

Original paper

A redescription and family placement of *Buemarinoa patrizii* Roewer, 1956 (Opiliones, Laniatores, Triaenonychidae)

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Summary. *Buemarinoa patrizii* Roewer, 1956, from a Sardinian Cave and *Fumontana deprehendor* Shear, 1977, from the Appalachian Region of eastern North America, are closely related and are the only representatives of the temperate Gondwanan family Triaenonychidae in the Northern Hemisphere. Based on their relevant characteristics, these two species, together with *Flavonuncia pupila* Lawrence, 1959, from Madagascar, are placed into a new tribus Buemarinoini **tribus n.**, which represents an old phyletic lineage. It is a unique case of a phyletic lineage (tribus in this case) with three representatives present on three different continents. The elongated appendages in troglobite *Buemarinoa patrizii* are not treated as a troglomorphic trait. Elongation of appendages in troglobionts is not an adaptation, but a precondition for settling in a subterranean environment. The main morphological differences of *Fumontana deprehendor* in comparison with *Buemarinoa patrizii* are treated as apomorphic. The unique terminal structure of the male copulatory apparatus, which includes a pair of flanking setose arms, a pair of glans glands and bifurcated sperm duct, define the Buemarinoini tribus n. Based on the male penis structure, Buemarinoini **tribus n.**, shows closeness to a complex of species gathered around the genera *Ceratomontia*, *Austromontia* and *Monomontia* from South Africa and South America. The origin of Buemarinoini must be related to the areas of Northern Gondwana, from where *Fumontana* penetrated deeper into Laurasia. Lectotypes are designated for *Buemarinoa patrizii* type material.

Key words: ampho-Atlantic, Laurasia, lectotype, new tribus, Northern Gondwana, troglomorphic.

INTRODUCTION

Subordo Laniatores is a highly species-rich group of harvestmen with nearly 4,200 described species (Kury 2013). Its representatives are most common in the tropics, where they display the highest level of species diversity. Cyphophthalmi and Palpatores, the remaining two suborders of harvestmen, show a somewhat greater diversity outside the tropics. As for Palpatores, with the exception of the family Sclerosomatidae, its overall diversity is associated with Temperate Zone areas. The three suborders share the fact that their basal groups (early-diverging lineages) are present almost exclusively outside of the tropical belt, in cryophilic

habitats of the Temperate Zone. They have survived in these areas mainly as relict cryptobionts.

A disproportional presence of basal groups of Laniatores between Temperate Zones of the Southern and Northern Hemisphere is evident. Basal groups of Laniatores in the Temperate Zones of Northern Hemisphere include representatives of the superfamily Travunioidea (Travuniidae, Cladonychiidae, Paranonychidae and Cryptomastriidae), the family Phalangodidae and, symbolically, the family Triaenonychidae; while in the Southern Hemisphere they are represented only by the family Triaenonychidae. Such a picture is suggestive, and (among other factors) illustrates the great age of the family Triaenonychidae. The presence of the basal groups of subordo Palpatores shows a similar pattern of presence, exclusively in habitats of the Temperate Zone.

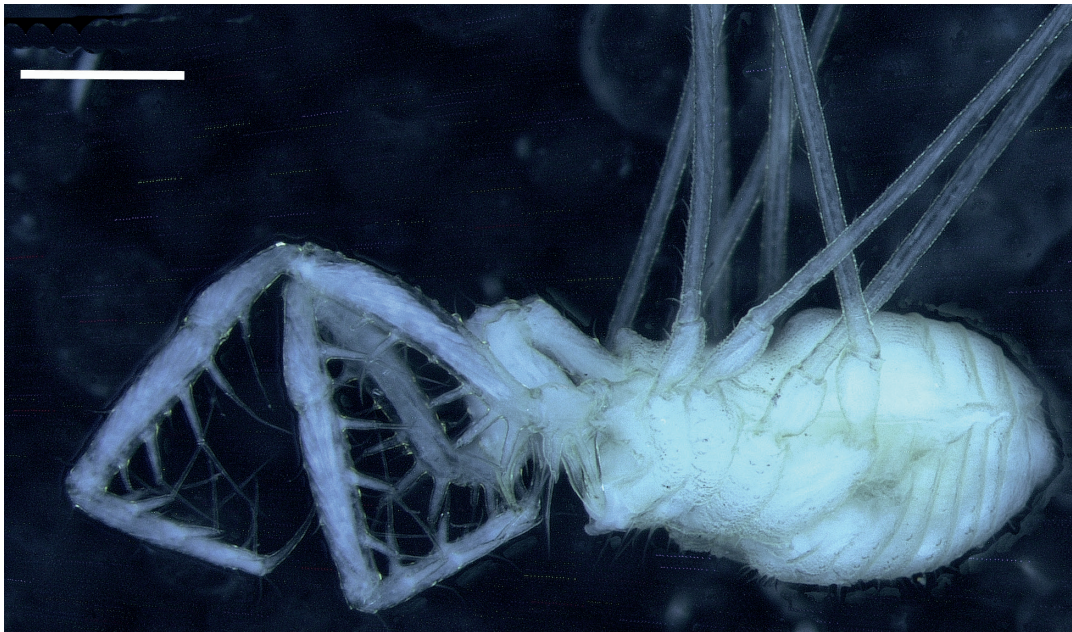


Fig. 1. *Buemarinoa patrizii*, paralectotype female 1.4 mm, side view. (Scale bar = 0.5 mm.)

Buemarinoa patrizii Roewer, 1956, a little-known cave species from Sardinia after its description was mentioned in a few publications, as one of the European representatives of the family Travuniidae (Martens 1978; Kury and Mendes 2007; Kury et al. 2014), in which Roewer originally placed it. Recently, Derkarabetian et al. (2018) classified this species in the Laurasian family Cladonychiidae. Kury and Mendes (2007) expressed doubts about the status of the genus *Buemarinoa*, but not about its family affiliation. In all of these important monographs and studies, which mentioned or briefly referred to *B. patrizii*, a mistake has clearly been made, because it was not possible to recognize the family affiliation of the species without insight into the actual specimens. Indeed, the original description of this species did not significantly differentiate it from other travuniids, as explicitly stated in the diagnosis of the genus. Also, a significant mistake in the description, where the typical triaenonychid type of the posterior leg claws in this species was listed as peltonychium type, appears to have misled the above listed authors. The great taxonomic significance that was previously attributed to this character could have been earlier identified, if it had been correctly interpreted, enabling experts to study this species in more details. In addition to these missteps, placement with the above mentioned families was considered to be “logical”, given the geographical position of Sardinia. This must have had a significant effect on speculations concerning species placement, which failed to take into account the highly complex biogeography of the Mediterranean and its limitrophic regions.

Examining type specimens of *Buemarinoa patrizii* (Fig.

1), I observed that it is actually a member of the family Triaenonychidae, close to the species *Fumontana deprehendor* Shear, 1977 (Fig. 2), from the Appalachian Region in North America, which is the only representative of this Gondwanan family in the Northern Hemisphere. The unique characteristics of these two species are reflected in the specific and complex structure of the male copulatory apparatus. A similar penis structure is present in the species *Flavonuncia pupila* Lawrence, 1959, from Madagascar. All three species based on this important and most indicative character stand in contrast to all other species in the family Triaenonychidae.

The family Triaenonychidae is not clearly defined. The reasons for this have been elaborated in detail by Hunt and Hickman (1993), and have been attributed to the fact that it is an extremely old group and an old diversification. Almost all species of Triaenonychidae have limited distribution, which best illustrates their relic character.

Actual division of the family is based on the structure of the sterna and tarsal claws of the hind legs, homoplastic characters which are variable at all taxonomic levels. Because of this, many authors expressed doubts about the validity of the division (Forster 1954; Maury 1988; Hunt and Hickman 1993). However, division of the family into four subfamilies is still in use (Kury et al. 2014; Kury 2018): **Triaenonychiinae** Sørensen, 1886 (South Africa, Madagascar, New Zealand, Tasmania, Australia, South America, New Caledonia, Eastern North America); **Adaeinae** Pocock, 1902 (South Africa and Western Australia); **Triaenobuninae** Pocock, 1902 (Tasmania, Southeast Australia, New Zealand, South America, Madagascar) and **Soerensenellinae** Forster, 1954



Fig. 2. *Fumontana deprehendor*, male 1.65 mm, side view. (Scale bar = 0.5 mm.)

(New Zealand and South Africa). Species of the New Zealand monotypic family Synthetonychiidae differ from Triaenonychidae by their unusual appearance, but not in other relevant characters. Therefore, some authors have expressed doubts about the validity of its existence (Martens 1986; Hunt and Hickman 1993).

A comprehensive revision of Triaenonychidae is clearly necessary, in order for species of this family to be grouped into subfamilies that are based on real phyletic relationships and valid characters. Unfortunately, this is currently not the case. Therefore, I am placing genera *Buemarinoa*, *Fumontana* and *Flavonuncia* provisionally into the subfamily Triaenonychinae, as nominal one of the established subfamilies, and because *Fumontana* and *Flavonuncia* had been already placed in it by their authors. To emphasize the phyletic proximity of these three geographically very distant genera, I decided, although it is not common practice in the classification of Opiliones, to establish for them a new tribe - the *Buemarinsonini tribus n.*

MATERIALS AND METHODS

Photographs of habitus morphology as well some details (pedipalps, ocular tubercle) were taken using a Leica M205C stereo microscope equipped with a Leica DFC290 HD digital camera. Final images were taken at different focal planes and combined using Leica Application Suite V4.11 software. Photographs from slides were taken using a Zeiss Axio Imager A1 compound microscope equipped with an AxioCam MRc5 digital camera. Final images were taken at different focal planes and combined using Helicon focus stacking software. Drawings were made in Adobe Illustrator CS2 on a Genius EasyPen M610X graphics tablet. Dissected parts were mounted on slides in glycerol. After glycerol the ovipositor and penises were temporary mounted on slides in Faure's mounting medium (40 g chloral hydrate, 10 g gum Arabic; 5 g glycerin, 5 g glacial acetic acid, 5 g glucose, and distilled water).

For comparison a male specimen of *Fumontana deprehendor* from USA (Tennessee, Cocke Co, road to Cosby Campground, 27. 08. 2005, leg. M. Hedin et al.) has been studied.

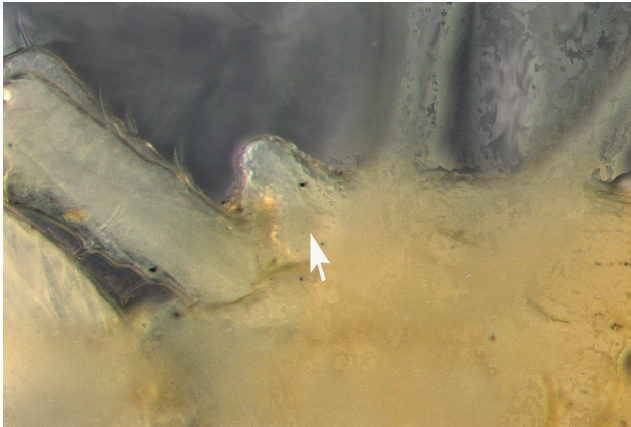


Fig. 3. *Buemarinoa patrizii*, paralectotype female 1.4 mm. Ocular tubercle (arrow).

RESULTS

Tribus Buemarinoini, tribus n.

Type genus

Buemarinoa Roewer, 1956

Diagnosis

The tribe is characterized by male genital morphology: Glans clearly separated from the stout truncus, elongated and terminally expanded, basally with two flanking setiferous arms. Each setiferous arm, on the basis of its apical half bearing three ventral and two dorsal setae. Glans ending with a complex structure of distally oriented projections, three paired and a single one which terminally protrudes (as

described in Thomas and Hedin 2006). In the drawings of *Flavonuncia pupila* provided by Lawrence (1959), three pairs of distally oriented projections are shown in a somewhat different spatial distribution. As the drawing may not be entirely accurate with respect to these details, in terms of this character *F. pupila* could be different within the tribe. Glans in Buemarinoini distally contains a pair of glans glands and a bifurcated sperm duct. *Buemarinoa patrizii* and *Fumontana deprehendor* are closely related, based on the structure of the penis and conspicuously elongated pedipalps in both species, compared to *Flavonuncia pupilla*.

Composition

Three known species of the tribe Buemarinoini are present on three different continents: *Buemarinoa patrizii* from a cave in Sardinia, *Fumontana deprehendor* from the Appalachian Region in North America and *Flavonuncia pupilla* from Madagascar (South-East and East Central Mts. and highlands).

Buemarinoa patrizii Roewer, 1956

(Figs 1, 3-7, 8B, 9A, 10)

Material examined

Lectotype male (here designated), 1 male paralectotype, 2 female paralectotypes, Sardinien, Grotta Bue Marino, leg. Patrizi, Coll. Senckenberg-Museum, Frankfurt/M, SMF 11402.

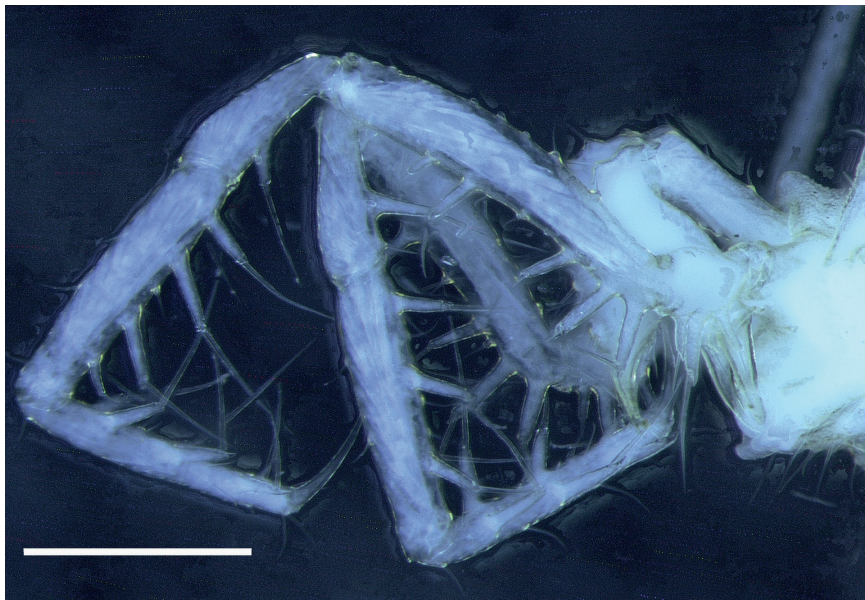


Fig. 4. *Buemarinoa patrizii*, paralectotype female 1.4 mm. Pedipalps, side view. (Scale bar = 0.5 mm.)

Remark

The type series comprises a lectotype male mounted on a slide, and a male and two female paralectotypes dissected by a previous researcher. The lectotype was deformed due to mounting on the microscope slide.

Redescription

Small blind troglobitic species (lectotype male 1.25 mm, male paralectotype 1.2 mm, female paralectotypes 1.3-1.4 mm long) with elongated pedipalps (Fig. 1) built in the form of a catching basket, armed with strong elongated spine-like tubercles. Conical ocular tubercle, small and smooth, situated on the anterior edge of the dorsal scutum (Fig. 3). Body unpigmented, uniformly granulated with small sparse granules.

Chelicerae elongated, basal segment slender, almost cylindrical with sparse setae on the dorsal surface, ventrally with few setae; second segment frontally set with sparse setae.

Pedipalps elongated (the femur length is two thirds of the body length) with thin articles (Figs 4-5); built in the form of a catching basket, armed with strong elongated spine-like tubercles, each bearing a strong elongate seta sub-apically; coxae ventrally with a low tubercle bearing small setae and a strong spine-like tubercle proximally; trochanter ventrobasally with 1 strong spine-like tubercle between 2 smaller ones; femur ventrally in the proximal part armed with a row of 3 strong spine-like tubercles, distally with 2 medial and 2 lateral (one smaller) spine-like tubercles; patella medially with 1 strong spine-like tubercle, laterally with 1 spine-like tubercle; tibia and tarsus with 3 strong spine-like tubercles on both sides (laterally and medially), terminally with 2 strong setae. Claw elongated.

Sternum narrow, basally widened, with two pairs of setae (basal pair shorter). Coxal lobes II anteriorly with small apophyses medially oriented.

Legs are elongated with cylindrical segments; coxae, trochanter, femur and patella granulated, with small sparse granules as body; coxae ventrally with a row of small sparse tubercles bearing setae. A stick like, frontally oriented, tubercle (Fig. 6) is present on the dorsal side of Coxa II, opposite to the ozopores. It seems it is connected with the functioning of the scent glands.

Each femur basally with a false articulation. Metatarsi divided into longer astragalus and shorter calcaneus. Calcanei I-IV elongated. Tarsal formula is wrongly presented in Roewer's description. Tarsal formula: I-3; II-13; III-4; IV-4. Basitarsi elongated, much longer than individual distitarsal segments. Measurements of legs (female 1.4 mm): I -5.5 mm; II-10.2 mm; III-6.8 mm; IV-9.3 mm.

Tarsal claws of the first and second legs simple (Figs



Fig. 5. *Buemarinoa patrizii*, paralectotype male 1.2 mm. Pedipalps, frontal (dorsal) view. (Scale bar = 0.5 mm.)

7A-B), first claw slightly sickle-shaped; second one elongated, straight in the proximal half, bent at the distal half; claws of the third and fourth legs (Figs 7C-D) with two lateral branches almost the same length as the median prong. Distal half of claws III and IV, bearing median prong and branches, bent at right angles to the proximal half.

Penis structure (Figs 8B-9A) is similar as in *Fumontana*, with a short, stout, muscular truncus and elongated glans with two flanking setose arms ventrobasally; glans apically expanded with a complex structure of ventrodistally oriented projections: three paired and one single protruded, with a pair of oval glands inside. Each setose arm on its apical half bearing three ventral and two dorsal setae. Medially, a pair of projections represent bifurcated, rigid end of sperm duct which opens subterminally, ventrolaterally from the base of the single projection - terminal setae. Orifices are with medially directed oblique openings. Two oval glands are present in widened, terminal part of the glans, aside from the bifurcate sperm duct. They open terminally, with a single orifice each, aside from the base of terminal setae.

Ovipositor cylindrical, short (Fig. 10), slightly longer than wide. Terminal rim surrounds two lateral, short non-conspicuous lobes and 12 setae. Vagina is short.

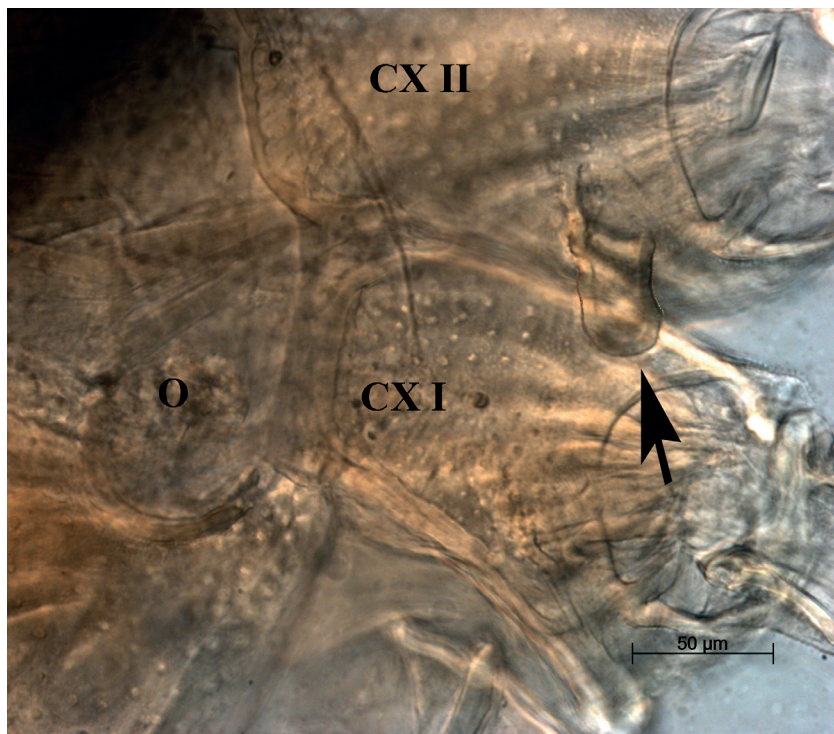


Fig. 6. *Buemarinoa patrizii*, lectotype. Stick like tubercle (arrow), O - ozophore, CX I, II - coxae of legs 1-2.

Remarks

Penis in *B. patrizii* in comparison with *Fumontana deprehendor*, is narrower with longer setose arms and more terminally positioned setae on them (Figs 9A-B). Also, glans distal projections show some differences in proportions and positions but they are not clearly visible on light microscope and are hardly comparable with clear SEM photos of *F. deprehendor* given in Thomas & Hedin (2006). A bifurcate structure and a pair of oval structures (glands?) with separate orifices, in the terminal part of the glans are indicated on the Lawrence drawing of *Flavonuncia pupila* (Fig. 9C).

Details of the complex structure of the male copulatory apparatus, based on the material and techniques I had available, remained unclear. It is thus necessary to continue this study using fresh material with application of histological techniques.

Ovipositor in *B. patrizii* is without dorsal and ventral lobes which are present in other Insidiatores (Travuniidae, Cladonychidae, Paranonychidae, Cryptomastriidae and genus *Yuria*) (Briggs 1971; Suzuki 1975a, 1975b; Martens et al. 1981; Karaman 2005; Starrett et al. 2016). Ovipositor morphology of *Fumontana deprehendor* and *Buemarinoa patrizii* do not exhibit remarkable differences. This observation is based on the drawing of the ovipositor of *F. deprehendor* made by Axel Schönhofer who kindly shared it with me.

Despite the fact that ovipositor musculature without adequate preparation is hardly visible, I have some observations

on it which I should mention. Area of seminal receptacle of *Buemarinoa patrizii* is surrounded by Inner Longitudinal muscles and Circular muscles, as presented in Martens et

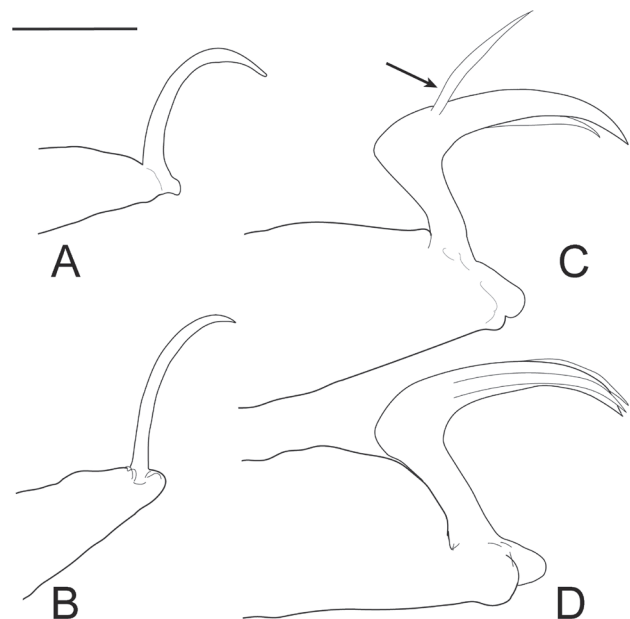


Fig. 7. *Buemarinoa patrizii*, lectotype. Claws of legs I-IV: A, claw I; B, claw II; C, claw III with a broken lateral branch (arrow); D, claw IV. (Scale bar = 50 µm.)

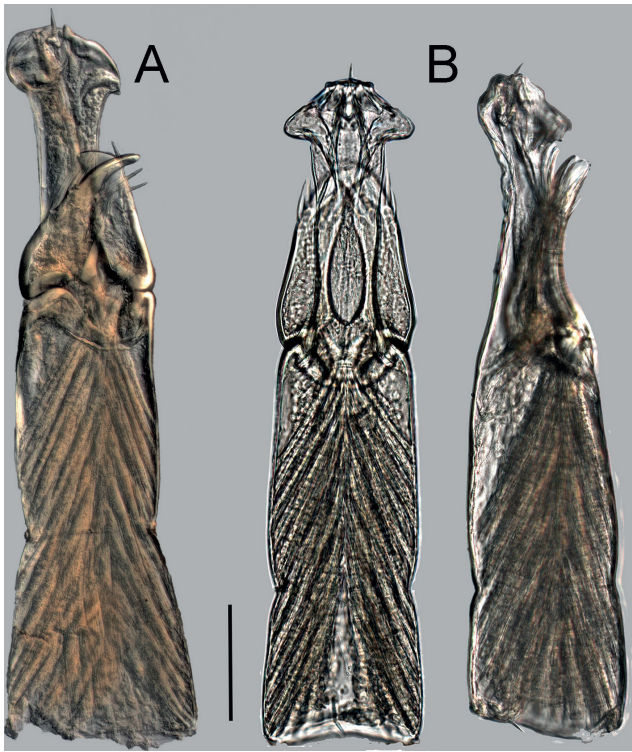


Fig. 8. A, *Fumontana deprehendor*. Penis, subventral view; B, *Buemarinoa patrizii*, paralectotype male 1.2 mm. Penis, ventral (left) and sublateral (right) view. (Scale bar = 100 μ m.)

al. (1981) for representatives of several Grassatores families. Outer Longitudinal muscles seems somewhat more complex than in Cladonychidae (Martens et al. 1981). Limitations of Light microscopy did not allow me to explore the details of taxonomically very important characteristics of inner ovipositor structure.

Stick like tubercle on Coxa II of *B. patrizii*, is present in *Fumontana deprehendor* in form of transverse bifurcate tubercle. In some South African triaenonychids it is in form of transverse ridge ending with tubercle. Currently, I have no knowledge about the presence of this character among Triaenonychidae nor its taxonomic significance.

DISCUSSION

The two closely related species of the tribe Buemari-noini represent two life forms: *Buemarinoa patrizii* is a troglobite, while *Fumontana deprehendor* is a terricole species. Although the first one could be treated as “highly specialized subterranean species”, a common statement regarding subterranean fauna, it has only reduced pigment and eyes as an adaptation to subterranean life. Its general appearance does not differ from the appearance of its epigeal ancestors. It retained the appearance of the early Laniatores. This refers to the pedipalps structure and the position of the ocular tubercles. I suspect that this is the case with the elongated legs

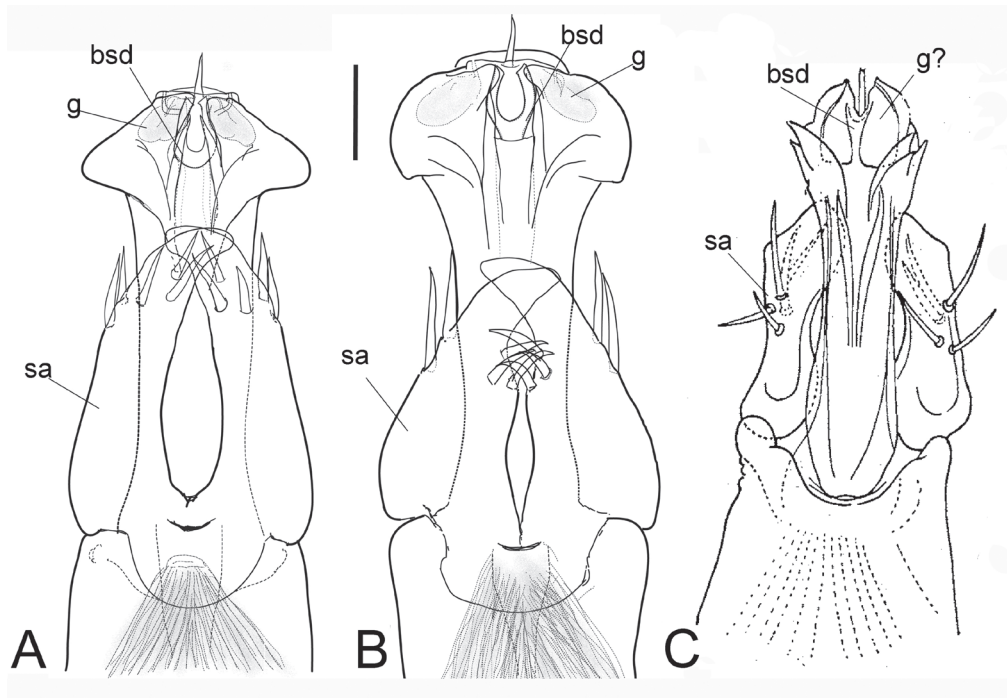


Fig. 9. Penis (terminal half), ventral view: A, *Buemarinoa patrizii*, paralectotype male 1.2 mm; B, *Fumontana deprehendor*; C, *Flavonuncia pupila* (drawing from Lawrence 1959) (g - gland; bsd - bifurcate spermal duct; sa - setose arms). (Scale bar A, B = 50 μ m.)

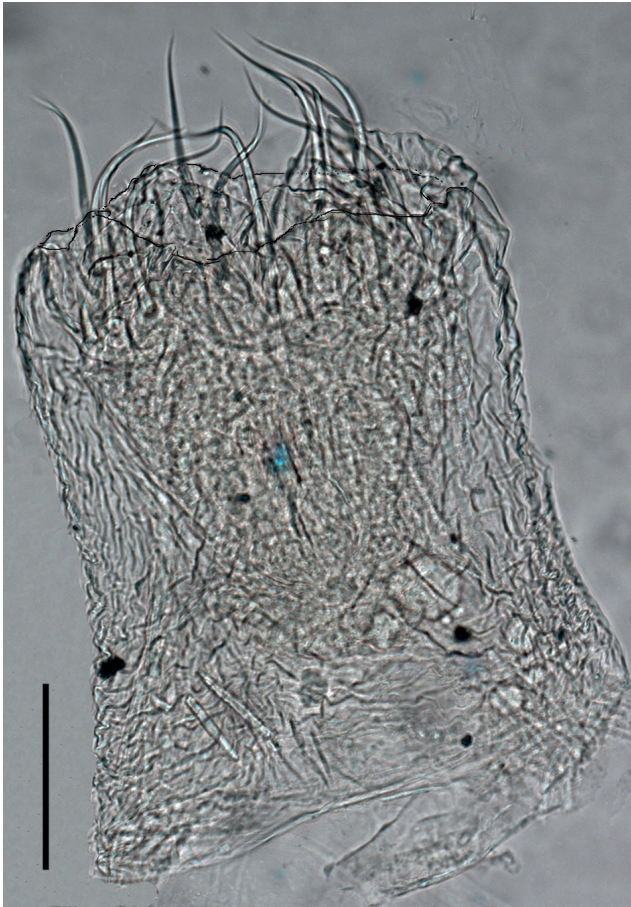


Fig. 10. *Buemarinoa patrizii*, paralectotype female 1.3 mm. Ovipositor. (Scale bar = 100 μm .)

of this species as well. Elongated legs are a prerequisite for life in a subterranean habitat, where vertical dimensions prevail. In biospeleology, “pre-adaptation” is a commonly used term, denoting expression of a previously committed step in the process of adaptation for life in underground conditions and a precondition for settling a subterranean environment. Regarding the elongation of extremities in troglobites, I think that the more appropriate term here is predisposition. This is a trait that has been acquired in conditions which are not in any way connected to any type of underground habitat. In an area very rich in subterranean fauna, in the Dinarides of former Yugoslavia, these are probably the earlier arboricolous forms of Tertiary forests covering the region. Karstification (and other processes) have provided underground cavities in which animals with appropriate skills are inhabited. One basic skill needed is the ability to move on vertical surfaces. Troglobionts are climbers, and elongated legs provide them with the ability to climb. Greater mobility is of primary importance for organisms living in an environment low in food sources, due to their constant need for foraging. It is thus very likely that the epigean ancestor of *Buemarinoa patrizii*

had elongated legs as well.

Life in an arid climate with unfavorable seasonal conditions (which occurred in the late Tertiary) likely favored shortening of the legs of the terricole, *Fumontana deprehendor*, so as to enable its retreat deeper into the cracks and cavities of substrate, trunks and logs etc.

I think that the type of pedipalps with elongated articles armed with long spines, as seen with *B. patrizii*, is the basic type in Laniatores and probably in Opiliones in general. This is indicated by the presence of long spines on the pedipalps of the most primitive Palpatores (*Acropsopilio*, *Austropsopilio*, *Caddella*, *Caddo*). This type of pedipalps functions as a catching basket (Karaman 2005), designed originally to capture and overcome highly mobile prey, such as Collembola. It is widely present among basic Travunioidea and basic Grassatores. Basic position of this type of pedipalps among Palpatores is suggested in Wolff et al. (2016), where they hypothesize that pedipalps “glandular setae evolved as an adaptation to capture small and agile prey, which are hard to catch with a capture basket”.

In the case of *Fumontana deprehendor*, pedipalps are in the form of a strong raptorial organ armed with spines of reduced length (Fig. 2), suggesting a less specialized function, i.e. to overcome more diverse, larger and stronger prey.

In the modified type of pedipalps of *F. deprehendor*, the function of structures that prevent prey from maneuvering (such as the “catching basket” in *Buemarinoa* and others) supersedes the rows of spines on legs I and II (Fig. 2). This substitute structure consists of a dorsal and a ventral row of strong spines on the femurs, similar to those on pedipalps in *B. patrizii*, and short ones on the patella and tibia of the extremities. These “armed” legs compensate for the reduction of the spines on the pedipalps of *Fumontana*. Similar and independent phenomenon and trends are present among representatives of various genera and families of Laniatores (as in Podoctidae, *Triaenobunus*, *Graemontia*), where extremely reduced spines on the pedipalps are compensated by similar structures on the fore legs.

In the process of further adaptations, the armament of these legs is reduced and its traces remain in the form of short sequences of shortened spines on some foreleg articles (as in *Ceratontia*, *Hendea*, *Lizamontia*,...) or in the form of tubercles (as in *Calliuncus*, *Nuncia*,...).

The position of the ocular tubercle of *Fumontana deprehendor* is also a result of the development of stronger pedipalps. Its initial position on the anterior margin of the dorsal scutum has changed. It has shifted posteriorly to the end of the prosoma of the dorsal scutum. This is a direct consequence of the strengthening of the femur of the pedipalps, which requires the space above the frontal dorsum when they are at rest and for balance during movement.

Based on the morphology of claws III and IV, *F. deprehendor* and *B. patrizii* are remarkable different. The first one possess claws with a pair of lateral branches shorter than the central prong, while the second one possess lateral branches equal to the central prong as in the New Zealand and South African subfamily Soerenenellinae.

Despite huge habitual differences between these two species, their complex male copulatory apparatus, which is almost identical, undoubtedly indicates their closeness. It is a synapomorphy shared with *Flavonuncia pupila* from Madagascar.

However, considering the triaenonychid close superfamily Travunioidea, this type of copulatory apparatus could be plesiomorphic. Penis structure in the Californian species *Zuma acuta* Goodnight & Goodnight, 1942 (fam. Paranonychidae) presented in Derkarabetian et al. (2018) indicates the possible homology of paired structures in the glans basis of this species and setiferous arms in Buemarinoini, which would then suggest paraphyletic Triaenonychidae. Such considerations have no support based on results from molecular analysis (Giribet et al. 2010; Fernández et al. 2017; Derkarabetian et al. 2018) which are often contradictory. I believe that a more realistic picture of the relationship between the early Laniatores will be obtained after analyzing of a much larger sample.

Maybe it is better to first invest more energy into the reconstruction of the phyletic relations at lower levels of classification and for some regions. At the current level of knowledge, overambitious reconstruction of early divergences within Opiliones may lead to more confusion than acceptable solutions.

Criteria for distinguishing families of Travunioidea, Grassatores, Palpatores and Cyphophthalmi often have less weight than differences among some genera of Triaenonychidae. This applies particularly to the structure of the copulatory apparatus, where, for example, an eversible complex glans is present in the genus *Triaenonychoides* (Pérez-González & Werneck 2018) while here flanking setose arms, a bifurcate sperm duct and glands are present in the non-eversible glans of Buemarinoini. Actually they all belong to the same subfamily Triaenonychinae.

All potentially indicative characters for the valid classification of this group have not been exhausted. Here, in the first place I propose the structure of the ovipositor that is compatible with the male's copulatory apparatus, which proved to be extremely indicative. It seems that internal ovipositor structure can be of greater importance, as it functionally supports the structure of the male copulatory apparatus. Most importantly, I recommend examination of the complexity of the ovipositor musculature, which may be of different levels, as Martens et al. (1981) has pointed out. In Laniatores, an active role of the ovipositor in insemination is quite possible.

With respect to male penis external structure, Tribus Buemarinoini shows closeness to a complex of species gathered around the genera *Ceratontia*, *Austromontia* and *Monomontia* (Mendes and Kury 2008; Schönhofer 2008; Iglesias et al. 2017) from South Africa and South America. The fused structures of the glans complex and chaetotaxy on the ventral setiferous plate in species of this species complex highlight this fact. The ventral setiferous plate of the penis is deeply cleft in the South African genus *Monomontia*, and

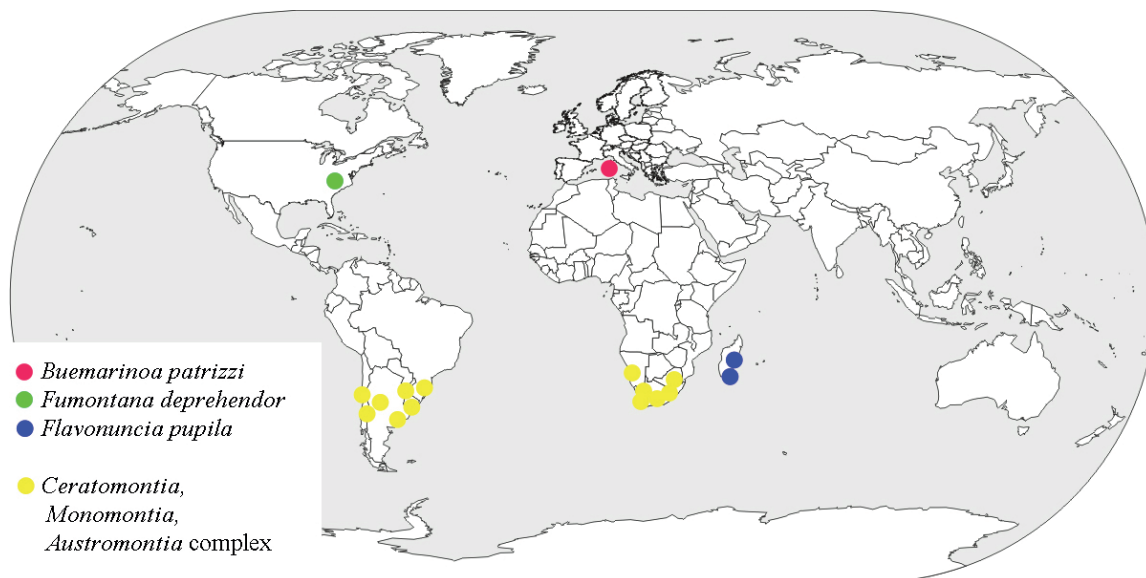


Fig. 11. The geographical distribution of Buemarinoini **tribus n.** and related triaenonychid generic complex.

could be a starting point for development of setiferous arms in Buemarinoini. Like the tribus Buemarinoini, the complex of these three genera is characterized by intercontinental distribution - amphi-Atlantic disjunction (Fig. 11), which suggests their great age.

The origin of the phyletic lineage represented by the tribe Buemarinoini must be related to the areas of Northern Gondwana, from where *Fumontana* penetrated deeper into Laurasia, and in areas where it is present today, before the full opening of the North Atlantic Ocean. Traces of its expansion in terms of the existence of populations of related species in the areas of western and possibly northern Europe were erased by Pleistocene events. *Fumontana* has penetrated into areas that belong primarily to the Laurasian fauna, specifically to the family Cladonychiidae.

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