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A new genus of Sensitibillini from Brazilian caves (Psocodea: 'Psocoptera': Prionoglarididae)

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A new genus of Sensitibillini from Brazilian caves (Psocodea: 'Psocoptera': Prionoglarididae). - The genus *Neotrogla* Lienhard gen. n. is described for three new cave-dwelling species from Brazil: *Neotrogla brasiliensis* Lienhard sp. n. (from Minas Gerais State), *N. aurora* Lienhard sp. n. (from Tocantins State) and *N. truncata* Lienhard sp. n. (from Bahia State). These species are the first Neotropical representatives of the subfamily Speleketorinae and the first New World representatives of the tribe Sensitibillini, previously known only from southern Africa. This distributional pattern of Sensitibillini is tentatively interpreted as due to Western Gondwanan vicariance. In the females of *Neotrogla* a complex of accessory structures to the spermathecal duct is described and denoted by the new term "gynosome". A hypothesis of functional complementarity, during copulation, between the "penis-like" gynosome and the strongly reduced male phallosome of *Neotrogla* is presented.

Keywords: New species - Brazil - cave fauna - gynosome - phallosome - copulation - Western Gondwanan vicariance - living fossils.

INTRODUCTION

The current knowledge of the Brazilian 'Psocoptera' (i.e. non-parasitic Psocodea, see below) fauna has been summarized by García Aldrete & Mockford (2009). It is clear that this picture is incomplete, and that the Neotropical fauna, especially of subterranean biotopes, is poorly known. Recent studies of Brazilian caves have yielded numerous as yet undescribed species, and suggest that an unexpected diversity of Psocoptera awaits discovery. This paper reports the results of a study of the family Prionoglarididae, which has not previously been recorded from Brazil.

Within the order Psocodea (*sensu* Yoshizawa & Johnson, 2006) the 'Psocoptera' family Prionoglarididae belongs to the basal suborder Trogiomorpha and has recently been placed in an infraorder of its own, the Prionoglaridetae (see Yoshizawa *et al.*, 2006). The family has been subdivided into two subfamilies by Lienhard (2004), Prionoglaridinae and Speleketorinae. The nominate subfamily contains three genera, the Palaearctic *Prionoglaris* Enderlein (3 species; see Lienhard & Smithers, 2002), the Oriental *Siamoglaris* Lienhard (monotypic; see Lienhard, 2004) and the Neotropical

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Speleopsocus Lienhard (monotypic; see Lienhard *et al.*, 2010). The subfamily Speleketorinae has been subdivided into two tribes by Lienhard (2007), the Speleketorini, containing the Nearctic genus *Speleketor* Gurney (3 species; see Lienhard & Smithers, 2002), and the Sensitibillini, containing the Aethiopian genera *Sensitibilla* Lienhard (4 species; see Lienhard, 2007 and Lienhard *et al.*, 2010) and *Afrotrogla* Lienhard (3 species; see Lienhard, 2007). Most of the previously known prionoglaridids live in caves or similar habitats.

In the following we describe the first Neotropical representatives of the subfamily Speleketorinae and of the tribe Sensitibillini, three new species from Brazilian caves which are assigned to a new genus closely related to *Afrotrogla* known from southern Africa (South Africa and Namibia). The biogeographical implications of the distributional pattern of Sensitibillini are briefly discussed. In the female of the new genus, a very particular "penis-like" structure of the spermapore region, associated to the spermathecal duct, is described and a hypothesis of its function during copulation is presented. The new term "gynosome" is introduced for this structure in analogy to the term phallosome, normally used for the male copulatory organ of Psocoptera.

MATERIAL AND METHODS

The collection of specimens in most caves was performed by manual capture. In addition, pitfalls containing formalin (5%) and liver baits were used in the caves Caboclo, Ossos and Janelão (Minas Gerais State). Dissection and slide-mounting followed the methods described by Lienhard (1998). The material examined is deposited in the following institutions: Universidade Federal de Lavras, Departamento de Biologia (Coleção de Invertebrados Subterrâneos), Lavras, Brazil (ISLA); Muséum d'histoire naturelle, Geneva, Switzerland (MHNG); Systematic Entomology, Hokkaido University, Sapporo, Japan (SEHU).

The following abbreviations are used in the descriptions: Ant = antenna (length); BL = body length (in alcohol); F = hindfemur (length); f1, f2, etc. = antennal flagellomeres (length); FW = forewing (length); HW = hindwing (length); IO/D = shortest distance between compound eyes divided by anteroposterior diameter of compound eye in dorsal view of head; P1-P4 = articles of maxillary palp; T = hindtibia (length); t1, t2, t3 = tarsomeres of hindtarsus (length, measured from condyle to condyle). Abbreviations of wing veins and cells are used according to Yoshizawa (2005). Details of genital morphology are explained in Fig. 10.

Bibliographical references of original taxa descriptions not given in this paper can be found in Lienhard & Smithers (2002) and Lienhard (2007).

DESCRIPTIONS

Neotrogla Lienhard gen. n.

DIAGNOSIS: Belonging to the subfamily Speleketorinae (as defined by Lienhard, 2004) and to the tribe Sensitibillini (as defined by Lienhard, 2007), but different from the previously known genera of this tribe due to the presence, in adults and nymphs, of a longitudinal row of articulated spines on anterior face of forefemur (Fig. 3a) and of a tarsal trichobothrium not only on second article of hindtarsus but also on second article of midtarsus (Fig. 4). Habitus similar to *Sensitibilla* (see Lienhard *et al*., 2010: fig. 4) and *Afrotrogla*. General morphology of adult and nymph as described for *Sensitibilla* (see Lienhard, 2000, 2007), with the following differences also present in the genus *Afrotrogla*. Hindwing (Fig. 1b) with M 2-branched. Third article of hindtarsus in females preapically with a dorsal pair of long curved hairs; the corresponding hairs much shorter in males and on foretarsus and midtarsus of both sexes. Female terminalia: ventral half of female paraproct with numerous short setae (Fig. 2c), lacking the circular field of long dense pilosity present in *Sensitibilla*; posterior lobe of subgenital plate at least slightly sclerotized and clearly visible medially between the pair of elongate ovipositor valvulae (external gonapophyses) (Figs 1c, 5, 8d); spermathecal wall with some sclerotized wrinkles near origin of spermathecal duct (Figs 2e, 7c). Male terminalia: paraproct (Fig. 3b) with a prominent ventral lobe (sometimes inconspicuous); phallosome with a narrow sclerite forming a simple aedeagal arch (Fig. 3e).

Differing from *Afrotrogla* not only by the above mentioned presence of a row of spines on forefemur and of a trichobothrium on second article of midtarsus but also by the following characters: spermapore region differentiated as an elongate "penis-like" gynosome (Fig. 2d, f; see also General Discussion), lacking the pair of lateral sclerotized struts present in *Afrotrogla* (see Fig. 10a:12' and Lienhard, 2007: figs 4g, 6d) [the gynosome of *Neotrogla* (see Fig. 10b, c) is a longitudinal structure composed of a weakly sclerotized posterior sac bearing the spermapore at its tip and enclosing the distal part of the spermathecal duct, a blister-like median part consisting of denticulate membranous structures and an anterior sclerotized rod]; internal lobe of basal part of external gonapophysis weakly differentiated (Figs 1c, 10b:4'), this gonapophysis not wider in middle than its foliaceous distal process (contrary to *Afrotrogla*, Fig. 10a:4'); posterior lobe of subgenital plate (Figs 1c, 10b:2) basally narrowed (broad in *Afrotrogla*, Fig. 10a:2); dorsally of external gonapophyses two pairs of apically rounded membranous and glabrous lobes present (ventral and dorsal gonapophyses? – absent in *Afrotrogla*), more or less covered ventrally by the basal parts of the external gonapophyses and by the posterior lobe of the subgenital plate (Figs 1c, 8d); aedeagal arch of the phallosome (Figs 3e, 9b) about half as long as the distance between its apex and the posterior end of the ejaculatory duct (= de) (much longer in *Afrotrogla*, reaching the ejaculatory duct; see Lienhard, 2007: fig. 7c) (Note: The width of the aedeagal arch depends largely on the degree of squashing of slide-mounted terminalia); endophallus (Figs 3e, 9b) medially with a longitudinal area densely covered by sclerotized papillae between the aedeagal arch and the ejaculatory duct (endophallic papillae absent in *Afrotrogla*); membrane of forewing with some brown colouration along several veins in basal half (Fig. 1a) (entirely hyaline in *Afrotrogla*); apical half of P4 (Fig. 7d) with 2 thin-walled preapical conical sensilla (5 such sensilla in *Afrotrogla*); tufts of long backwards-directed sternal setae near midline at about basal one third of abdomen absent in both sexes (present in females of *Afrotrogla*; see Lienhard, 2007: figs 4c, 6g).

TYPE SPECIES: *Neotrogla brasiliensis* Lienhard sp. n.

OTHER SPECIES: *N. aurora* Lienhard sp. n. and *N. truncata* Lienhard sp. n.

ETYMOLOGY: The name of the genus is feminine in gender and refers to its Neotropical distribution (Neo-) and its close relationship to the African genus *Afrotrogla* (-trogla).

DISCUSSION: See General Discussion.

Neotrogla brasiliensis Lienhard sp. n. Figs 1-3 and 10b, c

HOLOTYPE: ISLA, ♀, Brazil (Minas Gerais), Januária, cave "Gruta Caboclo", 27.iii.2003, leg. R. L. Ferreira.

PARATYPES: 3♂, 2♀ ISLA; 2♂ SEHU (for DNA extraction); 1♂, 1♀ MHNG; same data as for holotype. – 1 ♀ MHNG, same data as for holotype, but 22.iii.2003. – 1 ♂ MHNG, Brazil (Minas Gerais), Januária/Itacarambi, cave "Gruta Janelão", vii.2003, leg R. L. Ferreira. – 1♂, 2 nymphs ISLA; 2 nymphs MHNG; Brazil (Minas Gerais), Januária, cave "Gruta Ossos", vii.2003, leg. R. L. Ferreira.

DESCRIPTION

Male and female: See generic diagnosis, with the following additions. Head, thorax and appendages in general light to medium brown. Wings transparent (pterostigma very slightly opaque), veins brown, some brown pigmentation on membrane in basal half, as shown in Fig. 1a, b. In forewing fused portion of Rs and M longer than basal portion of Rs (Fig. 1a). Head with several small patches of brown hypodermal pigment (similar to Fig. 7a), shape and extension of these patches somewhat variable; compound eyes black, relatively small in both sexes (see Measurements: IO/D); vertical suture brown, frontal suture not visible. Ocelli well-developed, arranged in a slightly flattened triangle (see Fig. 7a). Vertex on each side behind lateral ocellus with a slightly concave area. Antennae damaged in all specimens examined (the best-preserved antenna examined is broken within f6), flagellomeres finely annulate. Maxillary palp long and slender (see Lienhard, 2007: fig. 3e), P2 with a well-differentiated subbasal sensory spur, P4 with two subapical conical sensilla, the more distal one slender and sometimes difficult to observe (see Fig. 7d). Trichobothria-bearing tarsomeres medially slightly thickened, but this thickening less distinct in midtarsus than in hindtarsus. Abdomen yellowish white, dorsally and laterally with longitudinal rows of reddish brown patches of hypodermal pigment (similar to Fig. 7b), often some patches partly fused to form irregular segmental transversal bands; terminalia yellowish brown.

Female terminalia: Epiproct and paraproct simple (Fig. 2c); paraproct with a sense cushion bearing 6 simple trichobothria (lacking basal rosettes) and usually also one normal seta in middle; posterior margin of sense cushion with several short sclerotized wrinkles. Subgenital plate (Fig. 1c) subdivided into a broad membranous anterior part, bearing a posteriorly opened curved sclerotized area of somewhat variable shape (Fig. 10b:1), and a slightly sclerotized elongate posterior lobe (Fig. 10b:2). The latter basally bearing a bifurcate sclerite (Fig. 10b:3) covered ventrally by a membranous transversal fold formed by the hindmargin of the anterior part of the subgenital plate. Posterior lobe apically rounded and densely covered by fine microtrichia, with a pilose subapical area on each side and two weakly differentiated small lobes subapically on lateral margin; medially between these lobes a somewhat crescent-like sclerotization and anteriorly to it a smooth and less sclerotized oval area. A pair of long foliaceous external gonapophyses (ovipositor valvulae) present, each of

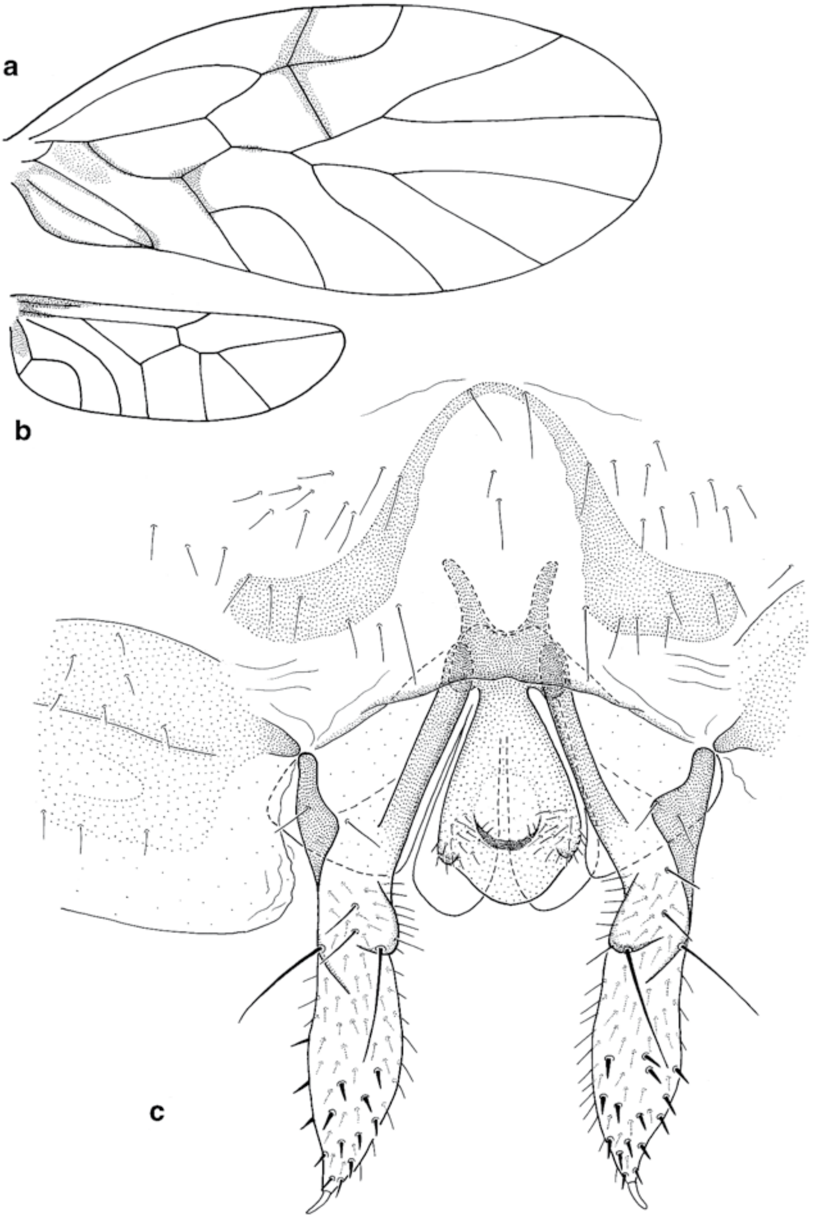

FIG. 1
Neotrogla brasiliensis Lienhard gen. n., sp. n., female: (a) Forewing. (b) Hindwing. (c) Subgenital plate and ovipositor valvulae with right ventrolateral parts of clunium, ventral view.

them with a long seta on a ventro-internal protuberance (Fig. 10b:4') about in middle of its length and with a similar seta on outer margin (Fig. 1c). Other pilosity of this ovipositor valvula (Fig. 1c): a claw-like spine on tip (Fig. 10b:6); ventrally numerous short stout spine-like setae in apical part and some longer hairs in basal half; numerous fine hairs on dorsal surface (represented by dotted lines in Fig. 1c). Valvula articulated near anterolateral margin of clunium by a condyle formed by its wavy marginal sclerotization; sclerotized inner margin of basal part of the valvula elongate and medially articulated to the above mentioned bifurcate sclerite at the base of the posterior lobe of the subgenital plate (Fig. 1c). Dorsally of the posterior lobe of the subgenital plate and of the basal part of the external gonapophyses two pairs of glabrous, apically rounded, membranous lobes present (Fig. 1c; homologuous to ventral and dorsal gonapophyses?). Spermapore region with an elongate gynosome (length about 0.8 mm), as described in the generic diagnosis (Figs 2d, f; 10b, c). Posterior sac of the gynosome (Fig. 10b:9), bearing the spermapore at its tip (Fig. 10b:8), *in situ* slightly ventrally curved (Fig. 2d) with its anterior opening (Fig. 10b:10) situated dorsally, at the base of the anterior rod (Fig. 10b:11"); blister-like part of the gynosome trilobate (Fig. 2f), the lateral lobes (Fig. 10b:12") membranous and finely denticulate, the dorsomedian lobe (Fig. 10b:13) somewhat asymmetrical (slightly bent to the left) and bearing numerous sclerotized denticles and ridges. Wall of the spermatheca thin, bearing small pores and a plate with characteristically arranged sclerotized wrinkles near the origin of the spermathecal duct (Fig. 2e). Spermatophores elongately oval, with a relatively long and more or less curved neck (Fig. 2e).

Male terminalia: Epiproct simple (Fig. 3c). Paraproct with a well-differentiated transversal fold between sense cushion and hindmargin and a relatively long ventral lobe; sense cushion as in the female, posteroventrally with some sclerotized wrinkles (Fig. 3b). Hypandrium simple (Fig. 3d), *in situ* ventrally rounded and almost dome-shaped, weakly sclerotized (some sclerotization also visible on 8th sternite), with two posterolateral pilose areas; the weakly sclerotized aedeagal arch usually only visible through hypandrium after clearing the terminalia. Phallosome strongly simplified and largely membranous (Fig. 3e), laterally towards the posterior margin of the hypandrium with some bulged membranous structures (see also Fig. 7e), between them the broadly rounded simple aedeagal arch (Fig. 10c:14), bearing a smooth apical thickening. Membranous posterior half of the endophallus delimited by the aedeagal arch, anterior half with a median zone of sclerotized papillae forming a longitudinal channel between the ejaculatory duct (= de) and the anterior end of the aedeagal arch (Figs 3e, 10c:15).

Nymph: As described for *Sensitibilla strinatii* Lienhard and *Afrotrogla oryx* Lienhard (see Lienhard, 2000, 2007 and Fig. 2a), but with a longitudinal row of articulated spines on anterior face of forefemur and with the following pattern of leg trichobothria: 2 on each tibia, 1 on second article of hindtarsus, 1 on second article of midtarsus (see generic diagnosis).

MEASUREMENTS

Female holotype: BL = 3.7 mm; FW = 4.5 mm; HW = 2.2 mm; F = 1060 μm; T = 1610 μm; t1= 705 μm; t2 = 155 μm; t3 = 166 μm; Ant (damaged); IO/D = 2.5.

Male allotype: BL = 3.6 mm; FW (damaged); HW = 2.2 mm; F = 1070 μm; T = 1700 μm; t1-t3 (damaged); Ant (damaged); IO/D = 2.4.

ETYMOLOGY: The specific epithet refers to Brazil, the country of the type locality.

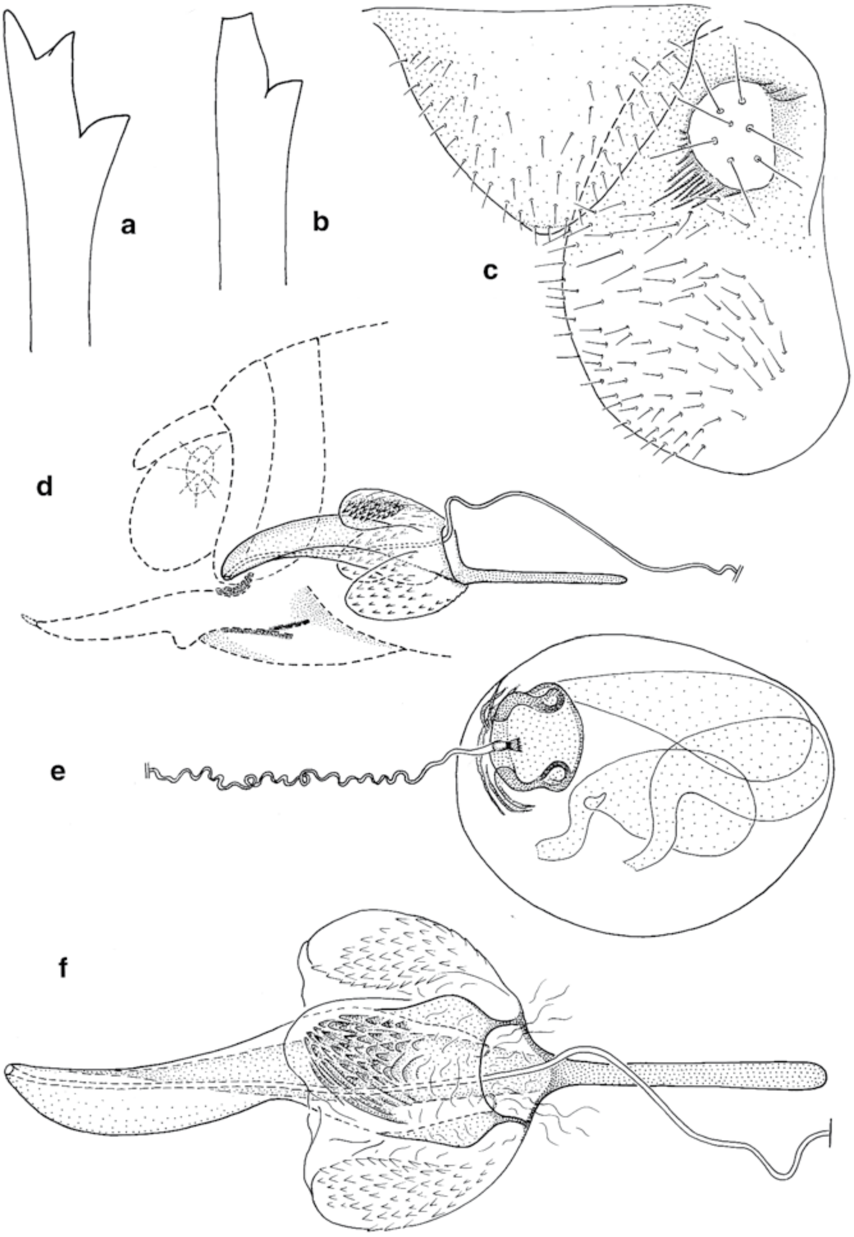

FIG. 2

Neotrogla brasiliensis Lienhard gen. n., sp. n.: (a) Lacinial tip, nymph. (b) Lacinial tip, female. (c) Epiproct and right paraproct, female. (d) Abdominal apex of female (interrupted line, schematic), with gynosome, lateral view. (e) Spermatheca (continuation of Fig. 2d), containing three spermatophores. (f) Gynosome, dorsal view (posterior part slightly asymmetrical due to slide mounting).

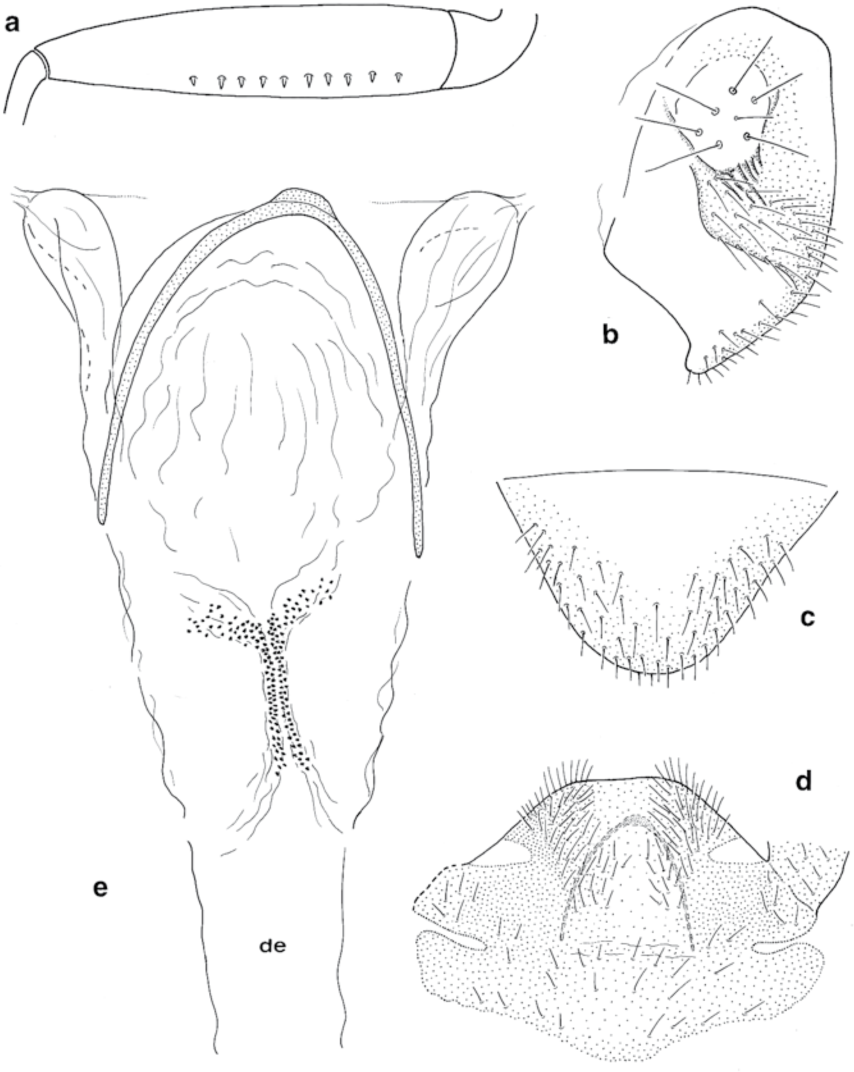

FIG. 3

Neotrogla brasiliensis Lienhard gen. n., sp. n., male: (a) Anterior face of forefemur with row of small spines. (b) Left paraproct. (c) Epiproct. (d) Hypandrium, ventral view (aedeagal arch visible through hypandrium). (e) Phallosome, ventral view (de: ductus ejaculatorius).

DISTRIBUTION: At present this species is known from three caves situated in the Peruaçu river valley. This area is located in the north of Minas Gerais State, between the townships of Januária and Itacarambi (Fig. 11). The area is nestled in a transitional area of two Brazilian phytogeographic domains: Cerrado and Caatinga (IBGE, 1993). These domains include several sub-types of vegetation presenting different levels of conservation, with most of them being well preserved. The limestone is part of the

Bambuí Speleological province. According to Piló (1997), the caves of the area can be divided in two main groups: the hydrologically active caves, directly related to the Peruaçu River (such as Janelão cave) and the dry caves positioned above the phreatic level. The dry caves are located in smaller canyons perpendicular to the course of the Peruaçu river (such as Caboclo cave), in residual outcrops or even in outcrops of the main canyon (such as Ossos cave). The three caves where the specimens of *N. brasiliensis* were collected are quite different, indicating that the species might not be adapted to any particular conditions. The area has dozens of caves. Since only few of these caves were prospected by biological surveys, it is possible that the species distribution is wider.

DISCUSSION: See discussion under *N. truncata*.

Neotrogla aurora Lienhard sp. n. Figs 4-7

HOLOTYPE: ISLA, ♀, Brazil (Tocantins), Aurora do Tocantins, cave "Gruta Biritite", 5.i.2009, leg. R. A. Zampaulo.

PARATYPES: 1♂ ISLA; 1♂, 1♀ MHNG; same data as for holotype. – 1♀ ISLA; 1♀ MHNG; Brazil (Tocantins), Aurora do Tocantins, cave "Gruta Asa Branca 1", 7.i.2009, leg. R. A. Zampaulo. – 1♂, 1♀ ISLA; 1♀ MHNG; 1♀ SEHU (for DNA extraction); Brazil (Tocantins), Aurora do Tocantins, cave "Gruta Couve-Flor", 7.i.2009, leg. R. A. Zampaulo.

DESCRIPTION

Male and female: See generic diagnosis and description of the type species, with the following differences. Pigmentation of wing membranes similar to that of *N. brasiliensis* but somewhat less extensive (Fig. 4) or even almost absent. Antenna with 13-14 segments, i.e. scape, pedicel and an apparently slightly variable number of flagellomeres (Note: Two intact antennae have been observed. One of them is the 14-segmented left antenna of the holotype. The 13-segmented antenna belongs to a female paratype. Both are considered as intact because the last flagellomere is slightly tapering to a regularly rounded tip and bears a conspicuous terminal sensillum).

Female terminalia: Posterior lobe of the subgenital plate (Fig. 5) apically clearly trilobate. Lateral lobes pilose, median lobe glabrous but densely covered by fine microtrichia or very small denticles. The more or less regularly sclerotized central zone of the posterior lobe of the subgenital plate almost reaching its base, in basal half with a field of tubercles. Both pairs of dorsal membranous lobes (ventral and dorsal gonapophyses?) almost completely covered by the basal part of the external gonapophyses and by the posterior lobe of the subgenital plate (Fig. 5). Gynosome (length about 0.7 mm) similar to that of *N. brasiliensis*, but mediodorsal lobe of its trilobate blister-like part strongly bent to the left (Fig. 6). Wrinkled plate of spermathecal wall (Fig. 7c) similar to that of *N. brasiliensis*. Spermatophores not observed.

Male terminalia: Paraproct with a relatively short ventral lobe (Fig. 7f). Smooth apical thickening of the aedeagal arch relatively wide (Fig. 7e).

Nymph: Not known.

MEASUREMENTS

Female holotype: BL = 2.75 mm; FW = 4.0 mm; HW = 2.0 mm; F = 865 μm; T = 1380 μm; t1 = 620 μm; t2 = 125 μm; t3 = 140 μm; Ant = 5.2 mm (14-segmented, see description); flagellomeres: f1 = 747 μm; f2 = 663 μm; f3 = 677 μm; f4 = 564 μm; f5 = 380 μm; IO/D = 2.2.

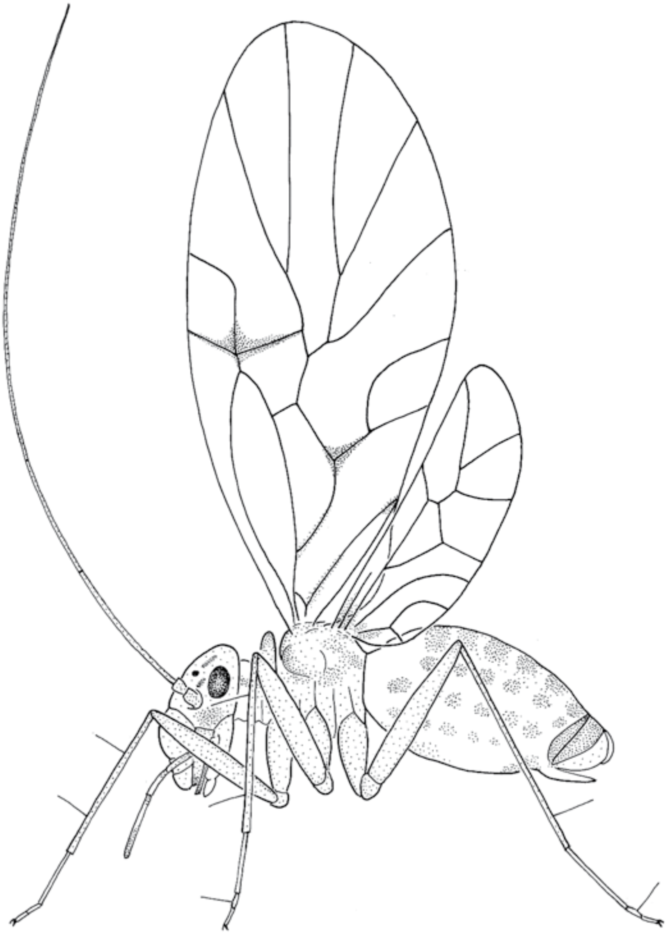

FIG. 4

Neotrogla aurora Lienhard gen. n., sp. n., female: Habitus, lateral view; pilosity, except for leg trichobothria, and right appendages not shown (body length 2.6 mm).

Male allotype: BL = 2.75 mm; FW (damaged); HW = 2.1 mm; F = 915 μm; T = 1490 μm; t1= 677 μm; t2 = 130 μm; t3 = 150 μm; Ant (damaged); IO/D = 2.2.

ETYMOLOGY: The specific epithet, a noun in apposition, refers to the type locality, Aurora do Tocantins.

DISTRIBUTION: At present this species is known from three caves situated in the municipality of Aurora do Tocantins which is located in southern Tocantins State, with an average altitude of 468m (Fig. 11). The area has a tropical climate and is inserted in the Cerrado formation (Brazilian Savana). The limestones of the area are also part of

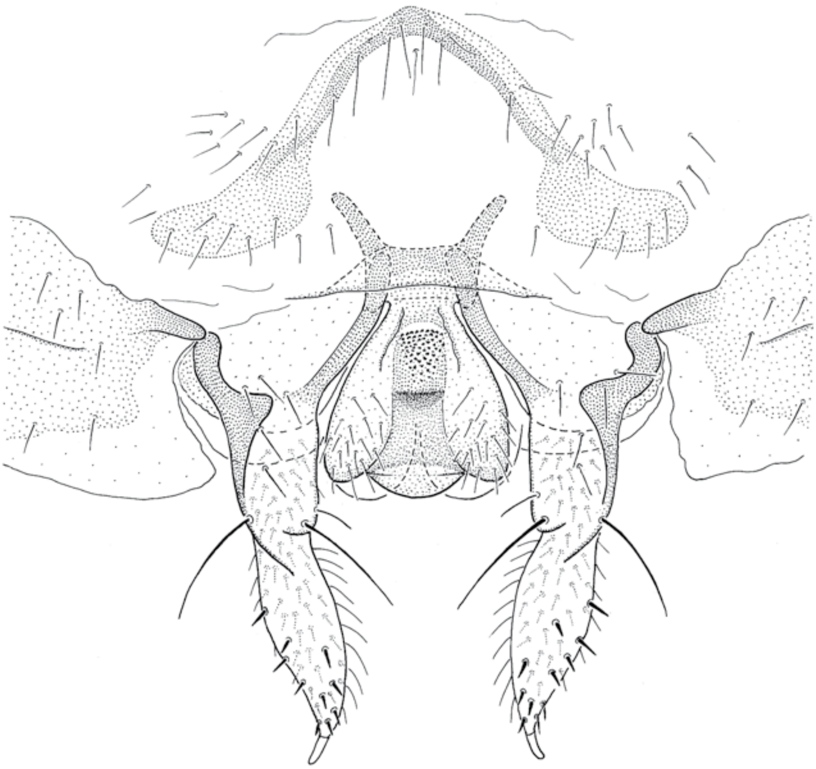

FIG. 5

Neotrogla aurora Lienhard gen. n., sp. n., female: Subgenital plate and ovipositor valvulae with ventrolateral parts of clunium, ventral view.

the Bambuí Speleological province. The caves of this area are mainly small, rarely longer than 200m (Couve-Flor cave 40m, Asa Branca 1 cave 70m, Biritite cave 200m). Six other caves in the area were also prospected, but no Prionoglarididae specimens were found in them. The collection of the *N. aurora* specimens was made by manual capture during one visit to the study area in the period of 05 to 10 of January of 2009. In all caves they were found near the entrance or in disphotic zones, always associated with rocky layers (cave walls or fallen blocks on the floor). The three caves in which the specimens were observed are distinct, but all of them are dry oligotrophic systems. The main resource in all caves is bat guano, although some piles of faeces of the rodent popularly known as mocó (*Kerodon rupestris*) may be found in some areas of the caves. The main vegetation type outside the caves is pasture, with some fragmented areas of Cerrado formation.

DISCUSSION: See discussion under *N. truncata*.

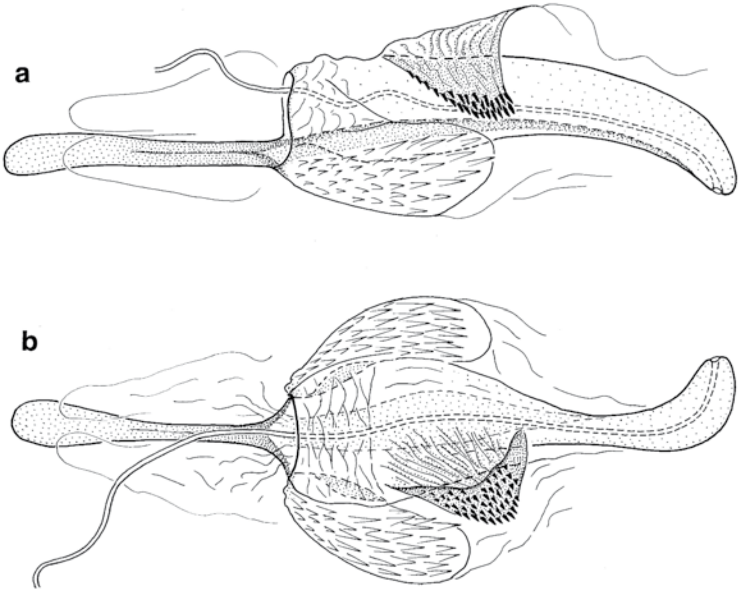

FIG. 6

Neotrogla aurora Lienhard gen. n., sp. n., female: (a) Gynosome, lateral view; posterior part at right in the figure. (b) Gynosome, dorsal view (posterior part slightly asymmetrical due to slide mounting).

Neotrogla truncata Lienhard sp. n. Figs 8-9

HOLOTYPE: ISLA, ♀, Brazil (Bahia), Campo Formoso, cave "Toca do Pitu", 10.vii.2008, leg. R. L. Ferreira.

PARATYPES: 1♂ ISLA; 1♀ MHNG; same data as for holotype. – 1♂ MHNG, Brazil (Bahia), Ourolândia, cave "Toca dos Ossos", 31.vii.2007, leg. R. L. Ferreira. – 5♂ ISLA; 1♂ MHNG, 1♂ SEHU (for DNA extraction); Brazil (Bahia), Palmeiras, cave "Gruta Ioiô", 1.i.2008, leg. R. L. Ferreira.

DESCRIPTION

Male and female: See generic diagnosis and description of the type species, with the following differences. In forewing (Fig. 8a) fused portion of Rs and M shorter than basal portion of Rs or at most of same length. Pigmentation of wing membranes similar to *N. brasiliensis* but hindwing with a distinct dark patch at the apex of vein R1 (Fig. 8b). Antennae damaged in all specimens examined; intact antenna with more than 11 segments (according to the best-preserved antenna examined, i.e. the right antenna of the allotype, broken beyond the tip of f9).

Female terminalia (Figs 8c, d; 9a): Posterior lobe of subgenital plate relatively short and broadly truncate, with some lateral pilosity; its apical part densely covered by distinct tubercles or denticles; a short transversal fold present medially in its apical half, and anteriorly to it a somewhat less sclerotized smooth central area. Bifurcate sclerite at the base of the posterior lobe of the subgenital plate with relatively short

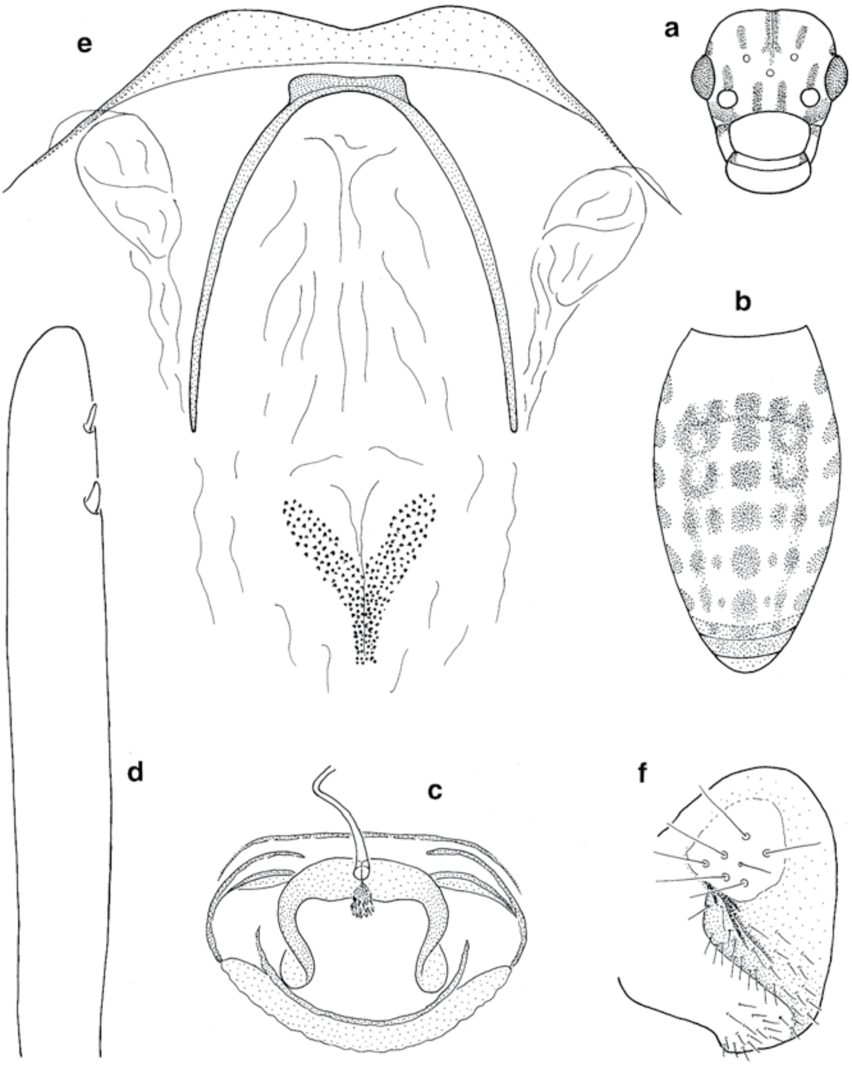

FIG. 7

Neotrogla aurora Lienhard gen. n., sp. n.: (a) Head of female, anterior view (antennae and palps not figured). (b) Abdomen of female, dorsal view. (c) Proximal part of spermathecal duct with wrinkled plate of wall of spermathecal sac (compare with Fig. 2e). (d) Apical half of P4 of female, with thin-walled subapical conical sensilla (general pilosity not shown). (e) Posterior margin of hypandrium (pilosity not shown) and phallosome, ventral view.

prongs. Distal part of external gonapophysis broadly foliaceous, ventro-internal protuberance weakly developed, external marginal sclerotization slender, not wavy as in the other two species. Pilosity of this ovipositor valvula similar to that of the other two species but stout ventral setae in apical part usually less spine-like and exceptionally two long setae present on external margin (see right valvula in Fig. 8d). Internal pair of dorsal membranous lobes (ventral gonapophyses?) clearly protruding from behind the truncate hindmargin of the posterior lobe of the subgenital plate, other pair of membranous lobes (dorsal gonapophyses?) shorter and inconspicuous, almost completely covered by the basal part of the external gonapophyses (Fig. 8d). Gynosome (length 0.63 mm) very characteristic (Figs 8c, 9a), its general shape similar to that of the other two species, but blister-like median part simple, not lobate, entirely membranous, regularly covered by fine scale-like or denticulate sculpture. Wrinkled plate of spermathecal wall and shape of spermatophore similar to *N. brasiliensis* (Fig. 9a).

Male terminalia: Paraproct (Fig. 9c) with a relatively long ventral lobe, lacking the transversal fold present in the two other species. Anterior part of hypandrium (8th sternite) weakly sclerotized (Fig. 9d). Phallosome similar to that of *N. brasiliensis*, but distal thickening of aedeagal arch bearing a fine sculpture of tubercles and short transversal ridges (Fig. 9b).

Nymph: Not known.

MEASUREMENTS

Female holotype: BL = 3.2 mm; FW = 4.0 mm; HW = 2.0 mm; F = 988 μm; T = 1520 μm; t1= 670 μm; t2 = 150 μm; t3 = 170 μm; Ant (damaged); IO/D = 2.5.

Male allotype: BL = 2.9 mm; FW = 4.0 mm; HW = 2.0 mm; F = 988 μm; T = 1510 μm; t1= 675 μm; t2 = 140 μm; t3 = 160 μm; Ant (damaged); IO/D = 2.6.

ETYMOLOGY: The specific epithet (truncatus, -a, -um) refers to the truncate posterior lobe of the female subgenital plate.

DISTRIBUTION: At present this species is known from three caves situated in the state of Bahia, near the municipalities of Campo Formoso, Ourolândia and Palmeiras (Fig. 11). The area is located in the Brazilian Caatinga, a semi-arid vegetal formation (IBGE, 1993). The caves are part of distinct carbonate domains, the Una carbonate province and the Caatinga limestones (see comments in General Discussion: Biogeography). The environment outside the caves is extremely dry and the degree of human impact is quite variable. The collections were done manually in one visit to each cave. Although some of the caves (Ioiô and Pitu caves) have subterranean lakes or ponds, the specimens were always found in the dry areas of the caves. Ioiô cave (length about 4 km) and Ossos cave (10 km) are considered as long caves, Pitu cave is smaller (about 500m). The specimens were always associated to areas near the cave entrance. *N. truncata* is the most widely distributed species of the genus (Fig. 11). Although the individuals were only found in few caves, the species certainly has a more extensive distribution, since there are hundreds of caves located in the same area.

DISCUSSION: The females of the three species of *Neotrogla* are easy to distinguish. Based on the similar structure of the gynosome and the subgenital plate *N. brasiliensis* and *N. aurora* seem to be more closely related to each other than to *N. truncata*. In the latter the gynosome is much simplified and the posterior lobe of the subgenital plate is short and apically truncate, not elongate and apically more or less trilobate as in *N. aurora* and *N. brasiliensis*. The central zone of this lobe is characteristically structured in each of the three species. The median lobe of the trilobate

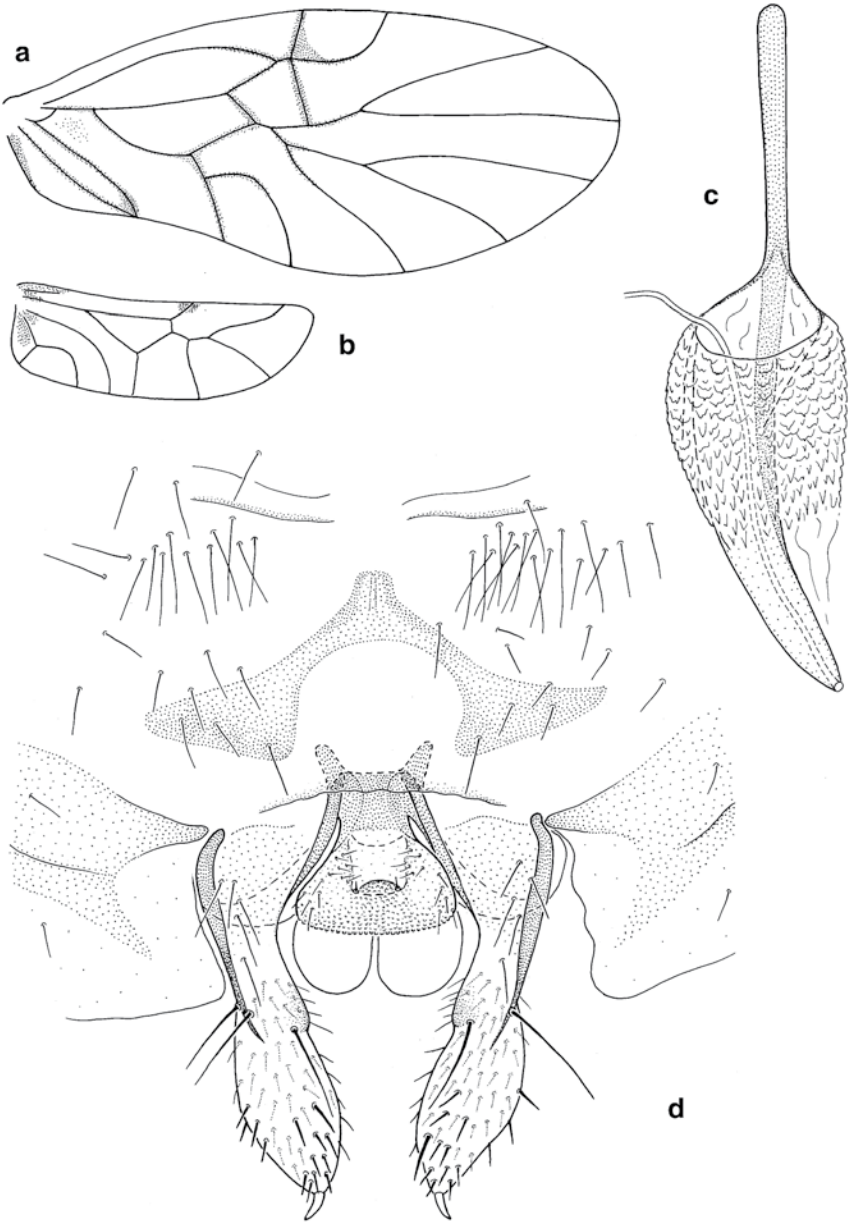

FIG. 8

Neotrogla truncata Lienhard gen. n., sp. n., female: (a) Forewing. (b) Hindwing. (c) Gynosome, dorsal view (posterior part downwards directed in the figure, slightly asymmetrical due to slide mounting). (d) Subgenital plate and ovipositor valvulae with ventrolateral parts of clunium, ventral view.

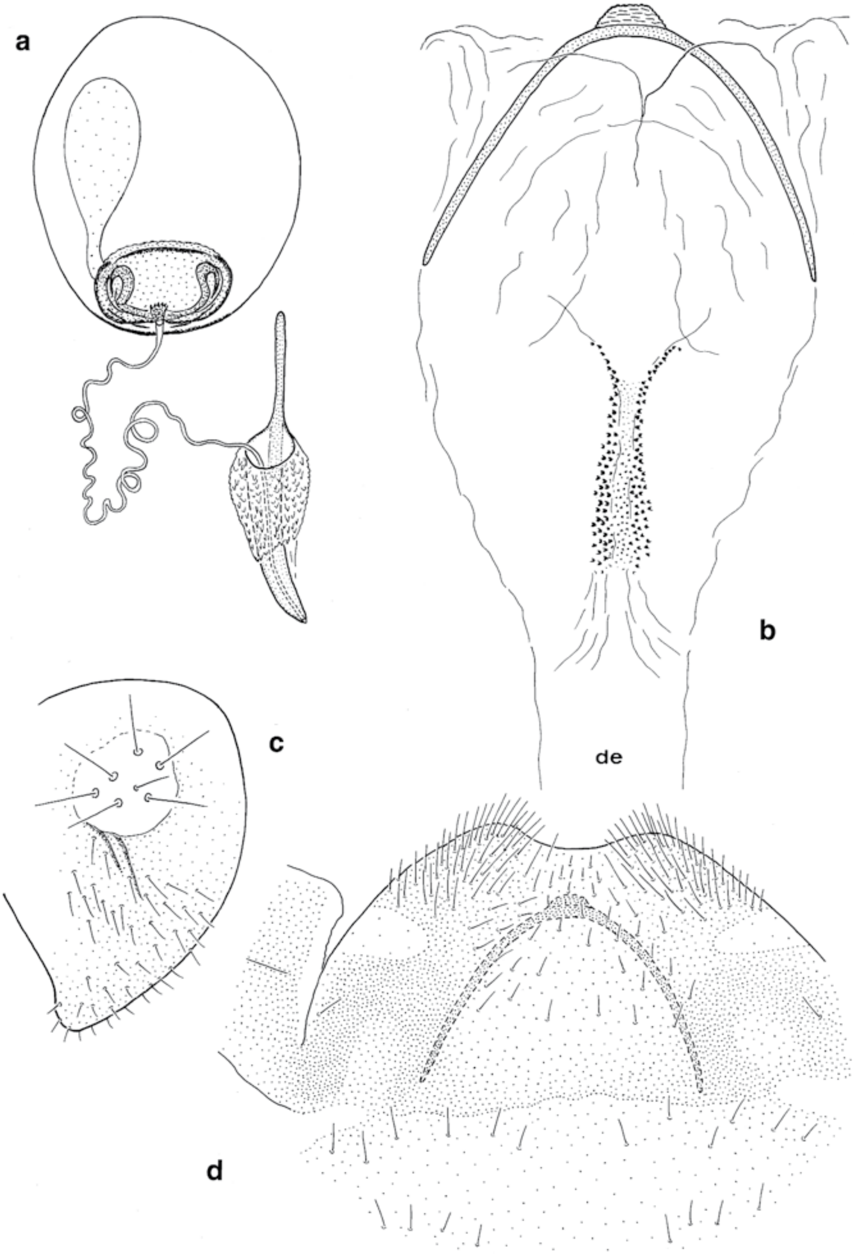

FIG. 9

Neotrogla truncata Lienhard gen. n., sp. n.: (a) Gynosome and spermatheca, containing one spermatophore. (b) Phallosome, ventral view (de: ductus ejaculatorius). (c) Left paraproct of male. (d) Hypandrium, ventral view (aedeagal arch visible through hypandrium).

blister-like zone of the gynosome is only very weakly asymmetrical in *N. brasiliensis* but strongly bent to the left in *N. aurora*; in *N. truncata* the blister-like zone of the gynosome is simple and not subdivided into lobes.

The males of the three species of *Neotrogla* are very similar. In *N. brasiliensis* and *N. aurora* the paraproct bears a transversal fold reaching from the sense cushion to hindmargin. This fold is not developed in *N. truncata*. In the latter the distal thickening of the aedeagal arch is finely sculptured while it is smooth in *N. brasiliensis* and *N. aurora*. The males of these two closely related species are particularly difficult to distinguish. In *N. aurora* the ventral lobe of the paraproct (Fig. 7f) seems to be somewhat shorter and the apical thickening of the eadeagal arch (Fig. 7e) slightly wider than in *N. brasiliensis* (Fig. 3b, e). However, nothing is known about intraspecific variability of these characters. The shape of the hindmargin of the hypandrium, which can be straight (Fig. 3d) or slightly concave (Figs 7e, 9d), seems to exhibit considerable intraspecific variation, but this is probably mostly due to position after slide-mounting.

The colouration of the three species is very similar, but in the hindwing of *N. truncata* a distinct brown patch seems always to be present apically on vein R1 (Fig. 8b). This patch is absent or very weakly developed in the other two species.

Biometrically both sexes of each of the three species are very similar. With a body length of 2.5-3.0 mm ($\bar{x}$=2.73, n=8) *N. aurora* seems to be slightly smaller than the closely related *N. brasiliensis* (BL 3.0-3.7 mm, $\bar{x}$=3.41, n=8). The relative length of the fused portion of Rs and M veins in forewing could be an additional character to distinguish *N. truncata* (fused portion shorter than basal portion of Rs or at most of same length, see Fig. 8a) from the two other species (fused portion longer than basal portion of Rs, see Figs 1a and 4).

GENERAL DISCUSSION

MORPHOLOGY

Several morphological structures observed in Speleketorini (see A) and Sensitibillini (see A, B, C) are unique in Psocoptera: (A) presence of trichobothria on legs; (B) external gonapophyses mediobasally joined (fused or articulated, see Phylogenetics) to the posterior lobe of the subgenital plate and bearing a spinose distal process; (C) spermapore with complex accessory structures partly enclosing the spermathecal duct. These structures have been described and discussed by Lienhard (2000, 2007). However, the very particular differentiation of the spermapore region in *Neotrogla* deserves some additional comment.

In female psocids the spermatheca, the spermathecal duct, its opening (spermapore sensu Badonnel, 1970) and the spermapore region are differentiations of the 8th abdominal sternum (Bitsch, 1979). The spermapore region is the area surrounding the opening of the spermathecal duct, it can be membranous or more or less sclerotized (gonopore plate or internal plate *sensu* Yoshizawa, 2005). Traditionally it has been regarded as belonging to the 9th sternum (Badonnel, 1970; Mockford, 1993; Lienhard, 1998; Yoshizawa, 2005) but according to Bitsch (1979) it is situated on the posterior part of the 8th sternum.

A very particular "penis-like" structure of the spermapore region has been described in detail for the new genus *Neotrogla* (see generic diagnosis and species descriptions), and the new term "gynosome" has been introduced, in analogy to the term phallosome, traditionally used in Psocoptera for the male copulatory organ (Badonnel, 1970). A similar structure was described some years ago for the genus *Afrotrogla* by Lienhard (2007). The schematic representation of these structures *in situ* for *Afrotrogla* and *Neotrogla* (Fig. 10a, b, interrupted lines), showing their position relative to the subgenital plate and the ovipositor valvulae, strongly suggests their homology (compare also detailed figures for *Neotrogla* spp. in the present paper and for *Afrotrogla* spp. in Lienhard, 2007). Therefore we propose to use the term gynosome also for the particularly differentiated spermapore region of *Afrotrogla*. In both genera the gynosome consists of a longitudinal membranous or slightly sclerotized sac (Fig. 10:9), enclosing the distal part of the spermathecal duct (Fig. 10:7) and bearing the spermapore at its tip (Fig. 10:8). The spermathecal duct leaves this sac anteriorly by a relatively wide circular opening (Fig. 10:10) situated dorsally of the longitudinal sclerotization which reinforces the sac ventrally (Figs 2d, 6a, 10:11). *In situ* the tip of the gynosome (broadly rounded in *Afrotrogla*, subacute in *Neotrogla*) is situated mediodorsally of the posterior lobe of the subgenital plate (Fig. 10:2). In *Neotrogla* the gynosome (Fig. 2d) is elongate and slender, bearing a denticulate and sometimes lobate blister-like zone about in the middle of its length (Fig. 10b:12",13) and ventrally a simple sclerotized anterior rod (Fig. 10b:11"). In *Afrotrogla* the longitudinal medioventral sclerotization is posteriorly prolonged towards the tip of the sac (Fig. 10a:11) and its anterior part, which corresponds to the simple anterior rod of *Neotrogla*, is a relatively short paired apodeme (Fig. 10a:11'). In *Afrotrogla* the blister-like zone is absent; but on each side of the sac there is a movable longitudinal strut (Fig. 10a:12') anteriorly joined with the paired medioventral sclerotization (see also Lienhard, 2007: figs 4g, 6d). In both genera, the width of the bifurcate sclerotizaton (Fig. 10:3) at the base of the posterior lobe of the subgenital plate (Fig. 10:2) apparently corresponds to the width of the sac of the gynosome (Fig. 10:9), i.e. bifurcate structure (Fig. 10:3) largely opened in *Afrotrogla*, narrowly forked in *Neotrogla*. Figure 10a represents the type species, *Afrotrogla oryx*; in *A. maraisi* the bifurcate sclerite at the base of the posterior lobe of the subgenital plate is not differentiated and the sac of the gynosome is posteriorly very broadly rounded (see Lienhard, 2007: fig. 6d).

Lienhard (2007) has already presented a hypothesis of functional complementarity between the complex gynosome and the strongly simplified phallosome in *Afrotrogla*, suggesting the transfer of the usual functions of a normally sclerotized phallosome of Trogiomorpha (i.e. establishement of close grip of male and female genitalia during sperm transmission) towards the gynosome. In Fig. 10c we propose here a corresponding hypothesis for *Neotrogla*, suggesting the insertion, during copulation, of the "penis-like" gynosome into the male phallosome through its papillate endophallic channel (Fig. 10c:15). It is evident that direct observations of specimens in copula are necessary to test this "topsy-turvy" hypothesis.

PHYLOGENETICS

Due to their basal position within Trogiomorpha and their similarity to fossils of this suborder, based on a plesiomorphic wing venation, the extant prionoglaridids are considered as "living fossils" (Lienhard, 2007). However, the different clades of

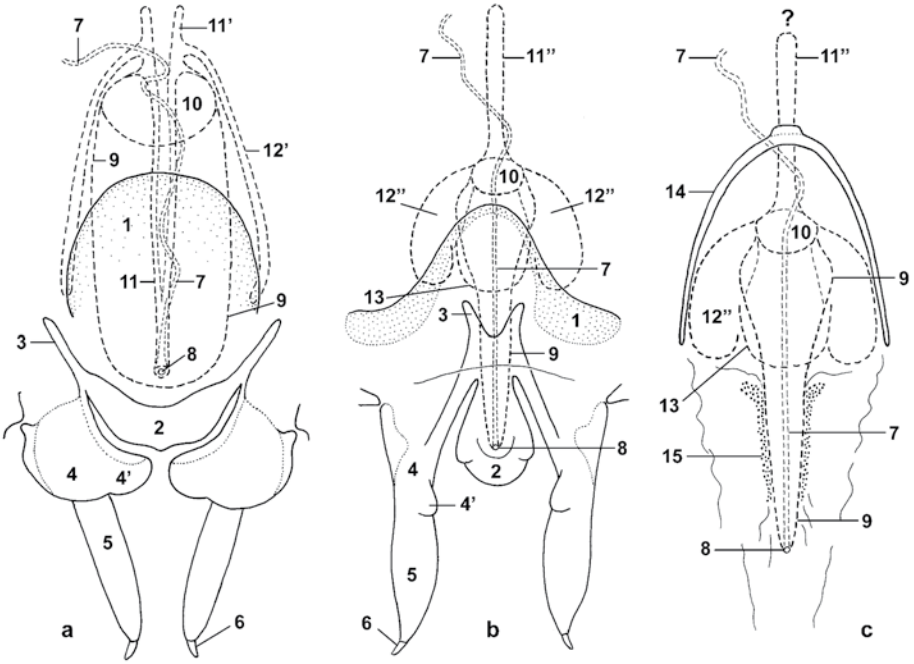

FIG. 10

Schematic genitalia of the type species of the genera *Afrotrogla* and *Neotrogla*, ventral view: (a) *Afrotrogla oryx* Lienhard: gynosome *in situ* with distal part of spermathecal duct (interrupted line), subgenital plate and ovipositor valvulae (based on Lienhard, 2007: fig. 4g). (b) *Neotrogla brasiliensis* Lienhard gen. n., sp. n.: ditto (based on Figs 1c and 2f). (c) *Neotrogla brasiliensis* Lienhard gen. n., sp. n.: hypothetical position of gynosome (interrupted line) inserted into phallosome during copulation (based on Figs 2f and 3e); the question mark indicates the strictly hypothetical nature of this figure. – Morphological details: (1-6) Female, subgenital plate and ovipositor valvulae: (1) subgenital plate, sclerotized area of anterior part; (2) subgenital plate, posterior lobe; (3) bifurcate sclerotization at the base of the posterior lobe of the subgenital plate; (4) external gonapophysis, basal part, with (4') its internal lobe or protuberance; (5) external gonapophysis, distal process; (6) external gonapophysis, claw-like apical spine. (7-13) Female, spermathecal duct and gynosome: (7) spermathecal duct; (8) spermapore on tip of gynosome; (9) gynosome, sac enclosing distal part of spermathecal duct; (10) gynosome, anterior opening of gynosomal sac; (11) gynosome, longitudinal ventral sclerotization, anteriorly differentiated as (11') a paired anterior apodeme or (11") a simple rod; (12) gynosome, lateral structures, differentiated as (12') a sclerotized strut or (12") a lobe of a blister-like zone; (13) gynosome, dorsomedian lobe of blister-like zone. (14-15) Male, phallosome: (14) aedeagal arch; (15) papillate endophallic channel.

this family are characterized by striking autapomorphies and surprising specializations unknown elsewhere in Psocoptera. Characters of Prionoglaridinae have been treated by Lienhard (1988, 1998, 2004) and Lienhard *et al.* (2010), those of Speleketorinae by Lienhard (2000, 2004, 2007). In the following we would like to mention some characters which are probably of crucial importance for the understanding of the phylogeny of the tribe Sensitibillini.

The most striking autapomorphy of the Sensitibillini mentioned by Lienhard (2007) can also be observed in the new genus *Neotrogla*, i.e. the presence of tarsal trichobothria, unique not only in Psocodea but in insects in general. The African representatives of the tribe, the genera *Sensitibilla* and *Afrotrogla*, have one trichobothrium on the second article of hindtarsus. In addition to this, *Neotrogla* has one trichobothrium also on the second article of midtarsus (Fig. 4). We consider the presence of this additional tarsal trichobothrium as an autapomorphy of *Neotrogla*. The very particular structure of the ovipositor, considered as another important autapomorphy of the African Sensitibillini by Lienhard (2007), is also present in the new genus. The external gonapophsis has a spinose distal process (Fig. 10:5) bearing a claw-like apical spine (Fig. 10:6). Mediobasally this ovipositor valvula is joined to the posterior lobe of the subgenital plate (Fig. 10:2) by fusion (in *Sensitibilla*) or articulation (in *Neotrogla*, see Fig. 1c, and in the type species of *Afrotrogla*, *A. oryx*; in *A. maraisi* the situation is not clear, because the laterobasal sclerotization of the posterior lobe of the subgenital plate is not differentiated in this species; see Morphology). These synapomorphies shared by the African genera and the Neotropical genus *Neotrogla* support the assignement of the latter to the tribe Sensitibillini. Within this tribe, *Sensitibilla* is characterized by the autapomorphic presence, on the spermathecal wall, of a kidney-shaped plate bearing a pair of short spines (see Lienhard, 2007: fig. 8) and by the reduction of vein M2 in the hindwing. On the other hand, *Afrotrogla* and *Neotrogla* show the following striking synapomorphies of genitalia which support their assignement to a clade forming the sister-group of *Sensitibilla*: in female, presence of a gynosome (see Morphology); in male, phallosome strongly simplified, its sclerotization reduced to a simple aedeagal arch.

The differentiation of sclerotized lateral struts of the gynosome (Fig. 10a:12') and the presence, in female, of a pair of tufts of long sternal setae at about basal one third of the abdomen (see Lienhard, 2007: figs 4c, 6g) can be considered as autapomorphies of *Afrotrogla*. The particular "penis-like" shape of the gynosome, bearing a blister-like median part (Fig. 10b:12",13), and the presence of a papillate channel anteriorly in endophallus (Fig. 10c:15) can be considered as autapomorphies of *Neotrogla*, together with the above mentioned presence of a trichobothrium on second article of midtarsus. The presence of a longitudinal row of small articulated spines on the anterior face of the forefemur seems to be homoplastic in Psocoptera. In the suborder Trogiomorpha this character is present in the prionoglaridids *Speleketor* (see Mockford, 1984) and *Neotrogla* (Fig. 3a), but it has also been reported from some members of the suborder Psocomorpha, belonging to the families Dolabellopsocidae and Amphipsocidae (see Smithers, 1990). A very similar character is also present in some Amphientometae, belonging to the suborder Troctomorpha. However, in the latter cases the conical spines are not articulated setae but rigid spiniform tubercles (see Lienhard, 1998), which are perhaps not homologous to the above mentioned spines.

The presence of a well-developed and more or less sclerotized posterior lobe of the subgenital plate in *Afrotrogla* and *Neotrogla* (Fig. 10:2) can probably also be interpreted as a synapomorphy of these genera, assuming that the short and membranous posterior part of the subgenital plate generally observed in other Trogiomorpha, including *Sensitibilla* (see Yoshizawa *et al.*, 2006), represents the plesiomorphic character state. The presence, in females, of a pair of long curved subapical hairs on the terminal article of the hindtarsus (see Lienhard, 2007: fig. 4d) is probably also a synapomorphy of *Afrotrogla* and *Neotrogla*; as far as we know, this character has not yet been observed elsewhere in psocids.

It is somewhat doubtful if the two pairs of membranous and glabrous lobes (Figs 1c, 5, 8d), present in *Neotrogla* dorsally of the posterior lobe of the subgenital plate and of the basal part of the external gonapophyses (and absent in the other Sensitibillini), are really homologous to the ventral and dorsal gonapophyses, which are strongly reduced or absent in all other Trogiomorpha (see Yoshizawa *et al*., 2006). The presence of these gonapophyses in *Neotrogla* would be a plesiomorphic character. However, these lobes could also be an autapomorphic structure of Neotrogla, not homologous to the ventral and dorsal gonapophyses and perhaps functionally related to the very particular gynosome present in this genus.

Lienhard (2007) mentioned the surprisingly low and apparently variable number of antennal segments in Speleketorinae and suggested that this character could constitute an autapomorphy of this subfamily. The plesiomorphic character state, present in all other Trogiomorpha, would be an antenna with 19 or more segments (i.e. scape, pedicel and at least 17 flagellomeres; see Lienhard, 2007). Flagellomere counts of undoubtedly complete antennae are rare in Prionoglarididae (even completely lacking in the subfamily Prionoglaridinae according to Lienhard, 2007), because their antennae are very thin and fragile, thus broken in most of the specimens available in collections. In the genus *Speleketor* three complete antennae have been observed (Mockford, 1984), each of them with a different number of segments (7, 10, 15). Only two intact antennae of African Sensitibillini are known, one of *Sensitibilla* (13-segmented; see Lienhard, 2000) the other of *Afrotrogla* (11-segmented; see Lienhard, 2007). In *Neotrogla* we were able to observe two intact antennae, comprising 13 and 14 segments (see description of *N. aurora*). Thus, the reduction of the number of flagellomeres and its intrageneric and intraspecific variability have been confirmed by the present observations, suggesting that this character could be interpreted as an autapomorphy of the subfamily Speleketorinae. A certain reduction of the number of flagellomeres is also characteristic for the other suborders of Psocoptera. However, in each of them the variability is very low (i.e. antenna generally 15-segmented in Troctomorpha and 13-segmented in Psocomorpha; see Mockford, 1993). Possible homoplasy of this character relativizes its phylogenetic information within Psocodea.

BIOGEOGRAPHY

Vishnyakova (1980) tentatively placed the origin of the suborder Trogiomorpha in the Early Jurassic. Yoshizawa *et al.* (2006) showed that the prionoglaridids are the most basal members of this suborder and tentatively interpreted their very disjunct distribution (four genera, each of them known from a different zoogeographical region) as Pangaean relicts. As shown by Binford *et al.* (2008) for two genera of cave- and soil-dwelling spiders of the family Sicariidae, the biogeographical pattern observed in Sensitibillini could be due to Western Gondwanan vicariance, admitting that the most recent common ancestor of *Afrotrogla* and *Neotrogla* was present on Western Gondwana before the separation, in the Early Cretaceous, of the African and South

American continents, which was complete about 95 mya (Pitman *et al*., 1993). This scenario is supported by the present distribution of *Afrotrogla* in caves of SW-Africa (Namibia and northern South-Africa; see Lienhard, 2007 and Lienhard *et al*., 2010 and map in Lienhard, 2008) and of *Neotrogla* in caves of eastern Brazil (states of Minas Gerais, Tocantins and Bahia; see below and Fig. 11) and by the fact that the molecular tree presented by Yoshizawa *et al.* (2006) suggests that the origin and the diversification of the family is deep. However, Yoshizawa *et al.* (2006) insisted that more data (including clear fossil record evidence) are required for more precise dating of their Trogiomorpha tree. As suggested by Baz & Ortuño (2000), extant cave-dwelling species belonging to basal Trogiomorpha clades may be relicts from Cretaceous tropical forests. Several fossil Trogiomorpha resembling prionoglaridids, due to the presence of a similar plesiomorphic wing venation, were recently described from Early Cretaceous amber from Spain, France and Lebanon (Baz & Ortuño, 2000, 2001; Perrichot *et al*., 2003; Azar & Nel, 2004). Even if it is not possible to clearly assign any of these fossils to the extant family Prionoglarididae, due to lack of morphological information, there is no doubt that prionoglaridid-like Trogiomorpha were already most diverse in the Early Cretaceous (Perrichot *et al*., 2003; Azar & Nel, 2004).

This historical scenario represents a hypothesis for the interpretation of the close relationship between the Brazilian genus *Neotrogla* and the African genus *Afrotrogla* within the geologically probably relatively old group of Sensitibillini. On the other hand, the striking morphological similarity of the three modern species of *Neotrogla* suggests a relatively recent specific diversification of this genus in Brazil. The following analysis of the known distribution of these Brazilian cave species may contribute to understanding the relationships indicated by morphology, i.e. *N. brasiliensis* and *N. aurora* much more closely related to each other than to *N. truncata* (see Discussion under *N. truncata*).

The *Neotrogla* species were collected in three distinct carbonate geological groups (Fig. 11). The caves located at Peruaçu river valley (type locality of *N. brasiliensis*) and in Aurora de Tocantins (type locality of *N. aurora*) belong to the Bambuí Group. The carbonate rocks of the Bambuí Group were formed in the Neoproterozoic, dating from around 900 million years. They occur over a vast area in the states of Minas Gerais, Bahia, Goiás and Tocantins and host extensive karst landforms (Auler, 2004). The areal distribution of the carbonate rocks in relation to the surrounding topography forms several physiographic domains, lending distinct morphological patterns on the karst landforms. Although the caves from Peruaçu and Aurora de Tocantins are quite far from each other, it is plausible to assume that they might have some underground continuity (or might have had in the past). Furthermore, most caves located in the areas inbetween those previously mentioned were not sampled and, thus, may also have some populations of the two species.

On the other hand, the caves where *N. truncata* was collected occur in two distinct limestone units: the Una Group (Pitu and Ioiô caves) and the Caatinga Formation (Ossos cave). The Neoproterozoic carbonate rocks of the Una Group occur in the northern half of the state of Bahia, and comprise a series of separate basins divided by quartzite mountain ranges (Auler & Smart, 2003). Most of the carbonate bedrock surface is covered by a thick soil sequence. Surface karst features are represented

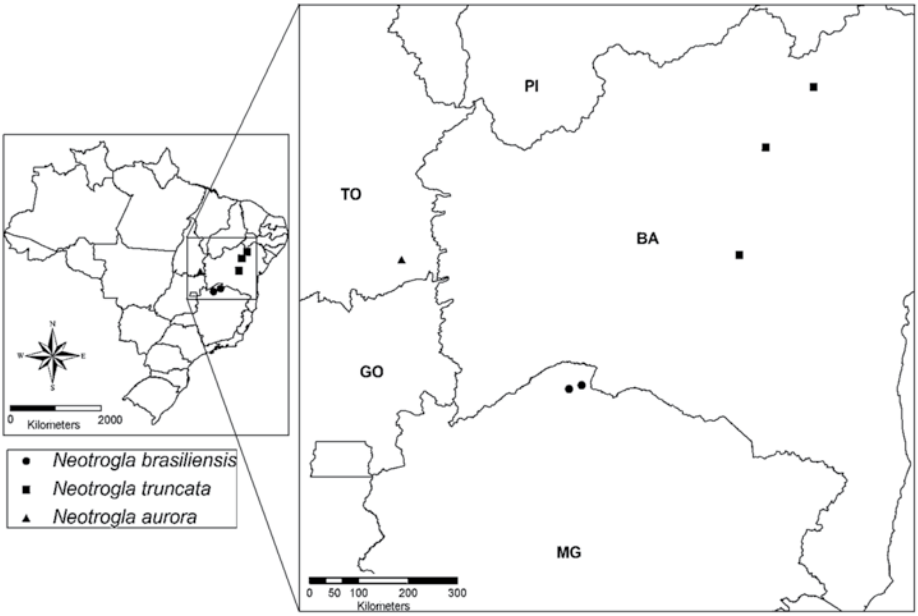

FIG. 11

Currently known geographical distribution of *Neotrogla* spp. in Brazil. States: BA = Bahia, GO = Goiás, MG = Minas Gerais, PI = Piauí, TO = Tocantins.

mostly by dolines, which can be extremely frequent, creating a very uneven terrain. Many of these dolines appear to be due to collapse with later smoothening of the slopes. Speleological research in the area is still in its infancy, and large tracts of carbonate outcrop remain to be checked (Auler, 1999). The freshwater Caatinga Group consists in a rather recent limestone, probably dating from the Pliocene. These limestones occur from the central-west to the northern portion of the state of Bahia, containing some inferred contact zones with the Una limestones. So, it is quite possible that these two domains, although formed in different ages and conditions, are physically connected at present.

The phylogenetic relationship between the three species may be partly explained by the geological formations in which the caves they inhabit are found. The relatively closely related *N. brasiliensis* and *N. aurora* are both known from caves in the Bambuí group of limestones, while *N. truncata* is known from caves in the Una and Caatinga limestones, which are contiguous with each other in some areas, but separated from the Bambuí formations.

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