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Witness of a lost world: *Meenoplus roddenberryi* sp. n., a new cavernicolous planthopper species (Hemiptera, Fulgoromorpha, Meenoplidae) from Gran Canaria

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Abstract

Meenoplus roddenberryi sp.n., an obligate cavernicolous and highly troglomorphic meenoplid species, is described from an artificial cave on Gran Canaria. Notes on its ecology are given. A key to the cave-dwelling Meenoplidae of the Canary Islands is provided. As Meenoplidae are not part of the present-day epigean fauna of the Canary Islands, the occurrence of cavernicolous species provides testimony of an ancient fauna which is now extinct. Despite their current relict status, it remains equivocal whether evolution of cave Meenoplidae was driven by allopatric speciation, or whether an adaptive shift to exploit a novel food resource triggered the colonization of caves.

Introduction

The Canary Islands harbour a rich and diverse invertebrate cave fauna. The islands are of volcanic origin, ranging in age from 0.8–21 Myr, and are characterized by a subtropical climate (Oromí 2004). According to the bioclimatic model proposed by Howarth (1980), these factors are ideal prerequisites for the evolution of terrestrial troglobites (obligate cave dwellers). To date, more than 132 cave-adapted terrestrial arthropod species have been described from the Canary Islands (Oromí 2008), 60 of them belonging to Coleoptera and 15 to Hemiptera. Among the latter, the most abundant are Fulgoromorpha (planthoppers) represented by 2 families, the Cixiidae (9 species: 4 on La Palma, 2 on El Hierro, 3 on Tenerife) (Remane & Hoch 1988; Hoch & Asche 1993) and the Meenoplidae (3 species: 1 on La Palma, 2 on El Hierro) (Remane & Hoch 1988; Hoch & Asche 1993). Previously, all obligately cavernicolous planthopper species were known from geologically comparatively younger islands in the archipelago, with historic or recent volcanism: La Palma (ca. 1.6 Myr), El Hierro (ca. 0.8 Myr), and Tenerife (max. 10 Myr) (Carracedo et al. 1998).

Gran Canaria is older (14 Myr according to Carracedo 2011) with no historic volcanic activity and relatively few recent terrains, making lava tubes much scarcer than in younger islands (Delgado 2002). It had been assumed that cave-adapted fauna on this island should be poor, and very little research was accomplished before 2000. As a result, only two adapted species were known before 2000: the spider *Spermophorides flava* Wunderlich, 1992 and the cockroach *Symploce microphthalma* Izquierdo & Medina, 1992; the latter occurring mainly in the *milieu souterrain superficiel* (Juberthie et al. 1980) or mesocavernous shallow substratum (Culver 2001), hereafter referred to as MSS. However, the active searching program developed in recent years by members of the Entomological Society Melansis, Gran Canaria, in lava tubes and old

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Figure 1. Landscape/vegetation in the Mina Los Roques area (inset: location within Gran Canaria).

artificial caves (see Naranjo et al. 2009), and by members of the University of La Laguna in the MSS (López & Oromí 2010), has unveiled a rich troglobitic fauna almost comparable to that of younger islands with abundant caves. Thus, a new *Chthonius* and four new *Lagynochthonius* pseudoscorpions have been described for the island (Mahnert 2011), three new *Dolichoiulus* millipedes have been described from artificial caves and the MSS (Enghoff 2012), the weevil *Laparocerus lopezi* was also discovered in the MSS (Machado 2008), and a couple of new troglobitic beetles, a Nicoletiidae silverfish and some spiders are currently being described. The particularly abundant mesocaverns of the underground in volcanic islands is likely to harbour an important cave-adapted fauna, even in old terrains without lava tubes as was previously stated for La Gomera and old areas of Tenerife (Medina & Oromí 1990, 1991; Pipan et al. 2010). This same pattern is now proving true also for Gran Canaria.

During a recent survey of cavities on this island a highly troglomorphic, obligately cavernicolous planthopper species was discovered in a water mine (artificial cave) at 1,105 m altitude, near the village of Tenteniguada on the eastern part of the island (Figs 1–3). The species is a member of the planthopper family Meenoplidae and is new to science.

Meenoplidae are one of the smaller Fulgoromorpha families. According to the FLOW database (Bourgoin 2012), there are currently 158 species in 22 genera, occurring in the Old World, Australia and the Western Pacific (Tsaur et al. 1986). Outside the Canary Islands, cavernicolous Meenoplidae are known from the Cape Verde Islands (Hoch et al. 1999), Western Samoa (Hoch & Asche 1988), Australia (Fennah 1973; Hoch 1990, 1993), and New Caledonia (Hoch 1996). As in the Cixiidae, the other Fulgoromorpha family which contains many cavernicolous species, meenoplid nymphs live close to or inside the soil, from where it might be a small step for an evolutionary switch to a permanent life underground (Hoch & Asche 1993).

Material and methods

Collecting. Specimens (nymphs and adults) were collected directly on the wall and floor of the cavity, in the dark zone, and preserved in 70 % ethanol.

Examination techniques, documentation, storage. External body parts were examined without treatment or manipulation, and drawings of relevant structures (habitus, tegmina) were made from specimens in ethanol. For examination of genital morphology, genital capsules were removed and macerated in 10 % KOH (24 h) at room temperature, washed in water, transferred to glycerine for storage, or to glycerine-jelly for drawings. Examinations and drawings were generated using a Leitz stereomicroscope with a camera lucida attachment.

In order to prepare morphological structures for drawing, dissections were made using stain-less steel insect pins. For permanent storage, genitalia were transferred to polyethylene vials and associated with the vial containing the relevant specimen.

Depositories. The studied material is deposited at the Department of Animal Biology, University of La Laguna (DZUL), Tenerife, Spain, and at the Museum für Naturkunde, Berlin (MFN), Germany.

Figure 2. Deep zone of Mina Los Roques where *Meenoplus roddenberryi* sp. n. was found.

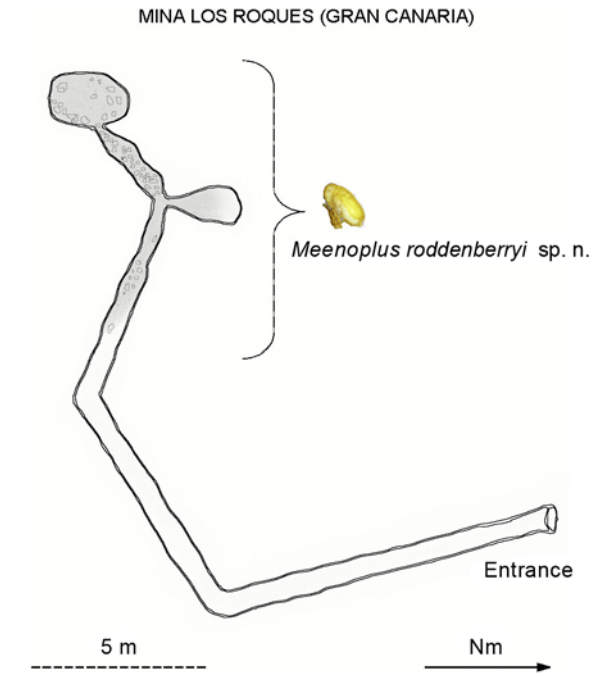

Figure 3. Mina Los Roques survey. *Meenoplus roddenberryi* sp. n. was observed in the shaded area.

Taxonomy

Meenoplidae Fieber, 1872

Meenoplidae Fieber 1872: 2

Meenoplidae are currently divided into two subfamilies: Kermesiinae (= Nisiinae) and Meenoplinae. According to the key provided by Tsaur et al. (1986), all hitherto described Canary Island cave Meenoplidae species belong to the subfamily Meenoplinae. The generic placement of the new species into *Meenoplus* is tentative as characters of the tegmen are – due to strong troglomorphic alteration (see below) – either difficult to homologize (venation) or do not correspond to the alternatives given in Tsaur's et al. (l.c.) key (topography of rows of sensory pits). The general morphology of the male genitalia is, however, sufficiently similar to the previously described cavernicolous *Meenoplus* species from the Canary Islands, thus the preliminary placement in the genus *Meenoplus* appears justified. In general, generic concepts in Meenoplidae are not based on phylogenetic analyses, i.e., many if not most genera are perhaps para- if not polyphyletic; however, clarification of this situation would have been beyond the scope of this work.

Genus *Meenoplus* Fieber, 1866

Genus *Meenoplus* Fieber, 1866: 498

Type-species: *Meenoplus albosignatus* Fieber, 1866: 510 (type-locality: in Greece), by original designation.

Cavernicolous Meenoplidae of the Canary Islands are as follows:

Meenoplus cancavus Remane & Hoch, 1988: Hierro (Cueva de Don Justo, Cueva del Lajial)

Meenoplus claustrophilus Hoch & Asche, 1993: La Palma (Cueva del Ratón)

Meenoplus charon Hoch & Asche, 1993: El Hierro (Cueva de La Curva)

Meenoplus roddenberryi Hoch & Naranjo sp. n.: Gran Canaria (Mina Los Roques)

Key to the cave-dwelling Meenoplidae of the Canary Islands

1. Mildly troglomorphic: compound eyes present, but small, lateral ocelli rudimentary, reduced; tegmina and hind wings well developed . . . . . *Meenoplus claustrophilus* Hoch & Asche, 1993 (La Palma)

– Strongly troglomorphic: compound eyes missing, tegmina with venation strongly reduced, hind wings vestigial or absent 2

2. Caudal margin of genital segment smooth; aedeagus short, tubular, apically not tapering 3
– Caudal margin of genital segment with lobe; aedeagus wide at base, distally tapering . . . . . *Meenoplus roddenberryi* sp. n. (Gran Canaria)
3. Aedeagus in lateral aspect with dorsal margin convex, apically evenly rounded . . . . . *Meenoplus cancavus* Remane & Hoch, 1988 (El Hierro)
– Aedeagus in lateral aspect with dorsal margin straight, apically truncate . . . . . *Meenoplus charon* Hoch & Asche, 1993 (El Hierro)

Meenoplus roddenberryi Hoch & Naranjo sp. n.

Figures 4–6

Description

Habitus (Fig. 4). Tiny species, with almost coleopterous appearance; strongly troglomorphic, compound eyes and ocelli absent, vestigial tegmina and light body pigmentation.

Body Length (measurements taken from tip of head to posterior margin of tegmen). Males: 1.6–1.8 mm ($n = 3$). Females: 1.8 mm ($n = 1$).

Colouration. Vertex and frons pale brown, lateral portions of head incl. antennae whitish; pro- and mesonotum as well as tegmina very pale brown; tegmina translucent; legs yellowish-brown except 2nd tarsal joints, these whitish, almost translucent; thorax and abdomen ventrally whitish; genital segment very pale brown.

Head. Vertex short, smoothly rounded onto frons, not compartmented by longitudinal or transverse carinae, anterior margin in dorsal aspect straight, medially not vaulted anteriorly. Maximum width of head in dorsal aspect ca. 3.7 times the length of vertex. Compound eyes and ocelli absent. Frons and clypeus smooth, lateral carinae of frons and vertex sharply ridged and furnished with a row of sensory pits; frontoclypeal suture straight, frons with 4–5 sensory pits in a transverse row adjacent to frontoclypeal suture. Rostrum elongate, well surpassing hind coxae.

Thorax. Pronotum ca. 1.3 times wider than maximum width of head; posterior margin only slightly concave, medially ca. 2/3 the length of mesonotum. Tegulae vestigial or missing.

Mesonotum ca. 2.4× as wide as medially long, posterior tip broadly rounded.

Pro- and mesonotum entirely smooth, without any longitudinal carinae.

Tegmina (Fig. 5) elytromorph, in maximal aspect subrectangular, longitudinally bent, covering the body dorsally and laterally; posterior margins parallel over most of their length; tegmina with posterior portion reduced; venation reduced except claval veins, each accompanied by two rows of well-developed sensory pits, fused at ca. 1/3 of total length of tegmen; a distinct vein (of uncertain morphological identity: Sc + R? M?) obliquely extending from the base of the anterior margin to the tegmen's distal margin displays a row of sensory pits. Costal margin in posterior half accompanied by a row of sensory pits parallel to costal margin; basal cell, cubital vein and claval suture entirely missing; area enclosed by first and second claval vein distinctly concave, common stem of claval veins finely granulate. Hind wings absent.

Metatibia laterally unarmed, distally with 6 teeth, arranged in a straight row; 1st and 2nd metatarsal joints distally with 4 well developed teeth, arranged in a slightly arched rows; 1st metatarsal joint ca. as long as 2nd and 3rd metatarsal joints together.

Male genitalia (Fig. 6). Genital segment in lateral aspect ventrally ca. 2.4× longer than dorsally, ventral margin posteriorly curved dorsad, caudal margin laterally with a distinct, rounded lobe at about midlength. Anal segment distally produced into two ventrocaudal lobes which are distally tapering and directed mediad. Parameres slender, narrow throughout, apically subtruncate, in lateral aspect shallowly S-shaped, medially concave, in repose directed ± caudad, in ventral aspect curved mediad. Connective elongate, narrow, in lateral aspect quartercircularly curved caudad. Aedeagus in lateral aspect ± bottle-shaped: wide at base, on dorsal side rapidly tapering at ca. midlength, distally produced into a narrow, syringe-shaped tip; phallotreme in repose exposed dorsocaudally; proximal apodeme of aedeagus ("tectiform structure" sensu Bourgoin 1997) elongate, narrow throughout.

Female genitalia as in other *Meenoplus* species from the Canary Islands strongly reduced, ventral valvifer laterodorsally rounded; ventral valvulae slender, narrow, tip rounded, directed mediocaudad; VII. sternite narrow, shorter than wide.

Diagnosis

Meenoplus roddenberryi sp.n. can be distinguished from all other cavernicolous *Meenoplus* species from the Canary Islands by characters of the head (anterior margin of vertex in dorsal aspect medially straight, not vaulted anteriorly as in the other species), the thorax (pro- and mesonotum dorsally smooth vs. pro- and mesonotum more or less weakly tricarinate as in the other species; pronotum medially about as long as mesonotum vs. pronotum medially distinctly shorter than mesonotum; posterior margin of pronotum only slightly concave vs. posterior margin of pronotum medially deeply incised) and the male genitalia (genital segment in ventral half strongly vaulted, almost bulbous, and caudal margin laterally with a distinct rounded lobe at ca. midlength vs. caudal margin laterally smooth, connective quarter-circularly curved vs. straight; parameres with distal margin subtruncate vs. rounded; aedeagus wide at base, rapidly tapering at ca. midlength, vs. short, tubular throughout).

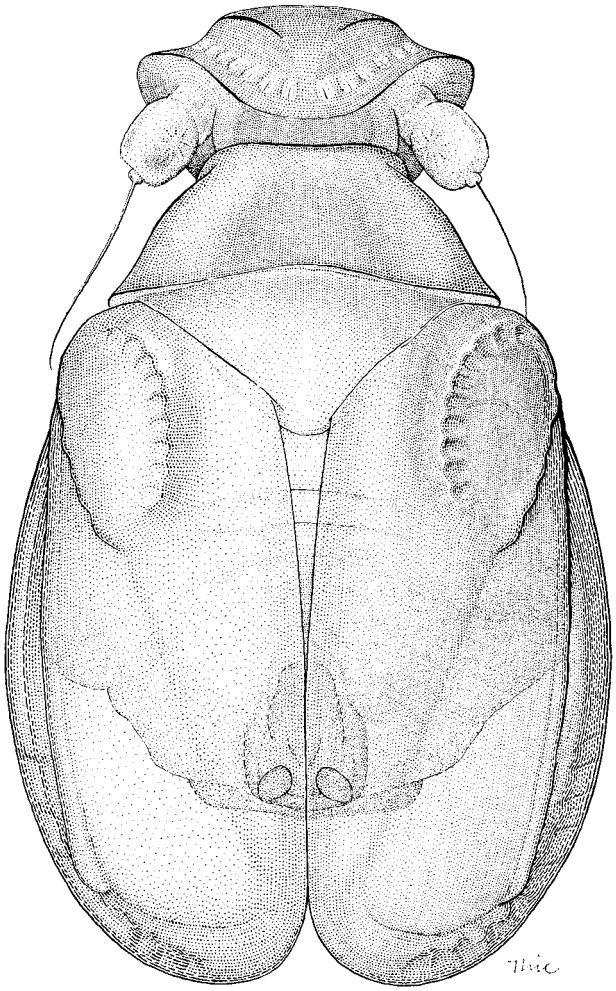

Figure 4. *Meenoplus roddenberryi*, habitus (holotype male). Total length 1.6 mm.

Distribution
Canary Islands. Endemic to Gran Canaria.

Ecology
Meenoplus roddenberryi sp. n. was collected in a small, 30 m long artificial water mine. This cavity (Mina Los Roques) is located at 1,105 m altitude, in an area with colluvial deposits of basaltic rocks, with an estimated age of 3.7–2.8 Myr (Cueto et al. 1990) (Fig 1). The planthoppers were found in the deepest part of the mine, where relative humidity is high (85–94 %) and temperature oscillates between 13–17 °C depending on the season; at the end of the mine the oxygen level can drop to 19 %. In this section of the cavity (Figs 2–3) there are roots which could belong to Sweet chestnut (*Castanea sativa*), or maybe to the local yellow broom (*Teline microphylla*), the blue Gran Canarian Tajinaste *(Echium callythirsum)* or the Escobón *(Chamaecytisus proliferus)* which are the three dominant shrubs on the surface. However, no *Meenoplus* specimens were detected on these roots.

Mina Los Roques is rich in hypogean fauna for an artificial mine, being the cavity of Gran Canaria with the highest density of the troglobitic cave-dwelling spider *Troglohyphantes* sp. (yet undescribed). Other troglobitic species have been collected here, such as the millipede *Dolichoiulus longunguis* Enghoff, 2012, as well as the yet undescribed weevils *Laparocerus* sp. and *Oromia* sp., and the pseudoscorpion *Lagynochthonius* sp. Some cixiid planthopper nymphs and aphid greenflies were observed around the roots, but they are not troglobitic species.

Etymology
The species epithet was chosen in honour of Gene Roddenberry (1921–1991), creator and producer of the famous U.S. science fiction tv-series *Star Trek*. The mission of its starship *Enterprise* "... to explore strange new worlds, to seek out new life ..., to boldly go where no one has gone before" applies – as much as to space – to biospeleology. Gene Roddenberry was fascinated by the exploration of the unknown, and we are sure he would be delighted about the discovery of the new life form described here.

Remarks
Meenoplus roddenberryi sp. n. is the smallest cavernicolous Fulgoromorpha species known to date, and one of the smallest Fulgoromorpha species of all.

Material examined
Holotype male. SPAIN: ISLAS CANARIAS, Gran Canaria, Mina Los Roques (1,105 m), 11.VIII.2011, M. Naranjo Morales leg. (DZUL 2630).

Paratypes. 2 ♂♂, same data as holotype, (DZUL 26031 and 26033); 1 ♂, 1♀, same data as holotype, except 23.I.2012, (MFN).

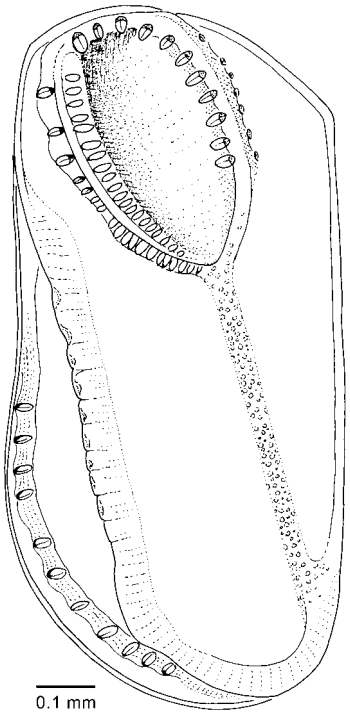

Figure 5. Tegmen, maximal aspect (paratype male, coll. 23.I.2012). Scale bar 0.1 mm.

Additional material. 2 nymphs (V. instar), same data as holotype; 2 nymphs (II., V. instar), same data as holotype, except 23.I.2012, (MFN and DZUL 26032).

Discussion

Possible epigean ancestors, relationship to other cave meenoplids from the Canary Islands.

It seems remarkable that potentially closely related epigean Meenoplidae are entirely missing in the present-day fauna of the pertaining islands (or elsewhere, see below); thus the cavernicolous meenoplid species are "classic" relicts, i.e., "persistent remnants of formerly widespread faunas ... existing in certain isolated areas or habitats" (Lincoln et al. 1982).

However, this currently observed pattern does not indicate whether the evolution of cave adaptation was driven by deteriorating conditions on the surface – and thus took place in allopatry (Climatic Relict Hypothesis, CRH: Vandel 1964; Barr 1968) – or was driven by the exploitation of a novel food resource (roots) and occurred in parapatry (Adaptive Shift Hypothesis, ASH: Howarth 1981). In other cave-adapted terrestrial arthropod taxa of the Canary Islands (the majority occurring on Tenerife, La Palma and El Hierro) both patterns are observed (Oromí & Izquierdo 1994). In Gran Canaria there are more cases of troglobites with no extant surface relatives, such as two species of the cockroach genus *Symploce* Hebard (H. López personal communication, used with permission) and four pseudoscorpion species of the genus *Lagynochthonius* Beier (see Mahnert 2011). Many troglobites from other islands of the archipelago are evident cases of ASH, such as the eyeless earwig *Anataelia troglobia* Martín & Oromí, 1988 living exclusively in lava tubes on La Palma, but closely related to the pigmented and eyed *Anataelia lavicola*; a lavicolous species sometimes collected in shallow places of the same caves as *A. troglobia* (see Martín & Oromí 1988). Furthermore, the three troglobitic species of *Wolltinerfia* Machado (Coleoptera, Carabidae) are closely related to the surface *Eutrichopus* Tschitschérine, all from Tenerife (Moya et al. 2004). The cave-adapted ground-beetles *Trechus minioculatus* Machado from El Hierro and *Trechus benahoaritus* Machado from La Palma are closely related to other *Trechus* species from the surface of these islands, very often with a sympatric distribution alongside the hypogean ones (Contreras et al. 2007).

Concerning the Meenoplidae, the presently observed absence of the surface fauna of the Canary Islands may either be the result of climatic changes – in the Miocene the climate in the Canary Islands was warmer and wetter (warm tropical) but it gradually shifted to an arid climate interrupted by irregular wetter periods (Fernández Palacios et al. 2011) – or may be due to faunal succession phenomena characteristic of oceanic islands (Ashmole et al. 1992) (see also Hoch & Asche 1993: 99).

The cave-dwelling Meenoplidae of the Canary Islands represent at least three (if not four) independent cave colonizations: 1) *M. claustrophilus* on La Palma, 2) *M. cancavus* and *M. charon*, both on El Hierro, and 3) *M. roddenberryi* on Gran Canaria. According to the configuration of the male genitalia, two morphological groups can be distinguished: 1) *Meenoplus claustrophilus*, *M. cancavus*, *M. charon*, and 2) *M. roddenberryi*. This suggests that in the past, there must have been at least two *Meenoplu*s epigean species present on the Canary Islands: one on Gran Canaria, the other perhaps more widely distributed on La Palma and El Hierro. It is remarkable that on Tenerife, which harbours three cave-dwelling Cixiidae (Hoch & Asche 1993) and which consequently has suitable cave planthopper habitats, so far no cavernicolous Meenoplidae have been found.

The cavernicolous Meenoplidae of the Canary Islands do not show any morphological affinities to epigean Meenoplidae from adjacent regions: the Cape Verde Islands and Africa. The Meenoplidae of the Cape Verdes are representatives of the Kermesiinae (Lindberg 1958, Hoch et al. 1999), and the African Meenoplinae species of the genera *Anigrus* and *Meenoplus* display entirely different morphological configurations pertaining to the male genitalia. Thus, there is no morphological evidence which may hint at the geographical source of the Canary Island colonization.

Occurence on Gran Canaria

Meenoplus roddenberryi is found on Gran Canaria which is, with 14 Myr (Carracedo 2011), much older than the other islands of the Canaries hitherto known to harbour obligate cavernicolous planthoppers. The main volcanic activity probably ceased approx. 1.6 Myr ago, although more reduced remnants of this activity have lasted until geologically recent times, producing some volcanic landscapes in the northern and eastern parts of the island. The south-western half of Gran Canaria, also called Tamaran or Paleocanaria (Araña & Carracedo, 1978; Anguita et al. 2002), is much older and has neither cinder cones nor recent lavas or lava tubes, and hardly any troglobitic species have ever been found there (only the cockroach genus *Symploce*), although it is a still unexplored area.

Hoch & Asche (1993) hypothesized that the absence of cave-dwelling planthoppers from the older and volcanically inactive islands, such as Gran Canaria and La Gomera, could be due to a decline of their primary habitat – roots of surface vegetation in mesocaverns – as a consequence of prolonged erosion and soil formation, the prevalent geologic forces subsequent to active volcanism. A similar phenomenon is observed on Hawaii where cave planthoppers are found to occur only on the younger, volcanically active islands (Hoch & Howarth 1993, 1999) where sufficient habitat is either constantly being generated or (still) available. The discovery of *M. roddenberryi* sp. n. on Gran Canaria at least partly rejects this hypothesis. In fact, one might think that an-

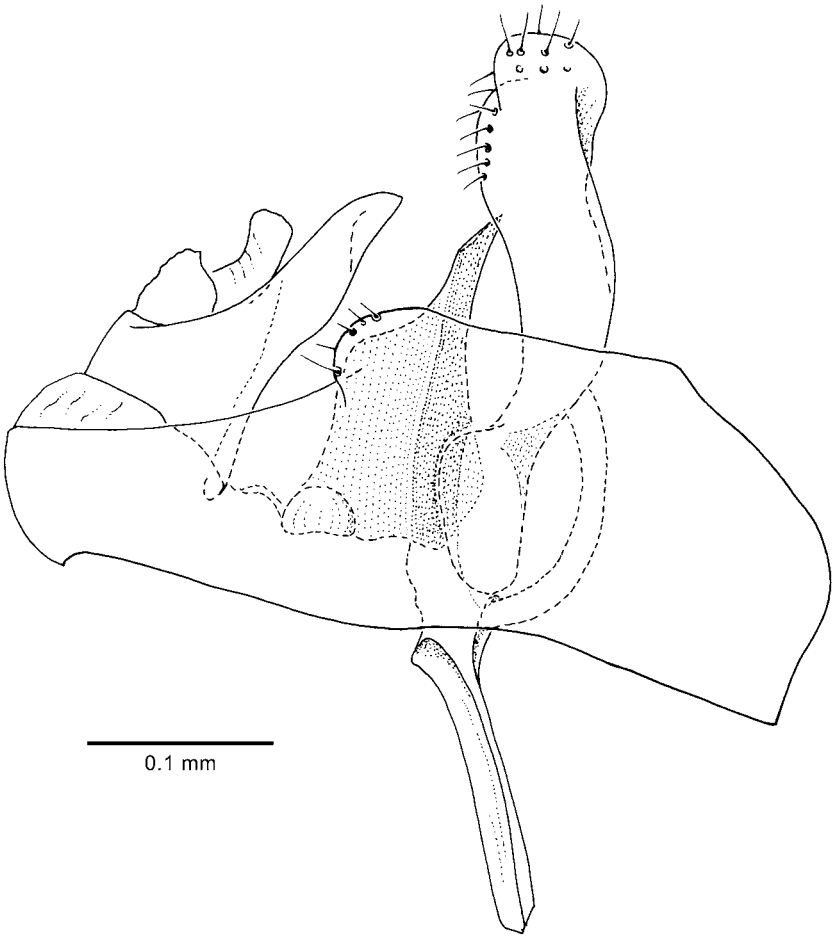

Figure 6. Male genitalia, left lateral aspect (paratype male, coll. 23.I.2012). Scale bar 0.1 mm.

cient islands like Gran Canaria can ”behave” as if younger than their surface geomorphology suggests: rock avalanches and landslides produce scree rich in mesocaverns, which can make up for the lack of recent eruptions. Thus older islands can stay ‘young’ and retain available habitats for cave-dwelling invertebrates.

Degree of troglomorphy: evolutionary time or habitat?
Interestingly, the degree of troglomorphy is comparatively higher in *Meenoplus roddenberryi* (from the at least 14 Myr old Gran Canaria) than in the other cavernicolous Meenoplidae from El Hierro (less than 1 Myr) and La Palma (less than 2 Myr). In cavernicolous Cixiidae from Hawaii and Australia, opposite trends were observed: the highest degree of troglomorphy is expressed in species occurring in relatively younger caves, indicating that cave-adaptation is not a gradual orthogenetic process (Wessel et al. 2007). Instead, Hoch and Howarth (1989) postulated that degree of troglomorphy may be correlated to physical parameters of the habitat. Apart from obvious troglomorphies, *Meenoplus roddenberryi* is characterized by its very small size and overall “smoothness” of the body surface. Hoch et al. (2006: 1881) hypothesized that a smooth body surface may facilitate movements in a dense soil substrate “. . .”. Thus, *Meenoplus roddenberryi* may in fact be an obligate soil dweller. This scenario is likely, because Mina Los Roques has abundant clay inside and runs close to the surface (less than 10 meters).

Also, the smoothness of the body surface (no carinae, wings covering the body dorsally and laterally), as well as translucent, nearly invisible 3rd tarsal joints, could be an adaptation against predation. Carabid and staphylinid beetles are present inside the cavity and are likely predators. In its natural habitat, *Meenoplus roddenberryi* specimens were observed to jump vigorously when disturbed, a behaviour which may serve predator avoidance.

There is a high probability that in the Canary Islands – with their wide range of geological ages, climatic conditions and abundance of suitable cave planthopper habitat – many more cavernicolous Fulgoromorpha await discovery and description. Continuing cave exploration on all islands, and especially on those where so far no cave planthoppers have been found, e.g. La Gomera, Fuerteventura and Lanzarote, and – as far as cave Meenoplidae are concerned – Tenerife, should be strongly encouraged as it may help to open a window into the faunas of the past even further.

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