A new genus of Prionoglarididae from a Namibian cave (Insecta: Psocoptera)

Charles LIENHARD

Muséum d'histoire naturelle, c. p. 6434, CH-1211 Genève 6, Switzerland.

E-mail: charles.lienhard@mhn.ville-ge.ch

A new genus of Prionoglarididae from a Namibian cave (Insecta: Psocoptera). - Sensitibilla strinatii gen. n., sp. n. is described and illustrated based on three females and several nymphs collected in Arnhem Cave (124 km SE of Windhoek). The new genus is closely related to the North American genus Speleketor Gurney. The description of its type species, Speleketor flocki Gurney, is complemented and the systematic position of both genera within the family Prionoglarididae is discussed. The presence of trichobothria on legs, unique in Psocoptera, is considered as a striking synapomorphy of Speleketor and Sensitibilla.

Key-words: Psocoptera - Prionoglarididae - new genus - new species - trichobothria - cave fauna - Namibia.

INTRODUCTION

The family Prionoglarididae (suborder: Trogiomorpha, family-group: Psocathropetae) groups some of the most astonishing psocids currently known. It contains two genera, Prionoglaris Enderlein, 1909 and Speleketor Gurney, 1943, each comprising 3 species which have been revised by Lienhard (1988) and Mockford (1984) respectively. The Palaearctic genus Prionoglaris is characterized by the absence of a bulging postclypeus and the corresponding reduction of hypopharyngeal structures (which are present in all other psocids and implicated in the active uptake of water vapour from the atmosphere, cf. Lienhard, 1988: 104) and by the strong metamorphosis of mouthparts during the last moult, also unique in the order Psocoptera: adults nearly lack laciniae (only a microscopical remnant is visible at high magnification), while nymphs have normal laciniae; adults have strongly modified sickle-shaped mandibles, while these organs are of the normal chewing-type in nymphs (cf. Lienhard, 1988, 1998). In the Nearctic genus Speleketor only a slight tendency to such a metamorphosis of mouthparts can be observed (Mockford, 1984), postclypeus and hypopharynx are not modified and exhibit the characters which are typical for the suborder Trogiomorpha. Both genera have very similar wing venation characterized by a strongly developed, arched basal segment of sc, joining r1 close to the base of the pterostigma. The very particular morphology of male genitalia, unique in Psocoptera, can also be interpreted as a synapomorphy of these genera.

In 1999 the Swiss biospeleologist Pierre Strinati discovered the first African prionoglaridid, a very distinct Namibian species which will be described in the following. It is much more closely related to *Speleketor* than to *Prionoglaris*. One of the most striking diagnostic characters is the presence of trichobothria on all tibiae and on hindtarsus, while in *Speleketor* such sensilla are only present on femora and on mid- and hindtrochanter. This feature and the very characteristic development of female genitalia warrant the erection of a new genus for this species, in spite of its close general resemblance to *Speleketor*. It would have been of particular interest to compare also the male genitalia, but unfortunately the male of the new species remains unknown.

Due to the kindness of my colleague Edward Mockford I have been able to examine a paratype female of *Speleketor flocki* Gurney, 1943, the type species of *Speleketor*. In the following comparative discussions some complements to the description of this species are made, enabling a better comparison of these closely related genera.

The following abbreviations are used in the descriptions: P1-P4 = segments of maxillary palp; f1, f2, f3, ...= antennal flagellomeres; t1, t2, t3 = tarsomeres of hindtarsus; c = costal vein; sc = subcostal vein; r1 = first branch of radial vein; rs = radial sector; m = medial vein; pcu = postcubital vein.

Sensitibilla gen. n.

Diagnosis. General habitus very similar to Speleketor (cf. Gurney, 1943: fig. 3). Differing form Speleketor by the following characters. Mandibles with slender incisor region lacking subapical tooth in adults (fig. 9), this region broader and with well developed subapical tooth in nymphs (fig. 13); chewing sculpture on molar region very weakly developed or absent in adults and nymphs. Distal segment of maxillary palp in apical half with a small subglobular sensillum on outer margin (figs 7, 8). Forefemur (fig. 17) lacking the row of articulated spines which is present in Speleketor (fig. 22). Legs with the following pattern of trichobothria on dorsal (outer) margin: 2 on foretibia (fig. 17) and midtibia (fig. 18) in adults and nymphs (one of them in proximal half, the other in distal half); 2 also on hind tibia in nymphs (fig. 21), but only the distal one present in adults (fig. 19); 1 on second article of hindtarsus in adults and nymphs (figs 19-21), this article is distinctly thickened at the place where the trichobothrium is located (fig. 20). Female paraproct concave in ventral half, this region densely setose, of about circular shape (fig. 29, the setose ventral part is transversally folded in slide mounted terminalia). Ovipositor valvulae (= third valvulae, fig. 28) with a long distal process, bearing several spinelike setae. Ovipositor valvulae basally articulated to their abdominal tergite on outer side and fused by a sclerified zone to the subgenital plate medially. Apical lobe of subgenital plate free but ventrally almost completely covered by the valvulae. Subgenital plate and main lobe of the ovipositor valvulae sparsely pilose (fig. 28). Spermapore (fig. 25) with a caplike structure and a longitudinal sclerite near the opening of the very long, narrow spermathecal duct. Distal part of the spermathecal duct spirally curled.

Spermatheca (fig. 25) thin-walled, its wall with irregular rows of small circular pores (fig. 26), near origin of duct a slightly sclerified oval region bearing 2 strong denticles directed to the inner side of the spermathecal sac. Spermatophore simple, more or less pear-shaped (fig. 25).

Type species. S. strinatii sp. n.

Etymology. The name is of feminine gender and alludes to the presence of trichobothria on tibiae [sensilis (lat.) = sensible].

Discussion. A detailed revised diagnosis of Prionoglaris has been published by Lienhard (1988, 1998), the diagnosis of Speleketor is given by Mockford (1984, 1993). One of the most striking diagnostic characters mentioned above is the presence of a characteristic pattern of trichobothria on legs. In other Psocoptera, trichobothria only occur on sense cushions of paraprocts. The genera Speleketor and Sensitibilla are the only psocids, so far as I know, where such sensilla are present on legs. In Prionoglaris the general pilosity of legs is short and uniform, similar to that in the two other genera of the family, but trichobothria are lacking. In Speleketor, the presence of trichobothria on ventral margin of femora has already been mentioned by Gurney (1943: 198), and Mockford (1984) considers the presence of two trichobothria on forefemur as a generic character. The reexamination of a female paratype of S. flocki showed the following pattern of trichobothria, which probably can be considered as diagnostic for the genus Speleketor (figs 22-24): 2 on forefemur; 1 on midfemur and 1 on midtrochanter; 1 on hindfemur and 1 on hindtrochanter; all trichobothria are situated on the ventral (inner) margin of the correponding segment. In Sensitibilla the trichobothria are located dorsally on tibiae and hindtarsus.

Female terminalia have been illustrated for *Speleketor* by Gurney (1943: figs 24-26) and Mockford (1984: figs 29-32). The only pair of well developed ovipositor valvulae (= third valvulae) are large rounded flaps bearing numerous slender setae on most of their margin and 2-3 stout setae close together in mediodistal region. They are not fused to the subgenital plate medially and no distal process is present. In *Speleketor* the paraproct is of normal shape, its ventral half is not concave as in the new genus and the paraproctal setal field is subdivided in a transversal median area and a roughly circular ventral area, both areas are separated by a large zone without hairs (cf. Gurney, 1943: fig. 26). Nothing is known about the spermatheca of *Speleketor flocki*, which is not present in the slide mounted genitalia of the paratype female examined by me. The spermatheca of the allotype female of *Speleketor irwini* Mockford can be characterized as follows (Mockford, *in litt.* 2000): the relatively short, straight duct is wide throughout, with a well-sclerotized cap but with no longitudinal sclerite at the spermapore end; the sac is thin-walled with no ornamentation; within the sac are three vague bodies which are probably spermatophores.

Female genitalia of *Prionoglaris* have been illustrated by Lienhard (1988, 1998). The subgenital plate is simple, with a broadly rounded somewhat sclerified distal margin. The ovipositor valvulae are not fused to the subgenital plate medially and no distal process is present; they are similar in shape to those of *Speleketor* but densely pilose throughout, with some stout setae near apical margin. The paraproct of *Prionoglaris* is simple, pilose and bears some stout setae resembling those on ovi-

positor valvulae. The spermatheca of Prionoglaris has a narrow, straight duct of medium length, and there are no ornamentations on the thin-walled sac; spermapore without sclerotized cap but with a longitudinal sclerite; spermatophore not yet observed.

The characters of trichobothrial pattern and female genitalia warrant the separation of Speleketor and Sensitibilla. Some other useful diagnostic characters are the presence of a row of small spines on anterior face of forefemur in Speleketor (fig. 22) (only a row of normal short hairs at the same place in Sensitibilla), the presence of a small flattened double sensillum in apical half of P4 in Speleketor (fig. 15) (unique subglobular sensillum in Sensitibilla) and the presence, on mandibles, of a small but distinct subapical tooth and a weakly but distinctly sculptured chewing plate in Speleketor (fig. 16) (no subapical tooth and no chewing sculpture in Sensitibilla).

Sensitibilla strinatii sp. n.

MATERIAL

Holotype ♀. NAMIBIA: Arnhem Cave (124 km SE of Windhoek), 1550m, 21 October 1999, leg. P. Strinati. Paratypes: 2♀ and 7 nymphs (different stages), same collecting data. The specimens were collected at the end of a large gallery going down from the entrance, at about 120 m from the entrance, in a completely dark zone (the gallery being straight, the opening of the entrance is visible from the collecting place), under stones on dusty and sandy soil (the psocids were sitting on the underside of the stones, not on the soil itself). Air temperature at this place: 21°C. At the same place, some pseudoscorpions and beetles were also collected. The cave is inhabited by many bats and guano deposits are important.

The type series is deposited in the Psocoptera collection of the Muséum d'histoire naturelle, Geneva, Switzerland: No. 7435 (♀ holotype, mounted on two slides), 7436 (♀ paratype, in alcohol), 7437 (\$\gamma\$ paratype, head mounted on slide, other parts in alcohol), 7438-7441 (4 nymphs paratypes, each mounted on a slide) and, without collection numbers,

3 nymphs paratypes, in alcohol.

ETYMOLOGY

The species is dedicated to its collector, Pierre Strinati, in acknowledgement of his tireless efforts in collecting psocids in caves all over the world.

DESCRIPTION (\mathcal{L} , with some indications on nymphal morphology)

Coloration. Head (fig. 5) marked with some light brown zones of cuticular pigmentation, a small and sometimes very indistinct crescent-like brown spot on each side near antennal socket. Compound eyes black, ocelli each with a dark brown pigment crescent on the inner side. Antennae and legs grey-brown, thorax brown, abdomen whitish with some red-brown hypodermal pigment on several tergites, arranged in irregular transversal bands. Wings clear, unmarked, pterostigma only very slightly opaque.

Morphology. Head shape in frontal view as in Speleketor flocki (cf. Gurney, 1943: fig. 1), compound eyes relatively small and very much in lateral position, close to antennal sockets. Vertical suture well visible, frontal suture absent, ocelli well developed (fig. 5). Antennae longer than body, one antenna of holotype damaged, the other apparently intact (i.e. with last flagellomere regularly rounded apically), with 13

articles. All flagellomeres very thin and densely annulated (sculpture), fl somewhat curved, f2-f11 straight. Lacinia with reduced apical denticles in adults (fig. 11), with three apical tines in nymphs (fig. 12). Maxillary palp (fig. 7) very long and slender, P2-P4 with annulated sculpture, general pilosity relatively dense, consisting of ordinary hairs of about the same length as the diameter of the palpal segments (not figured in fig. 7), 2 short and slightly thickend setae on P1, 1 small relatively weakly differentiated spur sensillum subbasally on P2, a very characteristic subglobular marginal sensillum in apical half of P4, slightly trilobate at apex (fig. 8). Mandibles as described in generic diagnosis (adult: fig. 9, nymph: fig. 13); molar lobe of right mandible subbasally with a well developed and slightly caudally directed fringed lobe. Cibarial sclerite of hypopharynx, epipharyngeal sclerite and oval lingual sclerites well developed, the latter with a distinct hexagonal sculpture, hypopharyngeal filaments separate (fig. 6), hypopharyngeal brush also well developed (not figured in fig. 6). Labial palp 2-segmented (fig. 27), first segment with a short, thickened seta on outer margin, second segment with a slightly sclerified tubercle near distal margin and 3 small thin-walled subapical sensilla. Labrum (fig. 30) with 4 spiniform marginal setae on each side, a row of 6 slender setae in the semicircular hyaline area in the middle of the anterior margin and a row of 5 small setiform marginal sensilla situated in a membraneous fold.

Legs with uniform short general pilosity (e.g. fig. 20, these hairs are not figured in figs 17-19). Forefemur with a longitudinal row of normal short hairs on anterior face (at the same place where in *Speleketor* there is a row of articulated spines, cf. fig. 22). Trichobothria pattern of legs as described in generic diagnosis (figs 17-21). Pretarsal claws symmetrical in nymphs and adults, lacking basal process or basal seta, with one preapical tooth in adults (fig. 10), in nymphs with a small additional tooth or short slender process just distally to it (fig. 14). Hindtibia with two ventral marginal spines in distal half and, on apex, 4 large ventral spines and 2 smaller dorsal ones. Hindtarsus with 2 apical spines and 5 plantar spines on *t*1 and 1 apical spine on *t*2. Same number of apical and plantar spines on tibia and tarsus of foreleg and midleg, the basal 2 or 3 plantar spines of foretarsus weakly differentiated, no ventral marginal spines in apical half of foretibia and midtibia. All leg spines with broadly rounded apex (fig. 20) (in *Speleketor flocki* the leg spines are pointed apically, cf. fig. 24). Midcoxa with a hyaline tubercle on ventral side. Pearman's organ of hindcoxa only represented by a mirror, coxal rasp not differentiated.

Forewing venation as in fig.1, distal segment of *sc* nearly perpendicular to *c* (much more inclined towards wing apex in *Speleketor flocki*), in one of the forewings of the holotype only anterior half of the crossvein between base of pterostigma and *rs* developed, wing margin and veins with very loose microscopical pilosity (fig. 2), *pcu* bald. Hindwing relatively small in comparison to forewing. Hindwing venation as in figs 3 and 4, *sc* with basal thickening on lower surface of wing, *rs* and *m* unbranched, *r*1 sometimes lacking. Pilosity very sparse or completely lacking on margin and veins of hindwing. Distal segment of *sc*, on lower surface of forewing, with a row of small denticles, diminishing in length towards wing margin (fig. 2) (no such denticles in *Speleketor flocki*), *c* in forewing with scale-like sculpture (fig. 2).

Terminalia of female as described in generic diagnosis (figs 25, 26, 28, 29), with the following complements. Epiproct simple, sense cushion of paraproct with 5-6 trichobothria in normal sockets (no basal rosettes) and 1 shorter ordinary hair. Proximal lobe of ovipositor valvulae with 5-6 long ventral hairs, 3 short hairs on inner margin and a transversal row of 4 short dorsal hairs basally to distal process. Distal process with 7-8 spiniform setae distributed throughout its length: 2 of them on dorsal face, 2-3 on inner margin, 2 on ventral face, 1 on apex. This terminal spine with flattened apex, slightly spoon-shaped (cf. detail of fig. 28). Subgenital plate on each side with a pair of long setae just anterior to the sclerified link with ovipositor valvulae. Basal part of subgenital plate with a characteristic pattern of cuticular pigmentation, apical lobe hyaline (fig. 28). Spermapore, spermatheca and spermatophore (= "sperm packet" of Mockford, 1993) as described in generic diagnosis (figs 25, 26).

Measurements ($\Pext{$^\circ$}$ holotype, mm). Body length = 2.5. Forewing length = 2.9. Hindwing length = 1.46. Length of hindfemur = 0.86. Length of hindtibia = 1.45. Length of hindtarsomeres (measured from condyle to condyle): t1 = 0.55; t2 = 0.15; t3 = 0.18.

Remark. The male is not yet known, but the presence of spermatophores in the spermatheca of the dissected female gives evidence of the bisexuality of the species.

GENERAL DISCUSSION

PHYLOGENETICS

Within the family Prionoglarididae the genus *Prionoglaris* is characterized by the autapomorphic characters of head morphology already mentioned in the introduction; another autapomorphy of this genus is the asymmetrical structure of pretarsal claws and their metamorphosis during the last moult (presence of a membraneous vesicle on inner side of anterior claw in adults, no vesicle in nymphs, cf. Lienhard, 1988, 1998).

The clade comprising the remaining two genera, *Speleketor* and *Sensitibilla*, is defined by the synapomorphic presence of trichobothria on legs. Within this group, *Speleketor* is characterized by the presence of a row of articulated spines on forefemur and *Sensitibilla* by the very specialized genitalia of females. The presence of trichobothria on ventral side of femur in all known species of *Speleketor*, mentioned by Mockford (1984), indicates that the trichobothria pattern is of diagnostic value on generic level. The more complex pattern seen in *Sensitibilla* may be interpreted as the apomorphic character state.

GEOGRAPHICAL DISTRIBUTION

The distribution of the currently known species of Prionoglarididae is the following (cf. Badonnel & Lienhard, 1994; Lienhard, 1988, 1996, 1998; Mockford, 1984, 1993):

Genus *Prionoglaris* (type species: *P. stygia*): *Prionoglaris stygia* Enderlein, 1909: Western Palaearctic, usually in caves, sometimes also under stones and within

rocky débris, recorded from the following countries: Belgium, France (type locality), Germany, Greece, Morocco, Portugal, Switzerland, Turkey, former Yugoslavia. – *Prionoglaris dactyloides* Lienhard, 1988: Greece: Peloponnese (type locality, within rocky débris) and Crete (in cave). – *Prionoglaris lindbergi* Badonnel, 1962: Afghanistan, only one nymph known (holotype), under stone.

Genus *Speleketor* (type species: *S. flocki*): *Speleketor flocki* Gurney, 1943: USA: Southern Arizona (Tucson Mountains, in cave, type locality) and Southeastern Nevada (near Las Vegas, in cave). – *Speleketor irwini* Mockford, 1984: USA: Southern California, on the skirts of dead leaves of the palm *Washingtonia filifera* in native stands. – *Speleketor pictus* Mockford, 1984: USA: Southern California, collected at a light (exact habitat unknown).

Genus Sensitibilla gen. n.: Sensitibilla strinatii sp. n.: Namibia, Arnhem Cave.

The few populations known are strongly localized, therefore all these species are considered as extremely rare, even the widely distributed *P. stygia* is very rarely collected. Two species, *Sp. flocki* and *S. strinatii* are only known from caves. *P. stygia* and *P. dactyloides* are also regularly found in caves. But probably none of the species is exclusively cave inhabiting; they are all fully winged, well pigmented and have well developed compound eyes and ocelli.

It is interesting to see that all species of *Speleketor* and *Sensitibilla* are known from desert regions only. The strikingly disjunct distribution pattern (SW North America and SW Africa) of these closely related genera may be interpreted as an indication of a relatively old age of this clade.

FUNCTIONAL MORPHOLOGY

Some of the morphological characters observed in the new genus reveal several interesting problems of functional morphology which have not been studied in detail but which I would like to point out here very briefly.

The presence of trichobothria on legs in *Sensitibilla* and *Speleketor*, unique in Psocoptera, has been described in detail in the discussion following the description of the new genus. These sensilla are very long and extremely fine smooth filiform hairs, inserted in very large and deep sockets (relative to the diameter of the hairs, cf. fig. 20). Their arrangement is apparently constant within a species and essentially the same in nymphs and adults. The absence, in adults of *Sensitibilla*, of the basal trichobothrium on hindtibia (fig. 19) can be explained by the position of the forewing, which touches and covers the basal half of hindtibia in resting position (cf. figs a and b of pl. 9 in Lienhard, 1998, showing the analogous situation in *Prionoglaris stygia* which has a very similar habitus). The resting position of wings is the same in *Speleketor flocki*, where the forewing covers also most of hindfemur and basal part of hindtibia; this situation is incorrectly figured by Gurney (1943: fig. 3).

These trichobothria are thin but relatively rigid hairs. When preserved specimens of *Sensitibilla strinatii* are moved in alcohol, near to the surface of the liquid, it can be observed that the trichobothria easily inflect at their base, without being bent. No histological investigation has been made but the observations mentioned above confirm the hypothesis that these sensilla are real trichobothria, as they are

known in arachnids, for example (cf. Foelix, 1996: 71-73). In spiders, the trichobothria are stimulated by air currents and low frequency air vibrations (sound). Probably their function could be the same in *Sensitibilla* and *Speleketor* and they may be interpreted as adaptations to cave life, even if only one of the three species of *Speleketor* is known to be cavernicolous. But they could also play an important role in the more general context of a life under the conditions of desert climate (cf. above: "Geographical distribution").

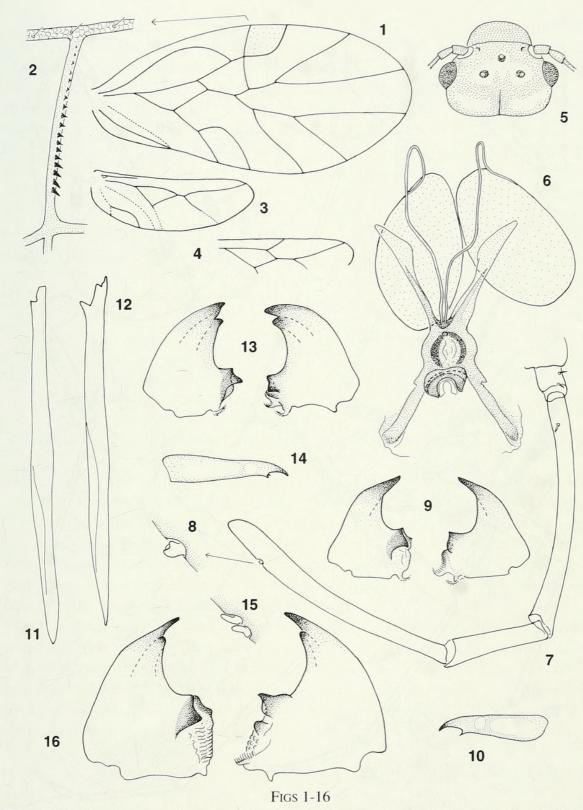
The different position of trichobothria in these genera (ventral side of basal segments of legs in *Speleketor*, dorsal side of apical segments of legs in *Sensitibilla*) may indicate a certain difference in function and therefore in biology of these species. The row of articulated spines on forefemur in *Speleketor* could perhaps also be related to this biological specialization. The row of denticles on distal segment of *sc* in forewing, present in *Sensitibilla* (absent in *Speleketor* and *Prionoglaris*) could eventually be involved in a specialized ethology; it could be interpreted as a sound producing rasp, but there is no evidence of a corresponding frictional structure.

The presence of morphologically different mouthparts (laciniae, mandibles) in adults and nymphs of *Sensitibilla* (and to a somewhat lesser extent in *Speleketor*) indicates a difference in nutritional biology of these life stages. As in *Prionoglaris*, an interpretation is not possible due to the lack of direct observations on animals in captivity (cf. Lienhard, 1988: 103). The reduction of chewing sculpture and the presence of a brush-like fringed basal lobe on right mandible of nymphs and adults could also be related to some nutritional specialization. In this context, it seems interesting to mention the presence of densely fringed mandibles in *Arixenia esau* Jordan (Dermaptera), which lives on bat guano in tropical caves (cf. Strenger, 1977).

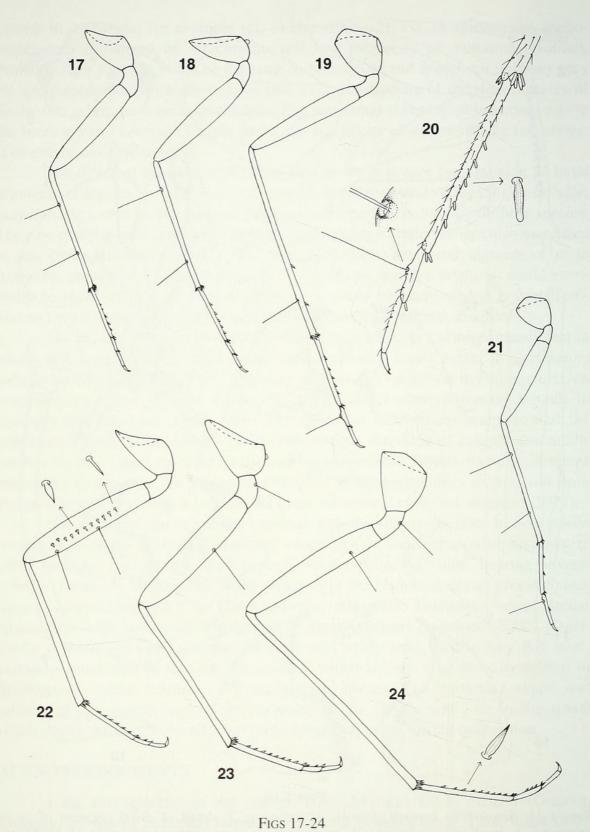
The fusion of the ovipositor valvulae with the subgenital plate in *Sensitibilla* results in a unique functional structure which in this configuration is unknown in other psocids. The strong distal process of ovipositor valvulae, bearing several spiniform setae, is reminiscent of the situation in the Namibian desert psocid *Spinatropos philippi* Lienhard, 2000 (Trogiomorpha: Atropetae: Trogiidae), where similar spines have been tentatively interpreted as digging organs (Lienhard, 2000). *Sensitibilla strinatii* lives under stones on dusty and sandy soils; that is why this interpretation could also be true for this species, which is only very distantly related to *Spinatropos* (same suborder, different family-group). The particular shape and pilosity of the ventral half of the paraproct in *Sensitibilla* could be in functional relation with the unit "ovipositor valvulae-subgenital plate" during oviposition.

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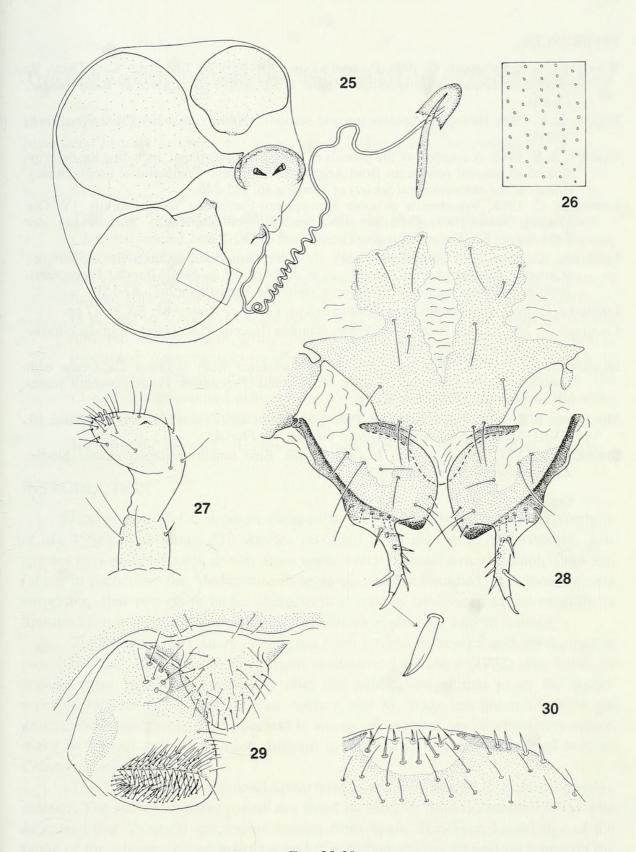
I am very grateful to the renown biospeleologist Dr P. Strinati (Geneva: Cologny) for having made this interesting material available to me. I also thank Dr E. L. Mockford (Normal, Illinois) for the loan of a female paratype of *Speleketor flocki* and for reading the manuscript and making some valuable suggestions. Dr P. Schwendinger (Geneva) kindly indicated to me some literature concerning problems of functional morphology.



Figs 1-11. Sensitibilla strinatii, female: 1, forewing; 2, detail of distal segment of sc in forewing; 3, hindwing (holotype); 4, variant of venation (anteroapical part of hindwing, paratype); 5, head (dorsal view); 6, hypopharyngeal sclerites (dorsal view); 7, maxillary palp (ordinary pilosity not figured); 8, marginal sensillum of P4; 9, mandibles (frontal view); 10, pretarsal claw; 11, lacinia. – Figs 12-14. Sensitibilla strinatii, nymph: 12, lacinia; 13, mandibles (frontal view); 14, pretarsal claw. – Speleketor flocki, female (paratype): 15, double marginal sensillum on P4; 16, mandibles (frontal view). – N.B. All corresponding figures of laciniae and mandibles at same magnification.



Figs 17-20. Sensitibilla strinatii, female: 17, foreleg; 18, midleg; 19, hindleg; 20, hindtarsus. – Fig. 21. Sensitibilla strinatii, nymph: hindleg. – Figs 22-24. Speleketor flocki, female (paratype): 22, foreleg; 23, midleg; 24, hindleg. – N.B. Figs 17-19 and 21 at same magnification, figs 22-24 at lower magnification. Ordinary pilosity not represented on these figures (only spinelike setae and trichobothria figured).



Figs 25-30

Sensitibilla strinatii, female: 25, spermatheca containing three spermatophores; 26, rows of pores on spermathecal wall (detail to fig. 25); 27, labial palp (ventral view); 28, subgenital plate and ovipositor valvulae (ventral view); 29, epiproct and left paraproct; 30, sensilla on distal margin of labrum (right side and middle).

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