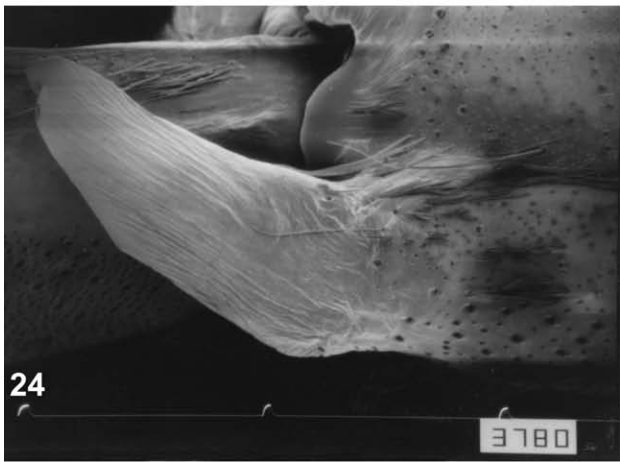
Species transferred

Phoneutria unilineata (Simon, 1897) was described under *Ctenus*. Lehtinen (1967) transferred it to

Phoneutria. Although the morphology of the epigynum of *Ctenus unilineatus* shows similarity with *Phoneutria*, this species lacks pedipalpal scopulae. Males also have a well-developed basal embolar projection, as described by Höfer *et al.* (1994) for *Ctenus*. For this reason this species is transferred to *Ctenus*.

Phoneutria niveobarbata Mello-Leitão, 1945, was synonymised with *Ancylometes bogotensis* by Schiapelli & Gerschman de Pikelin (1973: 32).

Phoneutria decora Gerstäcker, 1873: Holotype not examined, probably lost. This species was described based on a female from Zanzibar (Africa) by the



Figs. 22–26: Retrolateral tibial apophyses. 22 *P. boliviensis*; 23 *P. reidyii*; 24 *P. nigriventer*; 25 *P. fera*; 26 *P. bahiensis*. Scale lines=1.0 mm.

Taxon or Node	Tree 0
<i>Ctenus longipes</i>	char 19: 1 → 0 char 20: 0 → 1
<i>Oligoctenus ornatus</i>	char 10: 0 → 1
<i>Ctenus inaja</i>	char 4: 1 → 0 char 14: 1 → 2 char 16: 0 → 1
<i>Ctenus maculisternis</i>	char 22: 1 → 2
<i>Centroctenus auberti</i>	char 14: 1 → 0 char 17: 1 → 2
<i>Centroctenus ocelliventer</i>	char 6: 0 → 1 char 9: 1 → 0 char 14: 1 → 2
<i>Phoneutria nigriventer</i>	char 4: 1 → 0
<i>Phoneutria reidyi</i>	char 14: 1 → 0
Node 17	char 22: 0 → 1
Node 18	char 17: 1 → 2 char 24: 0 → 1 char 26: 0 → 1
Node 19	char 14: 1 → 0
Node 20	char 23: 0 → 1
Node 21	char 25: 0 → 1
Node 22	char 5: 1 → 2
Node 23	char 8: 0 → 1
Node 24	char 6: 0 → 1
Node 25	char 0: 0 → 1 char 1: 0 → 1 char 12: 0 → 1 char 16: 0 → 1
Node 26	char 14: 1 → 0
Node 27	char 19: 1 → 0
Node 28	char 21: 1 → 2
Node 29	char 10: 2 → 0
Node 30	char 17: 0 → 1
Node 31	char 2: 0 → 1 char 3: 0 → 1 char 4: 0 → 1 char 5: 0 → 1 char 7: 0 → 1 char 9: 0 → 1 char 11: 0 → 1 char 13: 0 → 1 char 15: 0 → 1 char 18: 0 → 1 char 19: 0 → 1 char 21: 0 → 1 char 22: 0 → 1

Table 2: Synapomorphies of the fittest tree.

coloration of the legs and the carapace colour pattern. The absence of pedipalpal scopulae (see Gerstäcker 1873: fig. 7) indicate that this species does not belong in the genus *Phoneutria*. The similarity with *Ctenus velox* Blackwall and *C. vividus* Blackwall from Zambesi, indicated by the author in the original description, suggests that this species belongs to the African *Ctenus*.

Doubtful species

Phoneutria rufibarbis Perty, 1833: F. O. Pickard-Cambridge (1897) considered this species as *forma ignota*, because the description given by Perty was very incomplete.

Phoneutria ochracea C. L. Koch, 1848: This species was described based on a male from Brazil, with no locality data. The author regarded it as close to *P. fera*, but distinguished it by the ochre coloration of the body. Because the holotype was not found, F. O. Pickard-Cambridge (1897) indicated that he had not

seen specimens fitting Koch's description. Mello-Leitão (1936) included *P. ochracea* in the Brazilian ctenids and recognised it by the length-width ratio of the pedipalp tibiae and the presence of two retrolateral tibial apophyses in the male. As can be seen in his fig. 37, the retrolateral apophysis corresponds to an example of *P. reidyi*. Eickstedt (1979) tried unsuccessfully to find Koch's holotype in the Munich Museum, so she suggested considering this species as valid until the holotype could be studied. Because of the imprecise locality and incomplete description of the holotype, we propose that this species be considered as a *species inquirenda*.

Key to species

1. Females.....2
– Males6
2. Epigynal middle field triangular.....3
– Epigynal middle field quadrangular4
3. Epigynal middle field convex with straight edges, anteriorly convergent and posteriorly divergent; lateral lobes with long, apically pointed spurs (Schiapelli & Gerschman de Pikelin, 1973: fig. 4).....
.....*P. boliviensis*
– Epigynal middle field with sinuous edges, with small spurs (Eickstedt, 1979: figs. 1–4).....*P. nigriventer*
4. Two posterior transverse lobes on epigynal middle field (Fig. 1)..5
– One posterior transverse lobe on epigynal middle field; concave anterior edge of epigynal middle field and anterior lobe less developed (Eickstedt, 1983: fig. 6).....*P. reidyi*
5. Anterior lobe elevated and convex (Eickstedt, 1983: fig. 5)..*P. fera*
– Anterior lobe less elevated and quadrangular (Fig. 20).....
.....*P. bahiensis* sp. n.
6. Distal tegular projection absent or less developed.....7
– Distal tegular projection well developed (Fig. 5).....9
7. Retrolateral tibial apophysis elongated, pointed at tip (Fig. 24).....
.....*P. nigriventer*
– Retrolateral tibial apophysis short8
8. Retrolateral tibial apophysis wide, truncated at tip (Fig. 22).....
.....*P. boliviensis*
– Retrolateral tibial apophysis very small (Figs. 19, 26)
.....*P. bahiensis* sp. n.
9. Embolus with apical laminar projection (Fig. 8), retrolateral tibial apophysis elongated, truncated at tip and separated from tibia (Fig. 25 and Eickstedt, 1983: figs. 1, 3).....*P. fera*
– Embolus without apical laminar projection, retrolateral tibial apophysis rounded at tip (Fig. 23).....*P. reidyi*

Phylogenetic analysis and discussion

One tree of maximum fit 167.0 (66%) was obtained using 53 steps (Figs. 27, 28). Synapomorphies are given in Table 2, and character steps and fits are given in Table 3.

This analysis confirms the monophyly of this group of ctenine genera, included at node 31 (Fig. 28, Table 2), by the following synapomorphies: five pairs of ventral spines on tibiae I, median field of epigynum as a lobe, female tibiae I with lateral spines absent, median field of epigynum with transverse lobe, presence of epigynal anterior lobes, copulatory openings in pockets, presence of epigynal tooth, simple copulatory ducts, basal fertilisation ducts, male metatarsus I with apical and lateral spines present, conical curved embolus, and cup-shaped median tegular apophysis. The lack of a cribellum is considered a secondary loss, as can be seen in some acanthothenine genera such as *Gephyroctenus*, *Enoploctenus* and *Caloctenus*. Brescovit (1996) suggested

that the genus *Centroctenus* Mello-Leitão, 1929 may be closely related to *Ctenus*. These results show that node 30 represents a lineage of Cteninae with spherical spermathecae, with head and base areas undifferentiated, and includes node 29 as a sister group of node 18. This last node comprises a group of species listed in *Ctenus* (*C. coxalis*, *C. longipes* and *C. taeniatas*), but because of their synapomorphies we consider these species may belong to *Isoctenus* Bertkau, 1880, which must be confirmed by the revision of that genus. This idea is supported by the presence of spherical spermathecae with head and base areas clearly differentiated, cymbial basal projection present, male pedipalpal tibiae as long as wide (and wider apically), retrolateral and ventral apophyses well developed, and median tegular apophysis with conical projection. Node 21 includes the genus *Centroctenus* and is the sister group of node 28 which includes the Cteninae with a prolateral groove in the dorsal concavity of the median tegular apophysis. Node 20 groups the Amazonian lineage of *Ctenus* (*C. inaja*, *C. crulsi* and *C. amphora*),

which are related by the presence of a basal embolar projection. We assume that the parallelism recorded between nodes 17, 19 and 26 with reference to character 14 is an independent derivation. Node 26 shows *Oligoctenus* as the sister group of *Phoneutria*. Node 25 is completely resolved and confirms the monophyly of *Phoneutria* by the presence of tarsal and tibial pedipalpal scopulae, defensive behaviour with erect position of the body with lateral movements, median position of the pockets in the epigynum, and copulatory duct simple and equal to or shorter than the spermatheca. The group of *P. nigriventer* and *P. boliviensis* at node 22 is related by the presence of a triangular lobe on the epigynum and is the sister group of node 24. This node includes the species of *Phoneutria* with an anterior lobe on the epigynum, within which *P. reidyi* is the sister group of node 23 comprising *P. fera* and *P. bahiensis*.

Lehtinen (1967) proposed *Ctenus* as the type genus of Cteninae, and he considered the related genera to be *Phoneutria*, *Isoctenus*, *Corinoctenus* Mello-Leitão, 1939, *Ctenopsis* Schmidt, 1954, *Oligoctenus* Simon, 1887 and

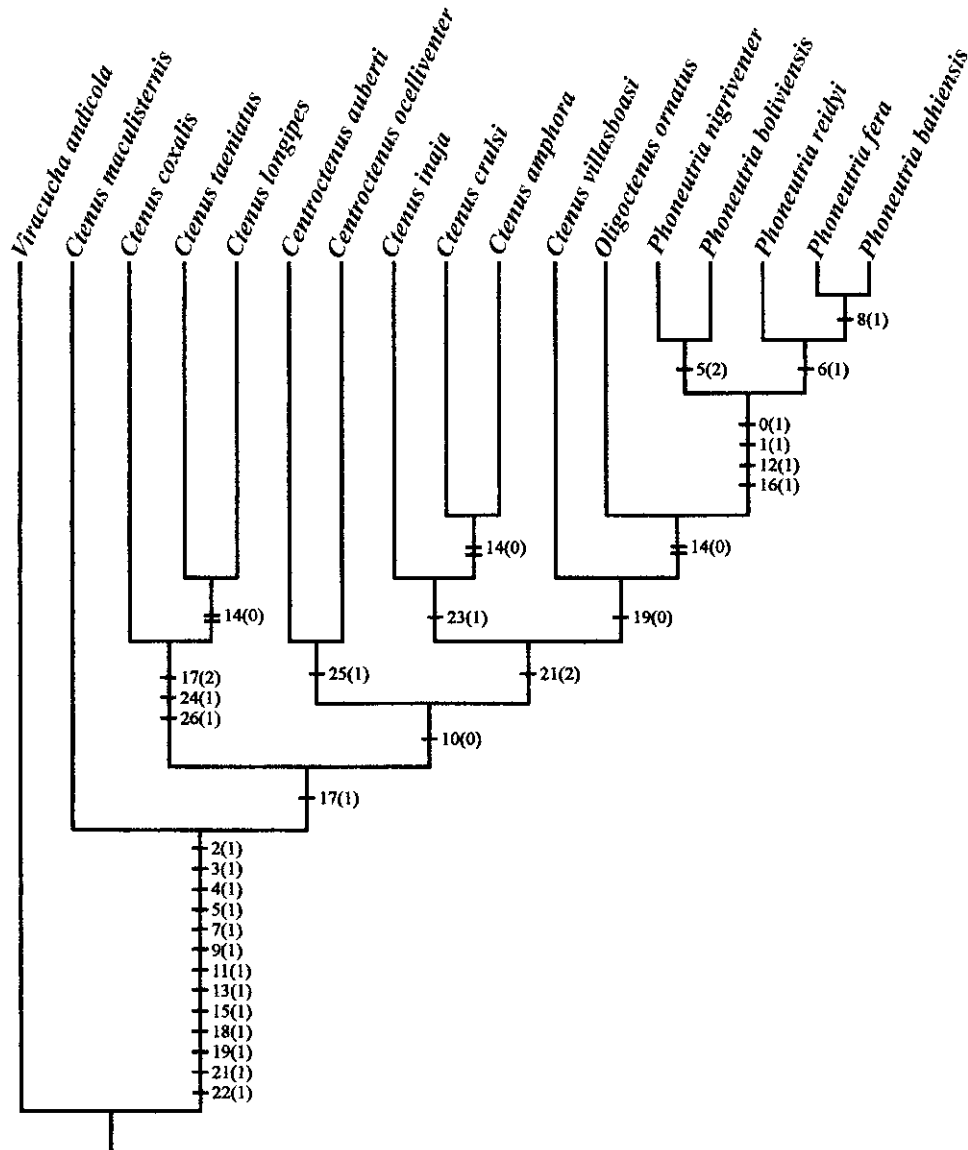


Fig. 27: Cladogram of the fittest tree of the species of *Phoneutria* and related Cteninae. Parallelisms are represented by two lines. Autapomorphies are omitted.

Tuticanus Simon, 1896. *Corinoctenus* was synonymised with *Ancylometes* Bertkau, 1880 (Pisauridae) by Schiapelli & Gerschman (1970) and we consider *Tuticanus* as more closely related to Acanthotheninae by its genital morphology: lateral fields of the epigynum well developed, long copulatory ducts, elongated and sinuous base of the spermatheca, spherical head of the spermatheca, and spine-like and curved embolus. Bücherl (1969a) characterised the Cteninae by the lack of dense scopulae on the pedipalpal tibia and tarsus, and included twelve genera from Central and South America, Africa, USA and Australia. He also proposed the subfamily Phoneutriinae based on the presence of dense scopulae on the pedipalpal tibia and tarsus, and he included only the genus *Phoneutria*. We consider that the characters used by Bücherl do not correspond to subfamilial characters because they are synapomorphies of the genus *Phoneutria*. Thus, the results obtained here confirm the inclusion of *Phoneutria* in Cteninae and for this reason Phoneutriinae is considered a junior synonym of Cteninae. The revision of *Isoctenus* and *Ctenopsis* and the inclusion of more terminal taxa in a future study (particularly species of *Ctenus*) will provide better information about the relationships of the Neotropical genera included in this subfamily.

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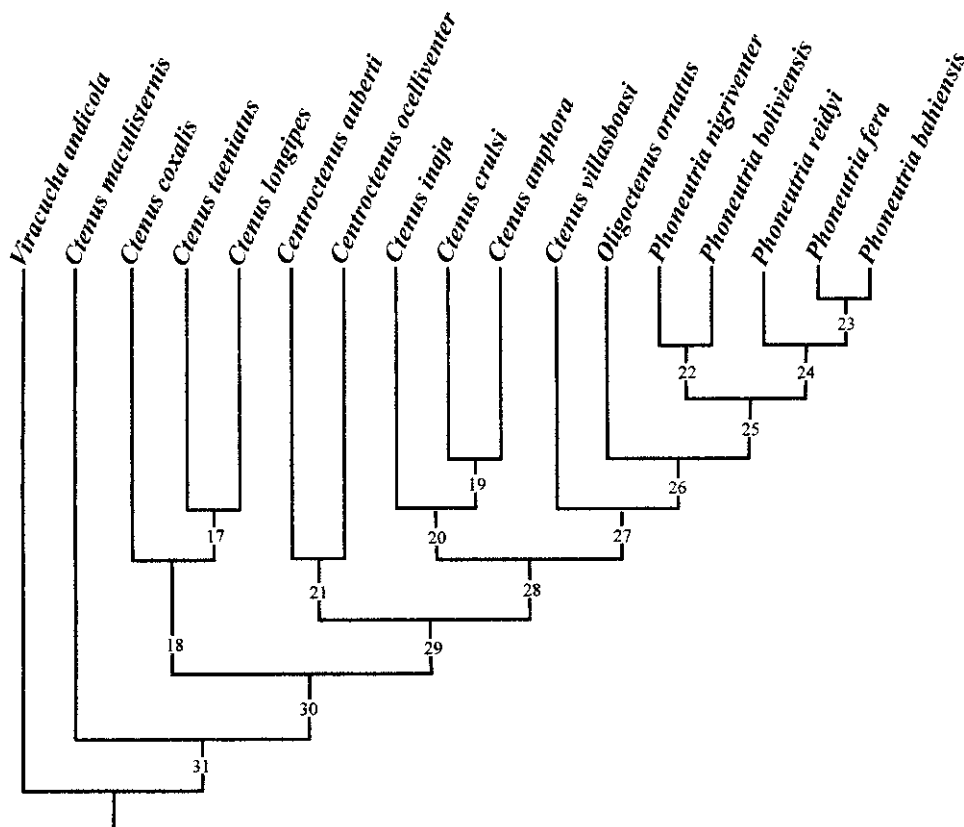


Fig. 28: Cladogram showing nodes of the fittest tree.

Character	Fit	Steps
0	10.0	1(0)
1	10.0	1(0)
2	---	---
3	---	---
4	6.6	4(3)
5	10.0	2(0)
6	8.5	2(1)
7	---	---
8	10.0	1(0)
9	8.5	2(1)
10	8.5	3(1)
11	---	---
12	10.0	1(0)
13	---	---
14	5.4	7(5)
15	---	---
16	7.5	3(2)
17	8.5	3(1)
18	---	---
19	7.5	3(2)
20	6.0	5(4)
21	10.0	2(0)
22	---	---
23	10.0	1(0)
24	10.0	1(0)
25	10.0	1(0)
26	10.0	1(0)

Table 3: Character steps and fit of the fittest tree.

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