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Stories behind names – The insect family Prionoglarididae (Psocodea: 'Psocoptera')

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Scientific naming of organisms is the first step towards communication about them among scientists; the description of species, allowing their reliable identification, is the foundation for studying biological diversity. Only when observations can be reliably tied to a species can a discussion of its ecology, behaviour, economic importance or evolutionary significance become meaningful, only then are studies capable of repetition and confirmation.

When a systematic entomologist encounters an insect unknown to him, and that he is reasonably sure has not been named before, he may decide to publish its description and to name the new species, assigning it to a known genus or to a new one. Today we follow the Rules of the International Code of Zoological Nomenclature (ICZN 1999), but this was not always the case. Naming is preceded by characterizing the organism using the scientific methods available to the person who intends to name it, and distinguishing it from other similar species. Thus, this insect is discovered for science by this systematic entomologist, although it might have been observed before by others or even be familiar to persons who are unaware that it is not yet known to science.

Morphology, the study of form and structure, has traditionally provided the information for characterizing newly discovered organisms and allowing their comparison with those already known. In entomology this approach is still primordial due to the high number of exoskeletal characters easily observable in most insects. However, morphology and systematics are often considered of secondary importance at the universities compared with ecology, physiology, genetics and molecular biology.

As I hope to show in this partly autobiographical article, systematic studies based on morphology not only provide the foundation for scientific investigation of an organism or biological phenomenon, they can also involve the systematic entomologist in fascinating collaborations with colleagues from other biological disciplines, such as ecology, evolutionary biology and molecular phylogenetics, all using different approaches and methods to understand nature. I think this summary of the evolution of our scientific knowledge of the psocid family Prionoglarididae, and of my personal study of this family, shows that systematic entomology is anything but boring. It opens access to new fields of research and, with its inherent historical and encyclopaedic aspects, can help to illuminate the bigger story of the History of Science. When comparing his observations with those already known, the systematic entomologist regularly needs to study old type material and literature, which always give fascinating insights about how our knowledge of a certain group of insects has evolved during past decades or centuries.

Most of the 8 genera and 23 species of the small psocid family Prionoglarididae were described and named less than 20 years ago (see Checklist below). However, the first scientist to become aware of

these insects, more than 200 years ago, was the great French entomologist Pierre-André Latreille (1762-1833).

Latreille had a very particular relationship to psocids! By establishing the genus *Psocus* he became the scientific "father" of these insects (Latreille, 1794). He assigned to this genus some new species and several species formerly assigned to the neuropteran genus *Hemerobius*, amongst them the type species *Psocus bipunctatus* (= *Hemerobius bipunctatus* Linnaeus, 1761). This was the first taxonomic decision leading eventually to the definition of the order Psocoptera by Shipley (1904); the psocids, or barklice and booklice, were nomenclaturally born. Today around 6000 psocid species are known worldwide, assigned to about 500 genera belonging to 40 families (Mockford, 2018). These small and delicate insects (body length between 0.6 and 10 mm) are considered as the non-parasitic members of the order Psocodea, which also includes the true lice (former Phthiraptera) (Yoshizawa & Johnson, 2006) which are strict ectoparasites. Recent molecular phylogenetic research has shown that the traditional 'Psocoptera' can no longer be considered as a monophyletic group because the true lice are phylogenetically embedded in the Psocodea suborder Troctomorpha (Johnson *et al.*, 2004; Yoshizawa & Johnson, 2010; Yoshizawa & Lienhard, 2010).

According to a hypothesis published by Yoshizawa *et al.* (2006), one of the most basal branches of the tree symbolizing the phylogenetic development of the Psocodea consists of the family Prionoglarididae, belonging to the suborder Trogiomorpha. However, the obvious morphological resemblance between the members of this family is essentially due to shared primitive wing vein characters. It was not possible to find any derived (advanced) morphological characters to support the monophyly of the family Prionoglarididae, but recent studies of the mitochondrial genome (Yoshizawa *et al.*, 2017) do support it.

Back to Latreille! When collecting an impressive winged specimen (female, forewing length 5.7 mm; see Enderlein, 1912) of an unknown psocid in France (handwritten locality label by Latreille: "Paris", collection date not indicated), Latreille realized that this insect was clearly different from the known *Psocus* species. He put it in his collection close to *Psocus longicornis* (F.) [= *Psococerastis gibbosa* (Sulzer)], the biggest European psocid (forewing length 5-7 mm), probably because of its somewhat similar habitus, but he did not give it a name (see Enderlein, 1919).

Some years after Latreille's death, Edmond de Selys Longchamps acquired part of his collection, including the above-mentioned specimen (Calvert, 1901; Wasscher & Dumont, 2013). Forgotten in the Selys Longchamps collection for almost a century, the specimen was rediscovered by the German Psocoptera specialist Günther Enderlein while he was working on the psocids of this collection. Enderlein described it briefly as the type species of a new genus, *Scoliopsyllopsis latreillei*, assigning it to the family Psyllipsocidae (Enderlein, 1912). In his important phylogenetic synthesis (Enderlein, 1911: table 27) he had already mentioned the name of this genus (*nomen nudum*), and some years later he gave a detailed and nicely illustrated final description of this insect (Enderlein, 1919), which he considered so extraordinary, compared to the known European psocid fauna, that he speculated about a possible mislabelling by Latreille or an accidental introduction to Paris from an exotic country.

About 20 years after the first description of the enigmatic *S. latreillei* by Enderlein, the French specialist André Badonnel must have been very excited when he received a female of an extraordinary psocid collected in 1925/26 by his colleague Lucien Berland in southern France (Dépt. Var: Callian). Comparison with Enderlein's description and figures of *S. latreillei* convinced him that the new specimen was the second known female of this species. After a detailed study of the very particular

mouthparts he placed the genus in a family of its own, the Scoliopsyllopsidae (Badonnel, 1931), which he considered as related to the family Psyllipsocidae, both belonging to the Trogiomorpha, the most basal suborder of Psocodea. Badonnel (1931, 1936) was impressed by the very particular morphology of the hypopharynx and mandible, and especially by the absence of the maxillary lacinia present in all other psocids as a characteristic chisel-like organ. This really was an unexpected and somewhat mysterious psocid (nothing was known about the biotopes where it lived), yet it seemed to be indigenous to France!

Just five years later, in 1936, this exceptional psocid had to change its name. Today its valid name is *Prionoglaris stygia* Enderlein, 1909. This name was given by Enderlein (1909) to a species he discovered when examining psocids collected by biospeleologists in French caves. He considered the 15 nymphs collected in January 1907 in the Compagnaga Lecia cave in the French Pyrenees as belonging to a new species, and also a new genus, because they differed from all known psocid nymphs (he even hesitated over whether they were nymphs or adults). Enderlein realized this insect was a typical psocid, having normal mandibles and a normal chisel-like lacinia, but he could not assign it to any of the known psocid families, and considered its position within psocids enigmatic (Enderlein, 1909, 1911: 287). His fascination with this interesting discovery is reflected by the aura of mystery attached to the species name proposed; an allusion not only to the subterranean habitat of the species but also to the River Styx, the underworld river of death in ancient Greek mythology. But scientists do not like persistent enigmas, so Karny (1930), without examining Enderlein's specimens, proposed including the genus *Prionoglaris* in the family Trogiidae, in a subfamily of its own, the Prionoglaridinae.

Some of the mystery surrounding the extraordinary psocids *Scoliopsyllopsis latreillei* and *Prionoglaris stygia* remained until the Belgian biospeleologist Robert Leruth collected an interesting winged psocid in the Hohière cave at Heyd-lez-Bomal (Belgium) on 16 July 1933, and gave it to his colleague Antoine Ball for identification. Realizing that this female was the third known specimen of *Scoliopsyllopsis latreillei*, Ball (1935) presented the discovery at the monthly meeting of the Belgian Entomological Society on 4 May 1935. He also asked Leruth to show him the place where he had collected this female in the cave. There they discovered several nymphs and adults of both sexes and Ball was able to describe the male of this species for the first time (Ball, 1936). While there was no doubt that the adults belonged to the species *Scoliopsyllopsis latreillei*, the nymphs corresponded exactly to Enderlein's description of *Prionoglaris stygia*. Ball reared some nymphs to obtain adults, and so observed the "transformation" of *P. stygia* nymphs into adults of *S. latreillei*! After comparing the nymphs to a specimen of Enderlein's type series of *P. stygia*, he proposed the synonymy of these two species (Ball, 1936), which was immediately accepted by his colleagues working with psocids. Thus, the same species had been discovered twice by Enderlein, once described as *P. stygia* Enderlein, 1909, once as *S. latreillei* Enderlein, 1912, the former name having priority. At present there is a consensus among psocid specialists, in agreement with Badonnel's opinion, that the isolated position of this genus deserves establishment of a special family. But the name Prionoglarididae Karny, 1930 has priority over Scoliopsyllopsidae Badonnel, 1931. One puzzle was cleared up by the studies of these systematic entomologists in the first half of the 20th century, but this psocid family continued to fascinate further generations of entomologists currently working with genomics and synchrotron micro-tomography to elucidate the remaining mysteries!

Soon, not only taxonomists but also general zoologists, such as Seeger (1975, 1979) and Nüesch (1987), became interested in *Prionoglaris*. The former made detailed morphological and embryological studies seeking better understanding of the phylogeny of the Paraneoptera, a supra-

ordinal group to which the psocids belong. The latter proposed a special type of metamorphosis for *Prionoglaris* in his review on metamorphosis in insects, based on the observation that this genus is the only psocid showing a very strong reduction of the lacinia in the adult, while this organ is present in the nymph (as opposed to being present in nymphs and adults, like all other psocids). In his classification of insect metamorphosis, Nüesch (1987: p. 478) considers *Prionoglaris* as paurometamorph (contrary to all other psocids which are ametamorph), a special type of metamorphosis within exopterygote insects characterized by the metamorphosis of only a few structures during adult moult.

Though the Prionoglarididae were thought to be one of the most basal groups among psocids, they were known only from the Old World until 1940. Between December 1940 and March 1941, the American entomologist R. A. Flock collected males, females and nymphs of an enigmatic psocid in a cave in the Tucson Mountains (Arizona). He sent these insects to the American psocid specialist Ashley Buell Gurney who identified them as a new species belonging to a new genus similar to *Prionoglaris* (Gurney, 1943). But this new species, *Speleketor flocki*, lacks the modified mouth parts observed in *Prionoglaris*; a well-developed lacinia is present not only in the nymph but also in the adult.

Impressed by the morphological differences between *Prionoglaris* and *Speleketor*, Courtenay Smithers, in his phylogenetic analysis of the Psocoptera, assigned each of these genera to a family of its own, Prionoglarididae and Speleketoridae (Smithers, 1972). At present two subfamilies of Prionoglarididae are recognized, Prionoglaridinae and Speleketorinae. The monophyly of each subfamily is well supported by morphological and molecular analyses (Lienhard, 2004; Yoshizawa *et al.*, 2006; Yoshizawa *et al.*, 2018b) while the monophyly of the family Prionoglarididae is only supported by a single study of the mitochondrial genome, as mentioned above (Yoshizawa *et al.*, 2017).

When describing his genus *Speleketor*, Gurney mentions some delicate sensory setae (trichobothria) on the femora. Such leg trichobothria had never been observed on psocids before. The presence of leg trichobothria is an important character to define the subfamily Speleketorinae within Prionoglarididae. Several genera of this subfamily also have such sensory hairs on their tibiae and tarsi and form a tribe of their own, the Sensitibillini. The representatives of this tribe are the most fascinating prionoglaridids known, due to their peculiar female genitalia, but the first representative of this tribe, the genus *Sensitibilla*, was not described until the year 2000 (Lienhard, 2000), so more about that later.

Meanwhile, two additional species of *Speleketor* were discovered in Southern California by Edward Mockford (1984), *S. irwini*, living on dead leaves of the palm tree *Washingtonia filifera*, and *S. pictus*, the habitat of which remains unknown because the only known specimen was taken in a light trap. So, three New World species of prionoglaridids were known by 1984. The Old World genus *Prionoglaris* remained monotypic, however, until the discovery of a nymph in the mountains of Afghanistan (Karghaleh, 3100m, under a stone) by the Swedish entomologist K. Lindberg. Based on this nymph, Badonnel (1962) described a new species, *Prionoglaris lindbergi*, but until the adult is discovered its identity will remain enigmatic.

In March 1982, during a spring excursion to Greece, I was collecting my first specimens of *Prionoglaris* and became involved in the investigation of the family Prionoglarididae. I had started work at the Geneva Natural History Museum in 1981 and was immediately confronted with some specimens, mostly nymphs, preserved in the Museum collections, which I recognized as belonging to the genus *Prionoglaris*. They came from caves in France, Greece, Turkey and Morocco and had been

collected by the Swiss entomologists Pierre Strinati, Villy Aellen, Bernd Hauser, Claude Besuchet and Ivan Löbl. The fascination of these insects marked my career as an entomologist and did not end with my retirement from the Museum in 2009!

Collecting adults of *Prionoglaris* in the field is a rare event, so most of the adults I have examined since 1981, originating from 14 localities, were reared from nymphs collected in caves or under stones; samples from 33 additional localities also contained only nymphs. We still cannot explain this phenomenon. Perhaps the adults have a particularly short lifespan due to their modified mouthparts: lacinia reduced to a microscopic rudiment, mandibles elongated and slender, lacking the rugose chewing part that is present in all nymphal stages. One wonders whether these mouthparts are really functional to feed on the fine layers of green algae that grow on rocks in the entrance zone of the caves where nymphs are usually found and which are used for rearing them in captivity. The first specimens I collected were three nymphs living under stones near Kastritsion in the Panachaikon Mountains of the Greek Peloponnese. Rearing two in the laboratory produced an adult of each sex and the surprising discovery that the morphology of the male genitalia (phallosome) was different from that of males known from Belgium, which were assigned to the species *P. stygia* by Ball (1936), while the females from Greece were indistinguishable from Belgian females. However, the type locality of *P. stygia* is not the Hohière cave in Belgium, from which Ball had described the male, but the Compagnaga Lecia cave in the French Pyrenees, from which only nymphs were known. The Greek specimens clearly could not be assigned to the same species as the specimens from the Belgian cave. But before giving a name to the Greek species, adults from the type locality of *P. stygia* had to be examined. With the help of Pierre Strinati, Bernd Hauser and especially of the French biospeleologist Michel Bouillon, an excursion to the type locality of *P. stygia* was organized in November 1986. Although we found only nymphs in the cave, it was possible to obtain several males and females by rearing them in the laboratory. The genitalia of the males from the type locality corresponded exactly to those of the specimens from Belgium. The tentative identification by Ball as *P. stygia*, based on the comparison of Belgian nymphs with one of Enderlein's nymphs (syntype), was correct. I was then able to publish a synthesis of the knowledge about the genus *Prionoglaris* together with the description of the new species from Greece, *P. dactyloides*, the name of which derives from the pair of very characteristic finger-like lateral appendices of the phallosome (Lienhard, 1988). A particularly exciting moment during this work was when I examined Latreille's specimen from Paris, the holotype of *Scoliopsyllopsis latreillei* Enderlein, which I had borrowed from the Institut Royal des Sciences Naturelles de Belgique in Bruxelles for this study.

But many questions about the real species diversity of *Prionoglaris* in the Palaearctic remained unresolved. A population of *S. stygia* from a Moroccan cave showed an intermediate morphology of the male genitalia between *stygia* and *dactyloides*, and a male of the latter from a cave in Eastern Crete does not correspond exactly to the holotype of *dactyloides* from the Peloponnese (see figures in Lienhard, 1998). Yoshizawa *et al.* (2018b) mentioned surprisingly large molecular differences between several European populations of *Prionoglaris* (see Checklist below: sp. 249, sp. 468). Perhaps there are some cryptic species? Due to the lack of adults for many populations it is often impossible to compare male genitalia, which seem to bear the most useful characters for defining species, so it is important that the Russian entomologist Sergei Kapralov collected a pair of adults of *Prionoglaris* in an Armenian cave in 2018. At the beginning of 2019 he sent me these specimens for identification. Detailed morphological and molecular studies of these perfectly preserved specimens may contribute to a better understanding of the systematics of this genus.

As we have seen, at the end of the 20th century, about 200 years after Latreille put the first specimen of *Prionoglaris* in his collection, the family Prionoglarididae was known from Europe and Afghanistan (three species of *Prionoglaris*) and from Arizona and California (three species of *Speleketor*). If this family were really a basal group within psocids, as generally suggested by specialists, it might also be present in the southern hemisphere... It is time for the second part of the prionoglaridid story!

At the end of 1999 I had the opportunity to examine the first representative of the prionoglaridid subgroup that would later (Lienhard, 2007) be named Sensitibillini and become famous, due to the unique reversal of sex organs in some of its members. On 21 October 1999 the renowned Swiss biospeleologist Pierre Strinati collected some cave dwelling insects in the Arnhem cave, near Windhoek, Namibia. Back home he gave these specimens to his friend Villy Aellen, former director of the Geneva Natural History Museum. Some of these insects were psocids. His life-long experience with cave insects told Aellen that these psocids were "special". Very sick at this time, he nevertheless handed them to me immediately in December 1999. Villy Aellen passed away on 22 January 2000. This was my last contact with my former director and my first contact with a representative of the fascinating group of Sensitibillini; simultaneously a personally very sad and scientifically very exciting moment. A new genus and new species had to be described for these insects (Lienhard, 2000): *Sensitibilla strinatii*. The presence of trichobothria on some parts of the legs indicated that the genus was related to *Speleketor*. In *Sensitibilla* the trichobothria are not present on femora and trochanters, as in *Speleketor*, but on tibiae and on the hind tarsi. This was the first time a tarsal trichobothrium had been observed in insects. These long and fine sensory hairs may be adaptations to the cave habitat; they are usually interpreted as receptors for air vibrations, more or less the "ears" of the Sensitibillini living in the darkness of caves!

In 2004 I sent a specimen of *Sensitibilla strinatii* to my young Japanese colleague Kazunori Yoshizawa for DNA analysis. I knew him personally, since he had attended the workshop on Psocoptera I organized in 1996 at the Geneva Museum. After finishing his PhD, he was not only an expert in psocid morphology but rapidly became an expert in molecular phylogenetics too. I was convinced that this material would one day be the key to understanding the phylogeny of the basal groups of psocids. This was the beginning of an important collaboration with my Japanese colleague on the biology of Prionoglarididae.

After the surprising discovery of *Sensitibilla* I contacted the National Museum of Namibia in Windhoek to see if any unidentified specimens of these interesting psocids were deposited in their collection. The entomology curator prepared a large parcel of all the non-identified psocids they had, and a Swiss friend of mine transported the parcel to Geneva after a private trip to Namibia. Among this very interesting material I discovered not only two new species of *Sensitibilla* but also three species of a closely related new genus that I named *Afrotroglia* (Lienhard, 2007). The strikingly coloured type species, *Afrotroglia oryx*, was collected in 1994 in a South African cave, near the Namibian border; I gave the name *oryx* to this species because the South African Oryx antelope has a somewhat similar dark brown colour pattern on its head.

Sensitibilla has normal genital organs, with a sclerotized phallosome in the male and no particular structures in the female beyond the characteristic ovipositor. When looking for the first time at a specimen of *Afrotroglia* I thought it must be a male, due to the presence of sclerotized structures in the apical part of the abdomen, but an ovipositor was also present... In another specimen, which lacked the ovipositor (and so was presumably male!), no sclerotized phallosome was visible... A very intriguing

situation! I carefully dissected one of each kind (not an easy task due to their small size: body length about 3 mm). The ovipositor-bearing insect was a female, but it also had a very striking, partly sclerotized structure enclosing the distal portion of the spermathecal duct (i.e. the duct that runs from the external genital opening (spermapore) to the spermatheca, where sperm is stocked after copulation before it is used for the fertilization of the eggs). Such a structure had never been observed in a female psocid. The other specimens were evidently male, but their external genital organs consisted only of a membranous cavity, except for a small, slender sclerite that can be interpreted as a rudiment of the phallosome as seen in *Sensitibilla*.

My hypothesis concerning the function of these very atypical organs was that the sclerotized structures of the phallosome of *Sensitibilla* are functionally replaced in *Afrotroglia* by the complex female structures associated with the spermapore and the spermathecal duct. Thus, in the genus *Afrotroglia*, responsibility for a close grip during copulation was probably transferred from the male organ (penis or phallosome) to a specialized female organ (Lienhard, 2007). Again, some *Afrotroglia* material was sent to Yoshizawa for DNA extraction for future phylogenetic study of the family Prionoglarididae. Some specimens of *Sensitibilla etosha*, the fourth species of *Sensitibilla*, collected in Namibia by the Czech entomologist Otakar Holusa in 2007, were, of course, also sent to Yoshizawa for DNA extraction after its description (Lienhard *et al.*, 2010a).

After discovering a new monotypic prionoglaridid genus, *Siamoglaris*, in a collection from Thailand made in 2003 by my colleague Peter Schwendinger from the Geneva Museum (Lienhard, 2004), I had also sent some material of the type species, *S. zebrina*, to Yoshizawa for DNA extraction. This genus does not belong to the Sensitibillini tribe and has normal genitalia in males and females, but it could immediately be included, with *Sensitibilla*, in the phylogenetic analysis of the suborder Trogiomorpha published two years later (Yoshizawa *et al.*, 2006). This molecular study confirms the monophyly of the two subfamilies Prionoglaridinae (*Prionoglaris* and *Siamoglaris*) and Speleketorinae (*Speleketor* and *Sensitibilla*) that I had defined morphologically (Lienhard, 2004). So the family was also known from the Oriental Region. A second species of *Siamoglaris* was later discovered in material collected by the Thailand Inventory Group for Entomological Research (TIGER) during their project on the insect fauna of Thailand (Lienhard, 2011). This species, *S. theresiae*, is dedicated to the former technician of the Geneva Museum, Ms Theresia Cuhe, who tirelessly sorted and labelled thousands of psocids from Thailand for this project. Recently the first fossil prionoglaridids have also been described from South East Asia: three species of the genus *Palaeosiamoglaris* from Cretaceous Burmese amber (Azar *et al.*, 2017). Based on their close relationship the genera *Siamoglaris* and *Palaeosiamoglaris* were separated from *Prionoglaris* as a new tribe, the Siamoglaridini, defined by these authors (see Checklist below).

By chance, the family Prionoglarididae had been discovered in the Oriental and the Ethiopian Regions within a short span of time. In a phylogenetic study on the suborder Trogiomorpha, Yoshizawa *et al.* (2006) speculated that the known prionoglaridid genera might be interpreted as Pangaeian relicts. Thus, the presence of the family in South America was implicitly postulated, but nobody knew that some South American prionoglaridids were already waiting in alcohol to be discovered and named by a psocid specialist!

In 2008 and 2009 the Brazilian biospeleologist and ecologist Rodrigo Lopes Ferreira sent me four parcels of psocids from Brazilian caves for identification. Among many other interesting psocids in this material I discovered three species of a new genus closely related to *Afrotroglia*. I carried out the morphological analysis and scientific description of these specimens, and named this New World

genus *Neotrogla*, containing the species *N. brasiliensis*, *N. aurora* and *N. truncata*. These results were published in a joint paper with Ferreira and his student Thais Oliveira do Carmo (Lienhard *et al.*, 2010b). The type material of the three species was collected between 2003 and 2009 in different caves of the Brazilian states Minas Gerais, Tocantins and Bahia by Ferreira and Robson de Almeida Zampaulo.

On examining the first specimens of *Neotrogla*, I was surprised by their great general similarity to *Afrotrogla*. The males have only a small sclerite embedded in a largely membranous genital cavity, very similar to the male external genitalia in *Afrotrogla*. I thought the female genitalia might also be similar to *Afrotrogla*. To examine this, the female was put into a liquid that makes the abdomen transparent before dissection. In the apical region of the abdomen I discovered a spectacular, partly sclerotized, partly membranous structure enclosing the distal portion of the spermathecal duct. The elongate and slender shape of this structure immediately suggested a comparison with a normal male psocid copulatory organ. This organ was so unusual for a female that I proposed the new term gynosome for this penis-like structure, analogous to the term phallosome generally used for the male copulatory organ of psocids (Lienhard *et al.*, 2010b). Having observed this spectacular genital structure in the female of *Neotrogla*, associated with the impressive reduction of the male phallosome, I proposed the hypothesis that the gynosome of *Neotrogla* might be an intromittent organ penetrating the male's membranous cavity during copulation. The presence, in the male genital cavity, of a papillate channel leading to the opening of the seminal duct (ductus ejaculatorius) situated at the bottom of this cavity, suggested that the tip of the gynosome might be introduced here to ensure contact between the opening of the male seminal duct and the opening of the female spermathecal duct during copulation for efficient sperm transfer (Lienhard *et al.*, 2010b: fig. 10c). I also proposed use of the term gynosome for the somewhat similar structure observed in *Afrotrogla*. Based on morphology, I considered these genera as the most closely related within the tribe Sensitibillini, supposing that their common ancestor had a similar structure of the genitalia, so the gynosome could be considered as a synapomorphy of these genera, absent from their sister-taxon *Sensitibilla*. However, the molecular phylogenetic analysis recently published in *Biology Letters* (Yoshizawa *et al.*, 2018b) showed that the African genera *Afrotrogla* and *Sensitibilla* are more closely related to each other than to the South American genus *Neotrogla*, and that the gynosome (or female penis) evolved twice independently in this group of insects, each time associated with the reduction of the male copulatory organ resulting in a sort of male vagina. The terminology "female penis" and "male vagina" was introduced by Yoshizawa *et al.* (2014) after direct observation of the function of these genitalia during copulation. This slightly shocking terminology used in the *Current Biology* paper to describe the reversal of sexual organs in these insects was probably the reason it was awarded the Ig Nobel Prize in the field of biology in 2017. Ig Nobel Prizes are awarded to "honor achievements that first make people laugh, and then make them think."

But this achievement was the result of the great efforts made by my colleagues, in the field and in the laboratory. Rodrigo Ferreira was especially important, because only he had direct access to the caves in which these insects were collected. When the taxonomic study was ready for publication Ferreira came to meet me in Geneva in September 2010. I showed him the microscope preparations of *Neotrogla* and insisted that now it would be crucial to observe the copulation of the *Neotrogla* species and to fix coupling pairs for detailed study of the function of the gynosome. I also said the distributional pattern of the Sensitibillini genera in southern Africa and Brazil could be a nice example of Western Gondwanan vicariance (this hypothesis was recently confirmed by Yoshizawa *et al.*, 2019b). The further development of research on these insects shows that my colleagues Rodrigo

Ferreira and Kazunori Yoshizawa found my fascination with it contagious. The *Neotrogla*-team was up and running!

I had already sent specimens of *Neotrogla* to Yoshizawa in 2009, and he prepared a preliminary molecular phylogenetic analysis of Prionoglarididae for the 4th Dresden Meeting on Insect Phylogeny (Dresden, Sept. 18-20, 2009). His results were included in my talk on Prionoglarididae, where the gynosome was presented to a scientific public for the first time. I explicitly asked the international experts attending this meeting whether they were aware of any male-female interaction during copulation similar to the postulated penetration of the male by the female penis-like gynosome. Apparently nothing similar had ever been observed in insects. Our conviction grew that this might be a phenomenon unique in the animal Kingdom.

Now the hard work began! Ferreira began a concentrated search for *Neotrogla* in Brazilian caves and Yoshizawa tried to understand the functional morphology of the gynosome. He came to see me in Geneva in September 2011, where he examined slides containing the dissected genitalia of *Neotrogla* for the first time. In my drawing, published with the original description of the genus (Lienhard *et al.*, 2010b: fig. 10c), the penetrating gynosome of *Neotrogla* is represented in resting position, as it was observed in the apical region of the female abdomen. However, after examining the slide-mounted genitalia Yoshizawa thought the membranous part of the gynosome might be reversed during penetration and that the small spines and spiny lobes present on this membrane (Lienhard *et al.*, 2010b: figs 2f, 6ab, 8c) might anchor the gynosome in the male genital cavity during copulation. And he realized that, in the male, the enigmatic membranous structures distally on each side of the rudimentary phallic sclerite (clearly figured in my initial drawings, see Lienhard *et al.*, 2010b: figs 3e, 7e), might be pouches for the insertion of these gynosomal structures. Back in Japan Yoshizawa tried to confirm this hypothesis by manipulating a non-dissected female. When pulling the tip of the gynosome out of the abdomen of this female with very fine pincers he observed that the spiny membranous parts of the gynosome were reversed by this artificial "erection" of the "female penis" and so were ready to be inflated for insertion into the membranous pouches of the "male vagina" for anchoring the female during copulation.

Due to the efforts and experience of Ferreira and Yoshizawa it was finally possible to confirm these hypotheses by analysing the micromorphology and the function of the gynosome of *Neotrogla* in coupling pairs, and to prepare the joint paper published in *Current Biology* (Yoshizawa *et al.*, 2014). Erection of the female penis and anchoring within the male vagina could be observed by Yoshizawa for all *Neotrogla* species in the coupling pairs fixed in alcohol by Ferreira. So it became evident that there is co-evolution of the male and female structures in this genus, the arrangement of the male vaginal pouches being adapted to the arrangement of the anchoring spines on the female penis. For this paper Yoshitaka Kamimura, a Japanese expert in evolutionary biology, was invited as a co-author, and he has since become an indispensable member of our team. In March 2016 Ferreira organized a joint field trip in Brazil for Yoshizawa and Kamimura, resulting in a more intense collaboration between these three enthusiastic biologists. They developed new techniques for future studies of population genetics in *Neotrogla* (Kamimura *et al.*, 2018).

In 2011 a fourth species of *Neotrogla* was discovered by Rodrigo Ferreira. The type material was collected by S. S. Salgado in several caves of the Brazilian state Bahia. Ferreira made the first dissection of female genitalia himself and was immediately convinced of having discovered an additional species, characterized by an apically curved gynosome. While the males of the four *Neotrogla* species are difficult to distinguish, due to the absence of characteristic genitalia, the females

are easily distinguished by the micromorphology of their gynosome. A possible fifth species (cryptic species?) from the Brazilian state Minas Gerais, the females of which are very similar to *N. aurora*, still awaits investigation (see Checklist below: sp. 501). The fourth species was described as *Neotroglia curvata* by Lienhard & Ferreira (2013) and became famous due to the figures of the coupling genitalia made by Yoshizawa for the *Current Biology* paper (Yoshizawa *et al.*, 2014: fig. 2A-E) and the observations of the coupling duration by Ferreira. He observed coupling duration in 12 pairs of *Neotroglia curvata*, varying from 41 to 73 hours! This is exceptionally long for insects and also for the humans watching the coupling pairs! Nothing was known about coupling duration in Sensitibillini before these observations, so Ferreira was expecting it to last up to about four hours, as mentioned in the literature for a related family of psocids (Trogidae). In view of the seemingly endless coupling he decided to check each pair every 30 minutes, if still in copula. All members of the lab were finally persuaded to take turns, over three days and nights for the most active couple!

Another intriguing structure of the female genitalia of *Neotroglia* is the very particular spermathecal plate, already figured in the original species descriptions (Lienhard *et al.*, 2010b: figs 2e, 7c, 9a). This sclerotized plate situated at the proximal end of the spermathecal duct can hold two spermatophores simultaneously (Yoshizawa *et al.*, 2014: fig. 3F). Based on the micromorphology of the spermathecal plate Yoshizawa postulated a switching valve mechanism for regulation of sperm flow between its two slots. This hypothesis was confirmed by the discovery of the first biological switching valve (Yoshizawa *et al.*, 2018a).

After publishing the results of the morphological and functional analyses of the reversed sex organs in the genus *Neotroglia*, together with the discovery of the switching valve in its spermatheca, and also the final results of the molecular phylogenetic analysis of the tribe Sensitibillini (Yoshizawa *et al.*, 2018b), the moment for evolutionary hypotheses had arrived. By chance Kazunori Yoshizawa was invited to write an article for the rubric "Hypotheses" of the scientific journal *BioEssays* (Yoshizawa *et al.*, 2019a), which allowed us to develop some thoughts about the question "Why did a female penis evolve in a small group of cave insects?" Detailed molecular phylogenetic investigations had shown that the female penis evolved twice independently in *Afrotroglia* and *Neotroglia*, together with the convergent reduction of the male phallosome towards a vagina-like cavity. This molecular result was supported by the considerable morphological differences between the female penis of *Afrotroglia* and *Neotroglia*. Several factors favouring the evolution of a female penis in the tribe Sensitibillini are postulated in the *BioEssays* article and several preadaptations that possibly reduced constraints against the reversal of sex organs are also discussed. One of the most interesting elements favouring the evolution of the female penis is probably the microscopical switching valve in the spermathecal plate (a novel structure possibly present in all Sensitibillini) which enables the female to stock simultaneously two sperm packages received from the same male during a particularly long copulation or from different males during two successive copulations.

Sex role reversal is known in other animals (Kamimura & Yoshizawa, 2017) but these inconspicuous psocids are the only animals where sex role reversal is combined with reversal of sex organs! These cave psocids are also unique among all known insects due to the presence of tarsal trichobothria. Apparently this isolated group constituted a testing-ground for evolutionary experiments. Further surprises seem possible in Prionoglarididae, like the one I had ten years ago when the Italian biospeleologist Giuseppe Grafitti sent me a vial with a tiny whitish and wingless psocid collected in February 2009 by his friend Corrado Conca in a cave in one of the famous inaccessible rocky tepuis in south eastern Venezuela.

Don't be snobbish! That is what I learned from the story of this Venezuelan cave psocid. Some years previously, Guiseppe Grafitti had already sent me all the psocids he collected in Sardinian caves, mostly whitish and wingless nymphs of the widely distributed species *Psyllipsocus ramburii*. These findings were not exciting because this species is very common in caves all over the world. "Another nymph of *P. ramburii*!" was my first reaction when I took this vial from the parcel, and without looking at it under the stereomicroscope I placed it in my cupboard for future examination. But I had to confirm arrival of the specimen to my Italian colleague, so a few days later I sorted out the vial again to check that the specimen was safely preserved. A quick glance under the stereomicroscope and my blood ran cold: this was not the nymph of a banal *Psyllipsocus* but a wingless adult prionoglaridid! In the absence of the typical wing venation of the family, I looked for another diagnostic character. I found it on the specimen's head. The bulging postclypeus, so typical for psocids, was not differentiated. The only psocid genera I knew that had the same shaped head capsule were *Prionoglaris* and *Siamoglaris*. The presence of 3-segmented tarsi was an unequivocal indication of adulthood, because psocid nymphs always have 2-segmented tarsi. My next step was to find out which sex it belonged to. It was a wingless female, about 2 mm long, with very long slender antennae, lacking any pigmentation and obviously blind... Or was it? A minute black point of pigment was visible on each side of the head, near the antennal socket. Further examination in the compound microscope showed this to be a unique flat ommatidium. The minimum number of ommatidia per eye known in psocids was two, observed in some species of the genus *Liposcelis*. So this new prionoglaridid is well adapted to cave life, if not completely blind, while all other members of the family are fully winged, well-pigmented and have well developed compound eyes. All known Prionoglarididae are usually found in caves but, surprisingly, this is the only species perfectly adapted to this habitat. So I named this new genus *Speleopsocus*, while the species name *chimanta* refers to the Chimanta massif where the type locality (the Auchimpe cave in the Churi tepui) is situated (Lienhard *et al.*, 2010a). Based on the morphology of the head capsule and particularly the mouthparts this new genus could be assigned to the subfamily Prionoglaridinae, which was known only from the Old World. Previously only representatives of the subfamily Speleketorinae were known from the New World (*Speleketor* and *Neotrogla*).

Speleopsocus is characterized by the reduction of pigmentation, eyes and wings, things apparently "superfluous" for a life in caves. However, evolution equipped our tiny cave psocid with a particularly "useful" novel structure. The antennae of *Speleopsocus* are extremely long and thin. They are important sensory organs for life in dark caves, more or less replacing the compound eyes usually present in insects. In the only known specimen of *S. chimanta* both antennae are damaged but, by extrapolation based on what we know about prionoglaridid antennae, we can estimate that the intact antennae of this species are several times longer than its body. When *Speleopsocus* touches the surrounding substrate with its antennae some dust particles adhere to the antennal flagellum. How can it be cleaned to ensure it remains an efficient sensory organ? Antenna cleaners, which are known in some other insects (e.g. ants, see Hackmann *et al.*, 2015), had never been observed in psocids. This minute cave prionoglaridid proudly paid tribute to the fact that it is a member of a very special family and offered me the pleasure of discovering the first antenna cleaner in psocids (Lienhard *et al.*, 2010a: fig. 1e-g). Though not yet observed in function, the supposed antenna cleaner consists of a spur-like apical extension of the first tarsomere of each foreleg and may be a very efficient tool for clamping the long antennal flagellum between this spur and the base of the second tarsomere while pulling it through the hairy notch at the base of the spur, the diameter of which exactly corresponds to the diameter of the antennal flagellum. Simply perfect! But will anybody ever have the chance to test this hypothesis by observing a living specimen of this tiny cave insect performing its ablutions?

Checklist of Prionoglarididae

(† = Extinct taxon)

Order: PSOCODEA ('Psocoptera')

Suborder: TROGIOMORPHA

Infraorder: PRIONOGLARIDETAE

PRIONOGLARIDIDAE Karny, 1930

Prionoglaridinae Karny, 1930

Prionoglaridini Karny, 1930

Prionoglaris Enderlein, 1909 (Palaeartic)

Synonym: *Scoliopsyllopsis* Enderlein, 1912

Prionoglaris dactyloides Lienhard, 1988 (Greece)

Prionoglaris lindbergi Badonnel, 1962 (Afghanistan)

Prionoglaris stygia Enderlein, 1909 (Europe, N-Africa)

Syn.: *Scoliopsyllopsis latreillei* Enderlein, 1912

[*Prionoglaris* sp. 249 from Greece, see Yoshizawa *et al.*, 2018b]

[*Prionoglaris* sp. 468 from Turkey, see Yoshizawa *et al.*, 2018b)]

Speleopsocus Lienhard, 2010 (in: Lienhard *et al.*, 2010a) (Venezuela)

Speleopsocus chimanta Lienhard, 2010 (in: Lienhard *et al.*, 2010a)

Siamoglaridini Azar, Huang & Nel, 2017 (in: Azar *et al.*, 2017)

†*Palaeosiamoglaris* Azar, Huang & Nel, 2017 (in: Azar *et al.*, 2017) (Myanmar, fossils in Cretaceous amber)

†*Palaeosiamoglaris burmica* Azar, Huang & Nel, 2017 (in: Azar *et al.*, 2017)

†*Palaeosiamoglaris inexpectata* Azar, Huang & Nel, 2017 (in: Azar *et al.*, 2017)

†*Palaeosiamoglaris lienhardi* Azar, Huang & Nel, 2017 (in: Azar *et al.*, 2017)

Siamoglaris Lienhard, 2004 (Thailand)

Siamoglaris theresiae Lienhard, 2011

Siamoglaris zebrina Lienhard, 2004

Speleketorinae Smithers, 1972

Speleketorini Smithers, 1972

Speleketor Gurney, 1943 (North America)

Speleketor flocki Gurney, 1943 (USA: Arizona)

Speleketor irwini Mockford, 1984 (USA: California)

Speleketor pictus Mockford, 1984 (USA: California)

Sensitibillini Lienhard, 2007

Afrotroglia Lienhard, 2007 (southern Africa)

Afrotroglia fabella Lienhard, 2007 (Namibia)

Afrotroglia maraisi Lienhard, 2007 (Namibia)

Afrotroglia oryx Lienhard, 2007 (South Africa)

Neotroglia Lienhard, 2010 (in: Lienhard *et al.*, 2010b) (Brazil)

Neotroglia aurora Lienhard, 2010 (in: Lienhard *et al.*, 2010b)
(Brazil: Tocantins)

Neotroglia brasiliensis Lienhard, 2010 (in: Lienhard *et al.*, 2010b)
(Brazil: Minas Gerais)

Neotroglia curvata Lienhard & Ferreira, 2013 (Brazil: Bahia)

Neotroglia truncata Lienhard, 2010 (in: Lienhard *et al.*, 2010b)
(Brazil: Bahia)
[*Neotroglia* sp. 501 from Brazil: Minas Gerais, see Yoshizawa *et al.*, 2018b]
Sensitibilla Lienhard, 2000 (Namibia)
Sensitibilla brandbergensis Lienhard, 2007
Sensitibilla etosha Lienhard & Holuša, 2010 (in: Lienhard *et al.*, 2010a)
Sensitibilla roessingensis Lienhard, 2007
Sensitibilla strinatii Lienhard, 2000

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