

Evolution and speciation of cave-dwelling Fulgoroidea in the Canary Islands (Homoptera: Cixiidae and Meenoplidae)

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Ten new cavernicolous Fulgoroidea species of the families Cixiidae and Meenoplidae are described from the Canary Islands: *Cixius palmeros*, *C. pinarcoladus*, *C. ratonicus*, *C. tacandus*, *Meenoplus claustrophilus* from La Palma, *C. ariadne*, *C. nycticolus*, *M. charon* from El Hierro, and *Tachycixius crypticus*, *T. retrusus* from Tenerife. Notes on their ecology and distribution are given, and where possible, phylogenetic affinities to existing epigeic species of the corresponding families are discussed. Despite the present-day relict status of the majority of cavernicolous species, it cannot be concluded with certainty whether their evolution has followed allopatric or parapatric modes of speciation.

ADDITIONAL KEY WORDS:—Homoptera – Fulgoroidea – Cixiidae – Meenoplidae – Canary Islands – lava tubes – troglobites – relict – parapatric and allopatric speciation.

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INTRODUCTION

Until little more than two decades ago, terrestrial obligate cavernicoles (trogllobites) were virtually unknown from oceanic islands and in tropical regions. This apparent impoverishment prompted the development of theories on their evolution and distribution in temperate regions where extinction of surface populations by changing climates (e.g. during glaciation) was assumed as an implicit prerequisite (Barr, 1973).

From results on faunistic research in various tropical areas, and especially from his own work on Hawaii, Howarth (1980) developed a bioclimatic model to explain the zoogeography of terrestrial trogllobitic animals. This model predicts the existence of obligate cavernicoles in areas yielding a subterranean environment suitable for colonization and adaptation, i.e. providing adequate moisture and food supply. Such an environment exists in limestone as well as in basaltic rocks and consists of interconnected labyrinthine voids of varying sizes ranging from small fissures (<0.1 cm; microcaverns), and medium-sized voids (0.1–20 cm: mesocaverns), to cave-sized passages (>20 cm: macrocaverns) (Howarth, 1983). Observations in Hawaii suggest that trogllobites probably inhabit the deeper mesocavernous zone (=MSP, *milieu souterrain profondeur*: Juberthie, Delay & Boullon, 1980; Juberthie & Delay, 1981), and colonize larger passages ('caves'), and the shallower mesocavernous zone (=MSS, *milieu souterrain superficiel*: Juberthie *et al.*, 1980; Juberthie & Delay, 1981) only when the environment is suitable (Howarth, 1983).

Subsequent investigations in tropical regions and on oceanic islands supported Howarth's bioclimatic model by revealing remarkably diverse trogllobitic arthropod faunas, e.g. in Australia (Howarth, 1988), and in the Canary Islands (Oromí *et al.*, 1991). A significant element of these trogllobitic faunas is represented by the homopterous insect group Fulgoroidea (=planthoppers), which has been recognized as rhizophages within the cave community (Howarth, 1973).

Hitherto, two trogllobitic planthopper species had been reported from the Canary Islands (Remane & Hoch, 1988), a cixiid from Tenerife (*Tachycixius lavatubus* Remane & Hoch) and a meenoplid from El Hierro (*Meenoplus cancavus* Remane & Hoch). Since then, 10 additional cavernicolous fulgoroid species have been discovered by or in collaboration with the *Grupo de Investigaciones Espeleológicas de Tenerife* (GIET). These species (eight Cixiidae from La Palma, El Hierro and Tenerife, and two Meenoplidae from La Palma and El Hierro) are described here.

With this concentration of cavernicolous taxa (12 species) the Canary Islands are among those regions of the world which show the highest known densities of cavernicolous Fulgoroidea taxa. Queensland, Australia (Chillagoe Tower Karst and Undara lava flow) has 12 species of the families Cixiidae and Meenoplidae (Hoch & Asche, 1988; Hoch, 1990) and Hawaii has six species of the family

Cixiidae (Howarth, 1987). Troglobitic Cixiidae have so far also been reported from Madagascar (one species), Mexico (two species), New Zealand (one species), the Azores (two species), and the Balears (one species), and troglobitic Meenoplidae are also known from Western Samoa (one species) (synopsis in Hoch, in press).

The high number of cave-adapted taxa within the families Cixiidae and Meenoplidae may be due to the fact that nymphs of all Cixiidae and Meenoplidae live, respectively, in or close to the soil. In epigeal species of these families, the adult leaves the nymphal habitat to feed and reproduce above ground. From this level of pre-adaptation it seems a comparatively small step to the evolution of cave-adapted taxa: the separation between nymphal and adult habitat, which may be interpreted as a strategy to avoid intraspecific competition by the emigration and dispersal to new areas by the adults (Remane & Hoch, 1988), is abandoned. The adults retain the nymphal habitat and mode of nutrition, sucking sap from roots.

This paper examines the degree of speciation observed in cavernicolous Fulgoroidea in the Canary Islands, and the geographic distribution of the species and their phylogenetic relationships to each other and to their (hypothetical) ancestral epigeal species. Possible modes of speciation are discussed.

DEPOSITORIES OF MATERIAL

AH=Private collection of M. Asche & H. Hoch, Marburg, Germany;
MSC=Museo de Ciencias Naturales, Santa Cruz, Tenerife, Canary Islands;
ULL=University of La Laguna (Biology Department), Tenerife, Canary Islands;
ZMU=Zoological Museum, Helsinki.

In the cavernicolous species, measurements of body length were made from specimens preserved in ethanol. Body length is taken to be the distance between the apex of the head and the tip of the abdomen or, where the tegmina surpass the tip of the abdomen, the distal margin of the tegmina. In surface-dwelling species, measurements of body length were made from dried specimens and equal the distance between the apex of the head and the distal margin of the tegmina. In the data given for the nymphs, Arabic numerals refer to the number of specimens, Roman numerals to the instar.

TAXONOMY

Family Cixiidae

Genus Cixius Latreille

***Cixius palmeros* sp. nov.**

(Figs 1, 2)

Description. Habitus strongly troglomorphic with reduced eyes, tegmina and bodily pigmentation.

Total length. Male 3.8 mm.

Colouration. Head and pronotum pale yellow, antennae, meso-, metanotum and first two abdominal segments white, abdominal segments 3–11 pale yellow, slightly darker than head and pronotum, tegmina translucent, venation pale yellow.

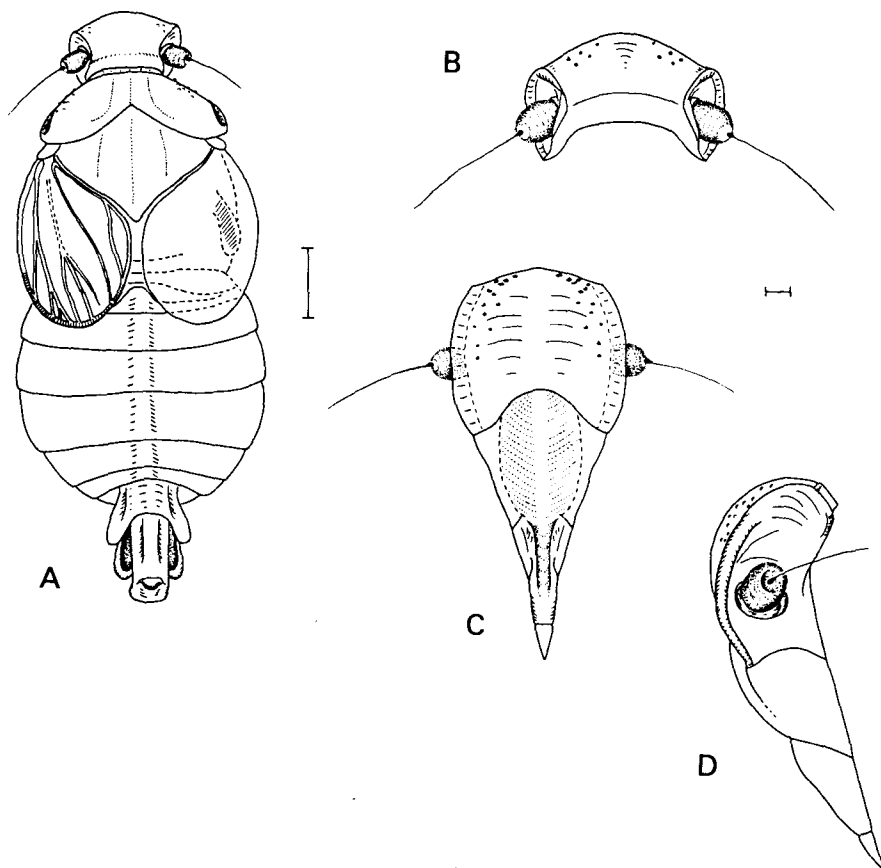


Figure 1. *Cixius palmeros* sp. nov., holotype. A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, same, left lateral aspect. Scale bar: A 0.5 mm, B-D 0.1 mm.

Head (Fig. 1). Vertex short, about 6.4 times wide as it is long in the middle line, indistinctly separated from frons by an obsolete transverse carina. Frons convex, about 1.7 times wider than medially high, lateral carinae ridged, median carina absent; upper portion of frons with numerous tiny pustules. Median carina of post- and anteclypeus rather feebly defined; lateral carinae of postclypeus in upper half continuing those of frons without interruption, in lower half extinct. Compound eyes and ocelli absent. Second antennal segment is approximately 1.3 times longer than it is wide.

Thorax (Fig. 1A). Pronotum short, medially about 2.75 times the length of the vertex, indistinctly tricarinate, lateral carinae not attaining posterior margin, lateral portions of pronotum pustulate, posterior margin obtuse angulately concave. Mesonotum nearly planate, faintly tricarinate, in midline about 2.6 times the length of pronotum. Tegulae vestigial. Tegmina strongly reduced, venation rudimentary, with sporadic bases of bristles along veins. Wings vestigial. Metatibiae laterally with two to three minute spines (individually varying), apically with six teeth. First metatarsal segment is about 1.3 times longer than the second and third together. First metatarsus with four, second with three apical teeth.

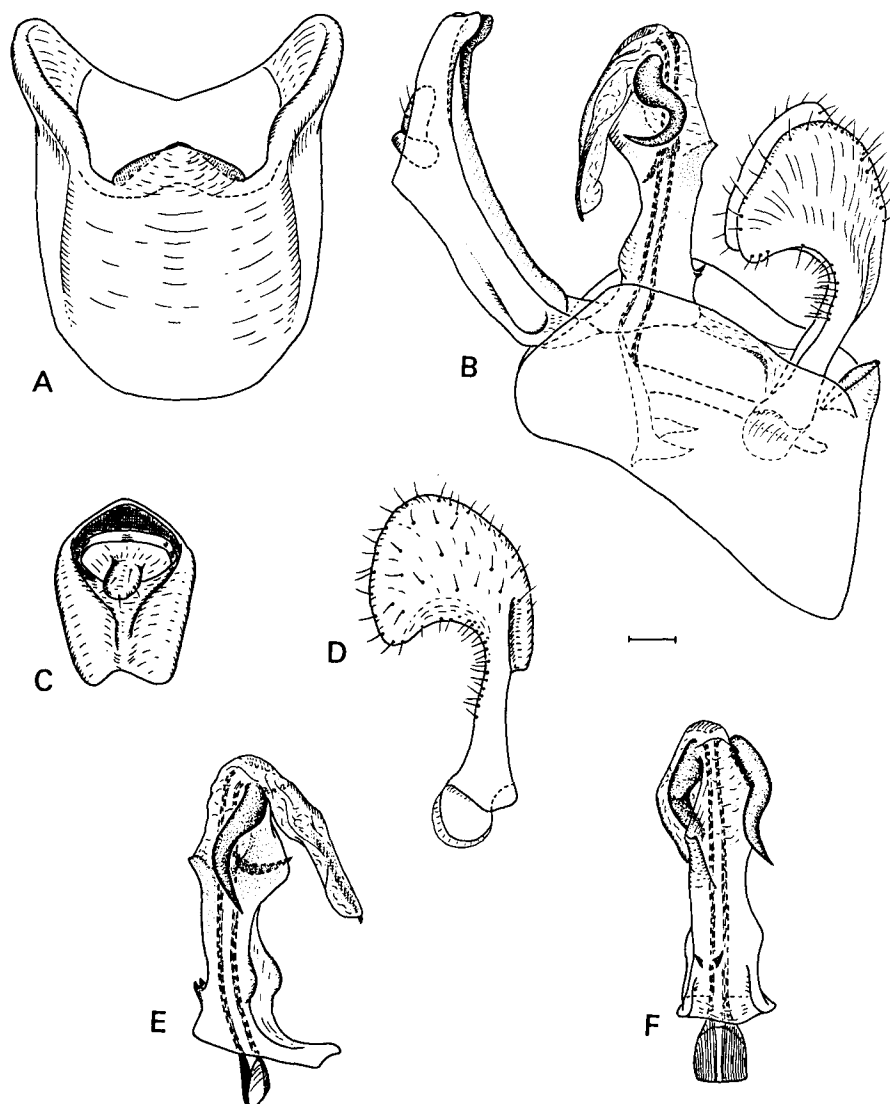


Figure 2. *Cixius palmeros* sp. nov., male genitalia, holotype. A, genital segment, ventrocaudal aspect; B, male genitalia *in situ*, left lateral aspect; C, anal segment, caudal aspect; D, left paramere, maximum view; E, aedeagus, right lateral aspect; F, same, ventral aspect. Scale bar: 0.1 mm.

Male genitalia (Fig. 2). Genital segment about 1.3 times higher than wide. Anal segment about 2.4 times longer than wide, distal portion slightly bent ventrad, laterodistal margins produced into two short, ear-shaped lobes. Parameres moderately long, narrow in basal half, then gradually expanding (Fig. 2B). Aedeagus basal part (shaft) (Fig. 2B, E, F) slightly compressed, slender; ventrally near base two minute, rigid spines directed caudad, ventral margin forming an obtuse projection directed ventrad; dorsal side of basal part subapically forming a bulbous protrusion, slightly grooved on left side. Shaft apically with two movable spinose processes: left lateral one hook-shaped, in

repose almost semi-circularly curved dorsad, right lateral one slightly sinuate, in repose directed basad. Distal part of aedeagus in repose reflected basad but not reaching base of shaft, dorsally with a longitudinal ridge which is produced into a short spine at apex.

Etymology. The name of this species is derived from its type locality, Cueva de los Palmeros, on the island of La Palma.

Holotype. Male: Canary Islands, La Palma, W. Fuencaliente (supra Las Indias), Cueva de los Palmeros, 14.ii.1988, M. Asche & H. Hoch leg. (ULL).

Additional material. Nymphs, same locality as holotype: 1 v (♂), 12.ii.1988; 1 iv, 14.iv.1990 (AH).

Diagnosis. Externally, this species displays a similar degree of troglomorphy as the other three cave-dwelling cixiid species from La Palma, but differs in characters of the male genitalia, especially in the shape of the two subapical spinose processes of the aedeagus shaft.

Distribution and ecology. *Cixius palmeros* is only known from Cueva de los Palmeros, W. Fuencaliente, La Palma (Fig. 38). The wide, tunnel-like and generally dry cave is located within a prehistoric lava flow at an altitude of about 650 m a.s.l., and is about 180 m long. The temperature measured in February and April was 15.2°C. A few roots, presumably of *Pinus canariensis*, are found very sporadically in the central part of the cave. All three specimens known have been found on a single rootlet emerging from a crack in the wall, about 50 m from the entrance, in an area which experiences comparatively strong air movements (transition zone, Howarth, 1973). Because of its high degree of troglomorphy *C. palmeros* is most probably restricted to underground environments, and is therefore ecologically classifiable as an obligate cavernicole, i.e. troglobitic.

***Cixius pinarcoladus* sp. nov.**

(Figs 3–5)

Description. In general, its appearance is similar to that of *C. palmeros*, but smaller.

Total length. Male 3.3 mm. Female 4.4 mm.

Colouration. In the male the body is generally white, the distal third of the abdomen yellow; in the female the head, pro-, mesothorax and abdominal segments 3–11 are pale yellow, the antennae, metanotum and first two abdominal tergites are white, the tegmina is translucent, and the veins pale yellow. In females the lateral portions of mesonotum anteriorly have a dilute light brown mark.

Head (Fig. 3). Vertex short, about 7 times as wide as it is long in the middle line, transverse carina inconspicuous, vertex continuously rounding onto frons. Frons convex, about 1.3 times wider than medially high, lateral carinae moderately produced laterad, median carina absent. Upper frons feebly pustulate. Carination of post- and anteclypeus as in *C. palmeros*. Compound eyes and ocelli absent. Antennae as in *C. palmeros*.

Thorax (Fig. 3A). Pronotum very indistinctly tricarinate, lateral portions anteriorly inconspicuously pustulate, in middle line about 2 times the length of the vertex, posterior margin shallowly emarginate. Mesonotum nearly planate, smooth in the male, feebly tricarinate in the female; medially about 2.8 times the

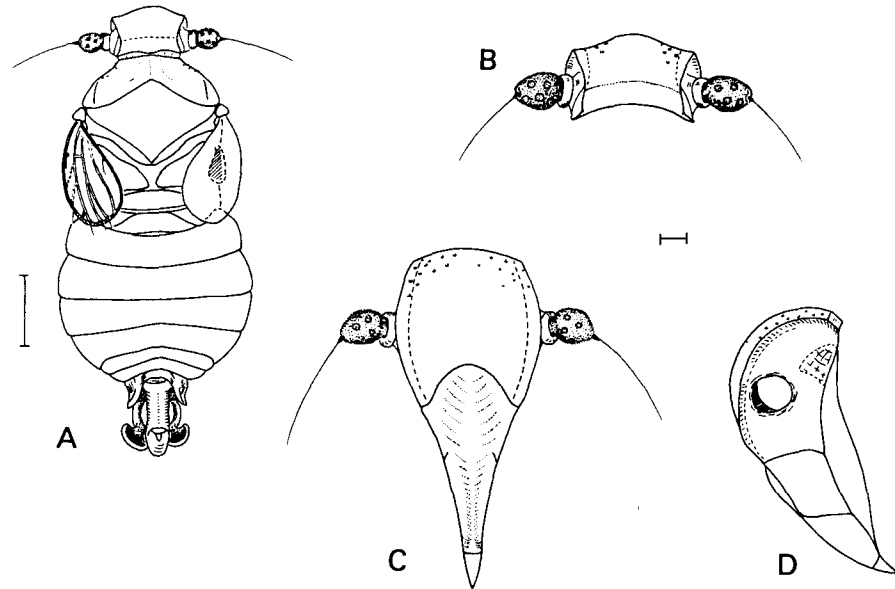


Figure 3. *Cixius pinarcoladus* sp. nov., holotype. A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, same, left lateral aspect. Scale bar: A 0.5 mm, B–D 0.1 mm.

length of the pronotum. Tegulae vestigial. Tegmina strongly reduced, venation rudimentary, with sporadic bristles along veins. Wings vestigial. Metatibiae laterally with three minute spines, apically with six teeth. First metatarsal segment 1.2 times longer than the second and third together. First metatarsus with four, second with three apical teeth.

Male genitalia (Fig. 4). Genital segment is similar in shape and proportions to that of *C. palmeros*. Anal segment slightly longer than twice its width, distally slightly bent ventrad, caudal margin shallowly concave. Parameres as in *C. palmeros*, but dilated distal portion more elongate, caudally obtusely angulate. Basal part of aedeagus slender, in lateral aspect almost parallel-sided, ventrally ridged near its base with two short, rigid spines (right one serrate) directed caudad. Shaft of aedeagus right laterally produced into an ear-shaped projection; dorsal side of this projection and lower two-thirds of left side of shaft distinctly sclerotized. Shaft subapically on each side with a ventrally exposed, movable, slender, terete spinose process: in repose left lateral one curved dorsad, right lateral one bent basolaterad. Distal part of aedeagus in repose reaching basal third of shaft, without any spine or velum.

Female genitalia (Fig. 5). Seventh sternite (pregenital sternite) with caudal margin medially slightly expanding caudad; ovipositor ensiform, slightly curved upward, distinctly surpassing anal segment; ninth tergite caudally truncate, wax-secreting field distinctly limited, medially separated by a triangular membranous area forming an inverse 'V'.

Etymology. The species is named from the location in which it is found: Cueva del Diablo is in a *colada* (Spanish for 'lava flow'), inside the Pine zone, the *pinar*.

Holotype. Male: Canary Islands, La Palma, Cueva del Diablo, supra Breña Alta (San Isidro: *Nucleo Recreativo Pared Vieja*), 23.x.1988, M. Asche & H. Hoch leg. (ULL).

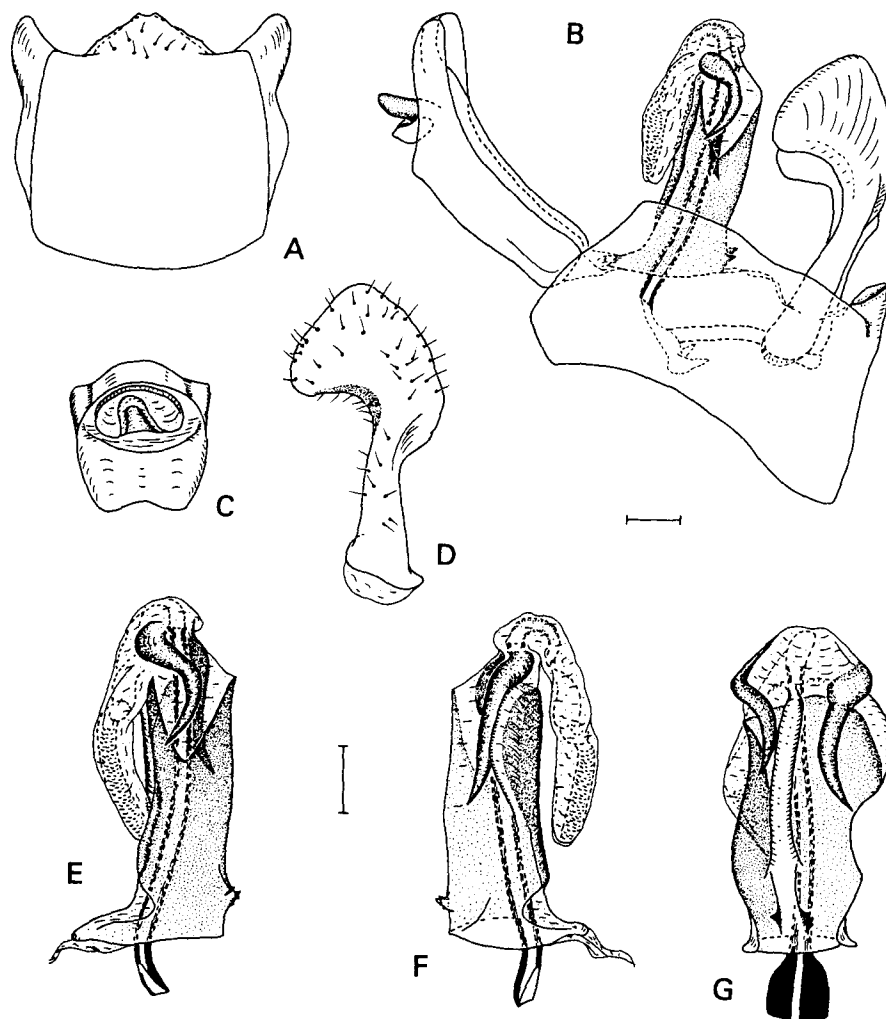


Figure 4. *Cixius pinarcoladus* sp. nov., male genitalia, holotype. A, genital segment, ventral aspect; B, male genitalia *in situ*, left lateral aspect; C, anal segment, caudal aspect; D, left paramere, maximum view; E, aedeagus, left lateral aspect; F, same, right lateral aspect; G, same, ventral aspect. Scale bar: 0.1 mm.

Paratypes. One female: same locality as holotype except 19.x.1988 (AH).

Additional material. Nymphs: 5 V (2 ♂♂, 3 ♀♀), 4 IV (1 ♂, 3 ♀♀), 2 III, same data as holotype except 19.x.1988 (AH); 1 V (♀), same data as holotype (AH). ? 1 V (♀), Cumbre Nueva, La Palma, 1.v.1989, A. L. Medina (ULL).

Diagnosis. *Cixius pinarcoladus* displays a similar degree of troglomorphy as *C. palmeros*, but differs in the following characters of the male genitalia: medioventral process of genital segment apically notched, laterodistal margins of anal segment rounded and not produced into ear-shaped lobes, subapical spinose processes of aedeagus less curved, tip of aedeagus distal part without spine.

Distribution and ecology. *Cixius pinarcoladus* is known only from Cueva del Diablo, supra Breña Alta, La Palma (Fig. 38). The cave is 116 m long, on average 3–4 m wide and lies in a prehistoric lava flow, at an altitude of 1400 m a.s.l. The

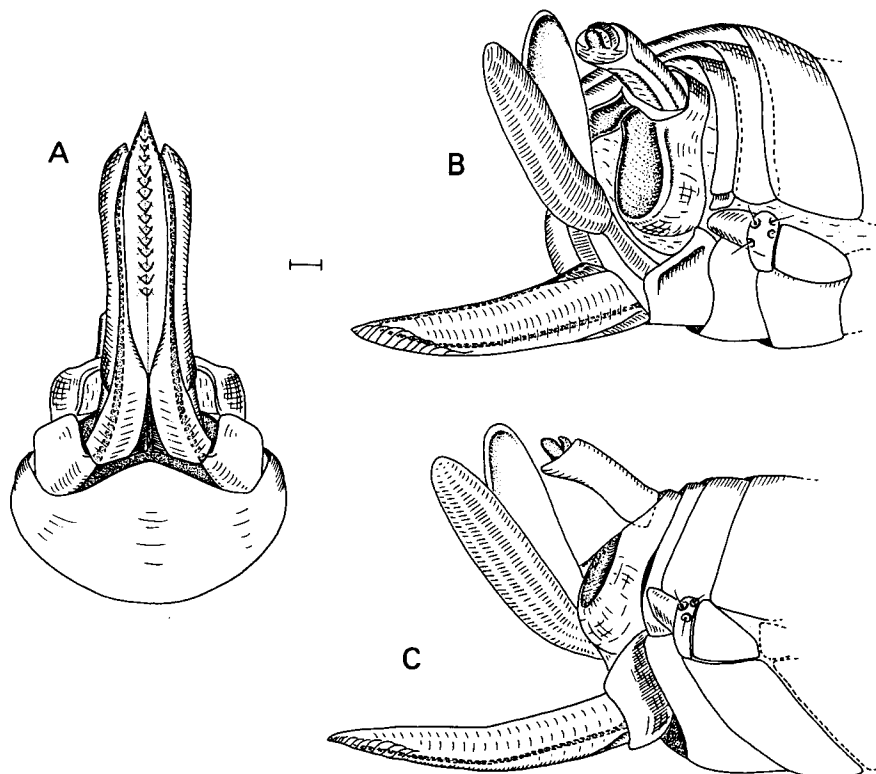


Figure 5. *Cixius pinarcoladus* sp. nov., female genitalia, paratype. A, ventral aspect; B, laterocaudal aspect; C, right lateral aspect. Scale bar: 0.1 mm.

temperature in the dark cave zone measured in October was 11.3°C. The surface vegetation is largely *Pinar*, with *Pinus canariensis* being the dominant plant species. Sparse roots, most probably of *P. canariensis*, hang from the ceiling or grow along the walls, mainly in the central and rear third of the cave. Due to its degree of troglomorphy and its ecology *C. pinarcoladus* is assumed to be troglotic.

A single fifth instar nymph collected in a pitfall trap within the mesocavernous rock layer along the Cumbre Nueva (approximately 2 km distance from Cueva del Diablo) had no eyes and lacked pigmentation. It obviously represents a troglotic species. Whether this species is conspecific with *C. pinarcoladus* can only be decided after comparison with adult specimens.

***Cixius ratonicus* sp. nov.**

(Figs 6–8)

Description. In habitus resembling *C. palmensis* and *C. pinarcoladus*, but distinctly smaller and more slender.

Total length. Female 2.85 mm. Male not measurable (see *Diagnosis and remarks*).

Colouration. Head, pro-, mesonotum and abdominal segments 3–11 pale yellow, metanotum, first and second abdominal tergites white, tegmina translucent, faintly yellow, veins concolorous.

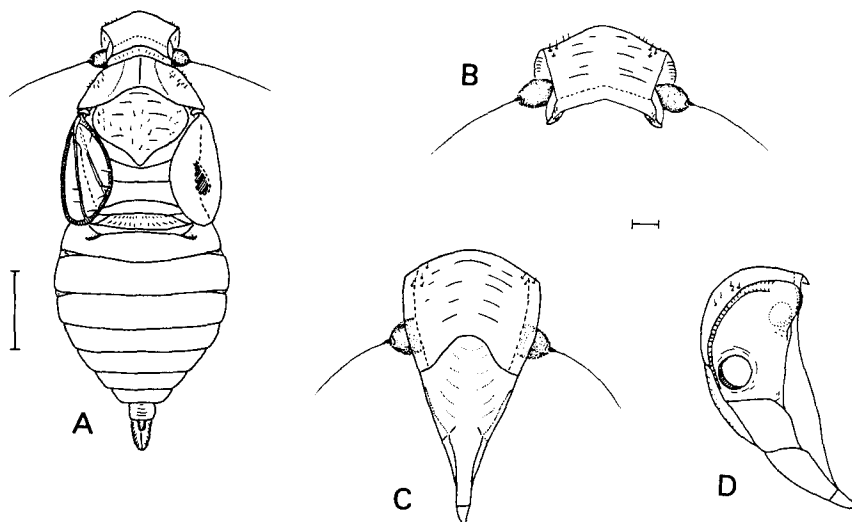


Figure 6. *Cixius ratornicus* sp. nov., paratype (female). A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, same, left lateral aspect. Scale bar: A 0.5 mm, B-D 0.1 mm.

Head (Fig. 6). Vertex short, about 6.2 times wider than medially long, indistinctly separated from frons by an obsolete transverse carina. Frons convex, about 1.5 times wider than medially high, lateral carinae ridged, median carina absent. Frontal area and clypeus beset with fine hairs. Median carina of clypeus absent, lateral carinae weakly defined. Compound eyes and ocelli absent. Second antennal segment subcylindrical, about 1.5 times longer than it is wide.

Thorax (Fig. 6A). Pronotum indistinctly tricarinate, lateral portions anteriorly with fine hairs, medially about 3 times longer than vertex, posterior margin shallowly excavate. Mesonotum shallowly vaulted, without carination, beset with fine hairs, in middle line about 2.4 times the length of pronotum. Tegulae vestigial. Tegmina strongly reduced, venation rudimentary, with fine bristles along veins. Wings vestigial. Metatibiae laterally with three minute spines, apically with four to five teeth (individually varying). First metatarsal segment slightly longer than second and third together. First metatarsus with four, second with two apical teeth.

Male genitalia (Fig. 7). Genital segment as in *C. palmeros* and *C. pinarcoladus*, medioventral process subconical, apically shallowly notched. Anal segment about twice as long as it is wide, distally slightly bent ventrad, caudal margin shallowly concave. Parameres similar to those of *C. palmeros* and *C. pinarcoladus* but distally stronger, expanding dorsad with dorsal and caudal margin rounded. Basal part of aedeagus compressed, ventrally ridged, with two small, rigid spines directed caudad near its base; right and dorsal side of shaft produced into a fold- and shield-like sclerotized structure, respectively. Shaft subapically on each side with a curved movable spinose process: in repose left lateral spine one curved dorsad, right lateral one directed lateroventrad. Distal part of aedeagus with a short but strong acute spine at apex.

Female genitalia (Fig. 8). Seventh abdominal sternite subtriangular, with distal margin medially bent dorsad; ovipositor ensiform, almost straight, distinctly surpassing the anal segment; ninth tergite caudally truncate, wax-secreting field

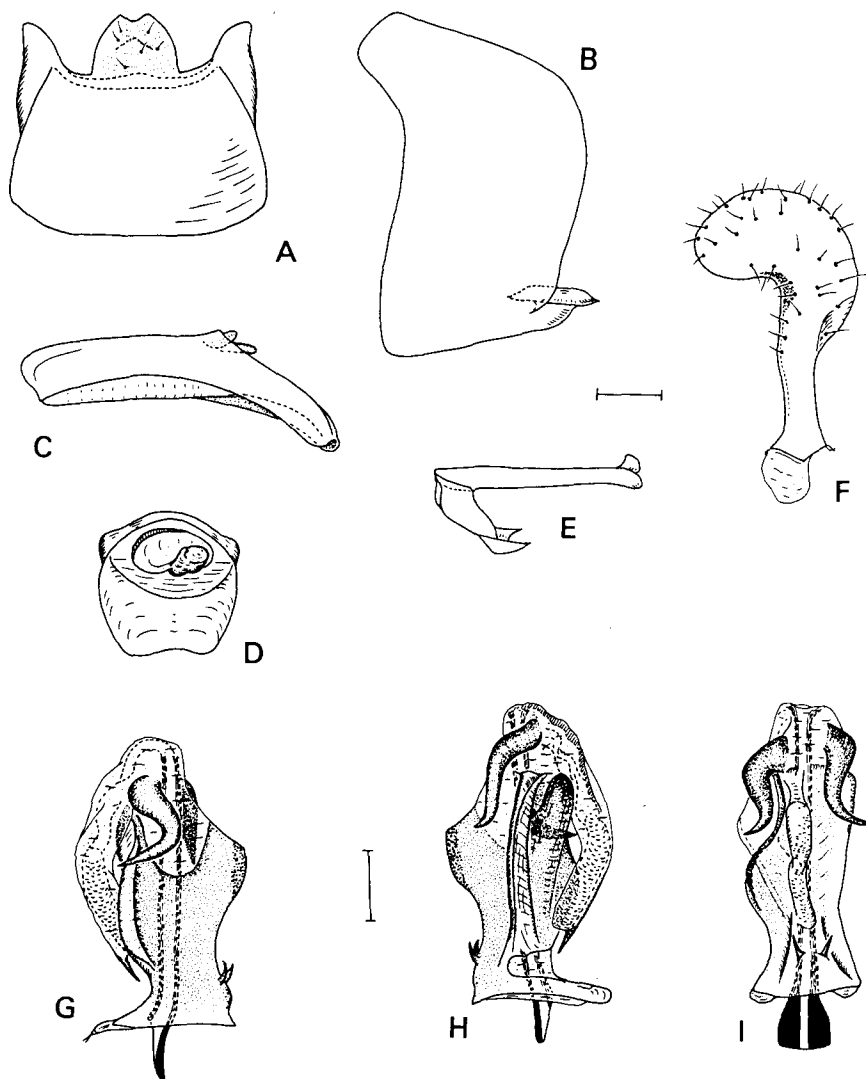


Figure 7. *Cixius ratonicus* sp. nov., male genitalia, holotype. A, genital segment, ventral aspect; B, same, left lateral aspect; C, anal segment, left lateral aspect; D, same, caudal aspect; E, connective, left lateral aspect; F, left paramere, maximum view; G, aedeagus, left lateral aspect; H, same, right lateral aspect; I, same, ventral aspect. Scale bar: 0.1 mm.

distinctly defined, medially completely separated by a membranous area forming two longitudinally expanded portions.

Etymology. This species is named after its type locality, Cueva del Ratón, on the island of La Palma.

Holotype. Male: Canary Islands, La Palma, S.E. Fuencaliente, Cueva del Ratón, 9.iv.1990, M. Asche & H. Hoch leg. (ULL).

Paratype. One female: same data as holotype (AH).

Diagnosis and remarks. *Cixius ratonicus* is similar to *C. palmeros* and *C. pinarcoladus* in its degree of troglomorphy, but differs considerably in size and male genital characters: genital segment with medioventral process strongly projected and

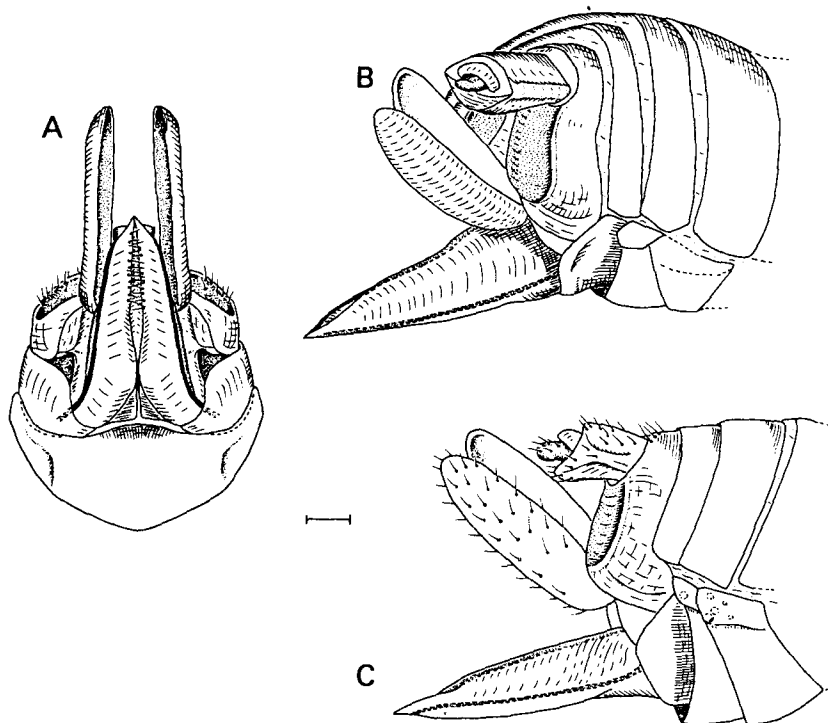


Figure 8. *Cixius raticus* sp. nov., female genitalia, paratype. A, ventral aspect; B, laterocaudal aspect; C, right lateral aspect. Scale bar: 0.1 mm.

apically conspicuously notched, dilated portion of parameres distally comparatively slender, with caudal margin evenly arched, aedeagus with central ridge more strongly pronounced, subapical spinose processes with different degree and direction of bending, tip of aedeagus distal part with a strong, acute spine.

The single known male was recovered from a spider's web and is badly damaged. However, the male genitalia were complete and proved to be sufficiently sclerotized. Its high degree of troglomorphy and its occurrence in the dark cave zone suggest that *C. raticus* is an obligate cavernicole, i.e. a troglobitic species.

Distribution and ecology. *Cixius raticus* is only known from Cueva del Ratón, S.E. Fuencaliente, La Palma (Fig. 38). The 260-m long lava tube is located in a historic lava flow of San Antonio volcano (the eruption of 1677), at an altitude of approximately 200 m; the temperature measured in April in the deep cave zone was 20°C. The entrance of Cueva del Ratón is located in a 'kipuka' (= island of older vegetation surrounded by young lava flows)-like situation: surrounded by fine lapilli of the 1971 eruption of Teneguía volcano. Roots, presumably of *Rumex lunaria* and/or *Schizogyne sericea*, are found sporadically throughout the cave, although concentrated in moister patches. In Cueva del Ratón, *C. raticus* occurs syntopically with a cave-adapted species of the family Meenoplidae described below. This is the only known locality on La Palma where two troglobitic Fulgoroidea species occur together.

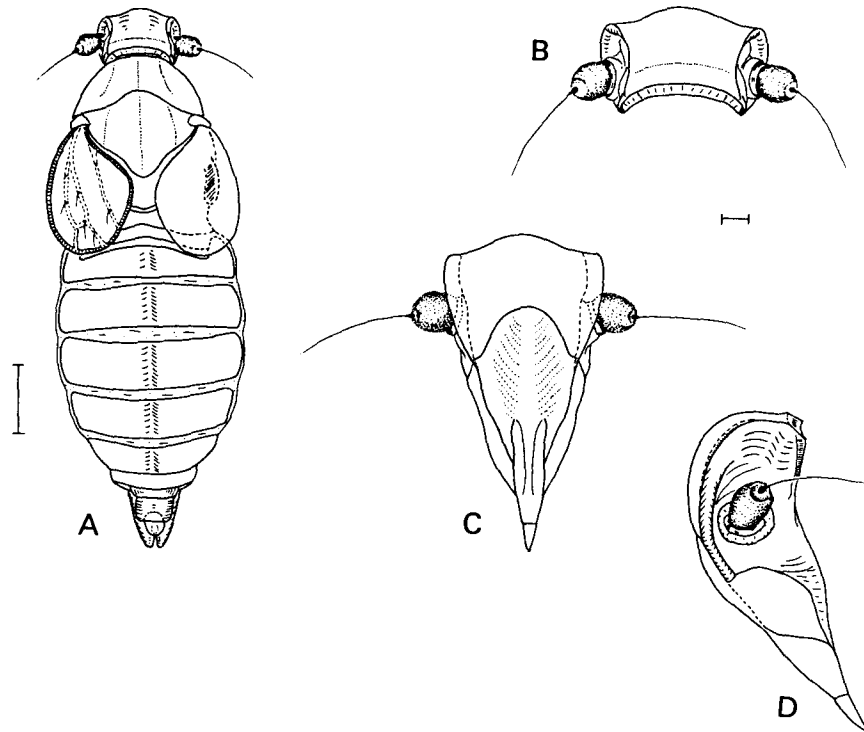


Figure 9. *Cixius tacandus* sp. nov., paratype (female). A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, left lateral aspect. Scale bar: A 0.5 mm, B–D 0.1 mm.

***Cixius tacandus* sp. nov.**

(Figs 9–11)

Description. Habitus as in *C. ratornicus*, but slightly larger.

Total length. Male 2.9 mm. Female 3.2–3.9 mm ($n=4$).

Colouration. Head, pro-, mesonotum and abdominal segments 3–11 pale yellow, metathorax and first two abdominal segments slightly lighter, antennae white, tegmina translucent, veins concolorous except for the pale yellow costal vein.

Head (Fig. 9). Vertex short, about 5.6 times as wide as it is long in the middle line, indistinctly separated from frons by a faint transverse carina. Frons convex, about 2 times wider than medially high, lateral carinae distinctly ridged, median carina absent. Frons and clypeus feebly pustulate. Compound eyes and ocelli absent. Second antennal segment subglobose.

Thorax (Fig. 9A). Pronotum faintly tricarinate, lateral portions anteriorly inconspicuously pustulate, in midline about 3.2 times the length of vertex, posterior margin shallowly excavate. Mesonotum nearly planate, smooth in the male, very faintly tricarinate in the female, medially about 2.2 times the length of the pronotum. Tegulae vestigial. Tegmina strongly reduced, venation rudimentary, bristles along veins very sporadic. Wings vestigial. Metatibiae laterally with two minute spines, apically with six teeth. First metatarsal segment

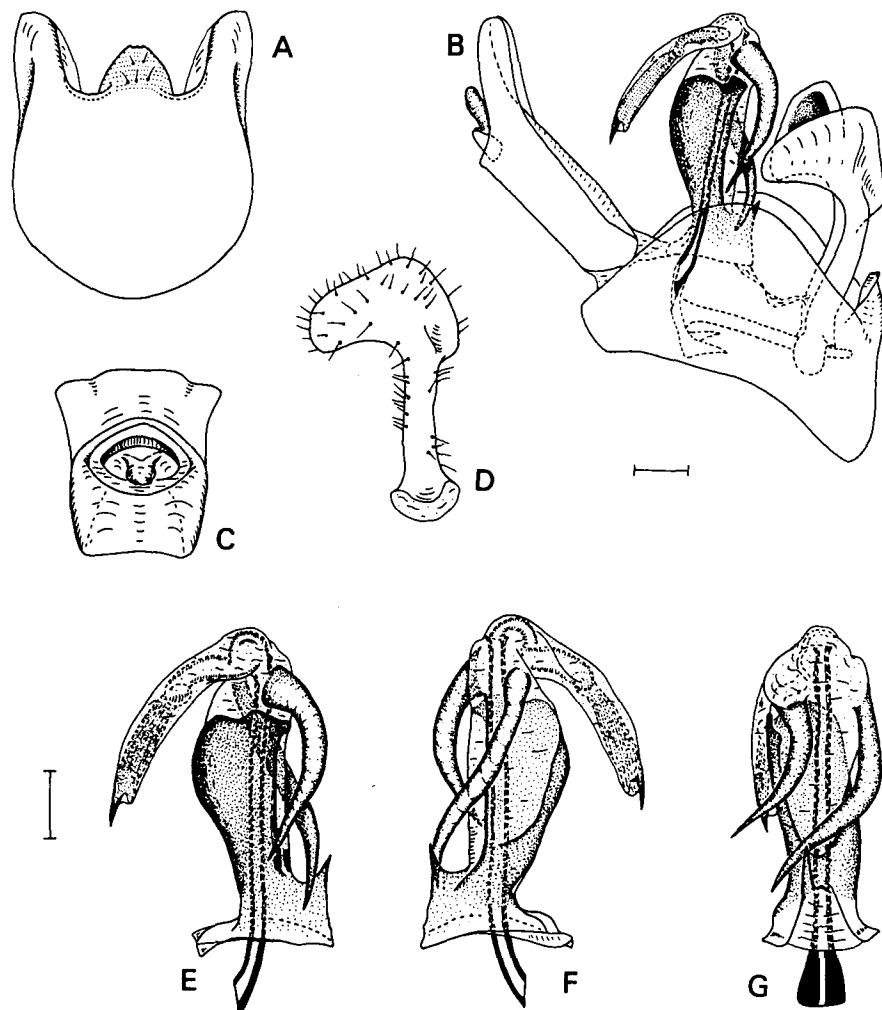


Figure 10. *Cixius tacandus* sp. nov., male genitalia, holotype. A, genital segment, ventral aspect; B, male genitalia *in situ*, left lateral aspect; C, anal segment, caudal aspect; D, left paramere, maximum view; E, aedeagus, left lateral aspect; F, same, right lateral aspect; G, same, ventral aspect. Scale bar: 0.1 mm.

about 1.3 times longer than second and third together. First metatarsus with four, second with two (male) or two to three (female) apical teeth.

Male genitalia (Fig. 10). Genital segment similar in shape and proportions to that of *C. ratornicus*. Anal segment as in *C. ratornicus*. Dilated portion of parameres strongly expanding dorsad with caudal margin forming an obtuse angle. Basal part of aedeagus slender, ventrally with a socle-shaped projection bearing a single solid spine directed caudad. Basal part dorsally and on its left side with a shield-like area of enhanced sclerotization; subapically with two rather long, slender, terete, movable spinose processes: in repose left lateral one directed basolaterad reaching the basal third of shaft, right lateral one curved ventrobasad and to the left side attaining almost the base of shaft. Distal part of

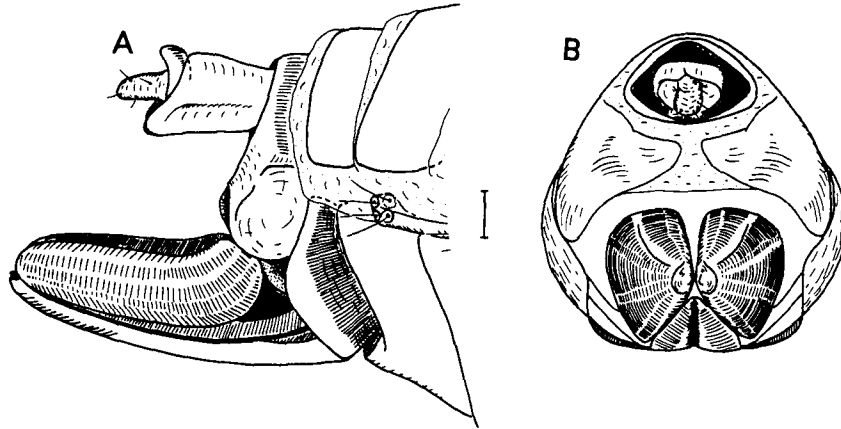


Figure 11. *Cixius tacandus* sp. nov., female genitalia, paratype. A, right lateral aspect; B, caudal aspect. Scale bar: 0.1 mm.

aedeagus in repose attaining the basal third of shaft, with a short, acute spine at apex.

Female genitalia (Fig. 11). Seventh abdominal sternite subtriangular; ovipositor ensiform, slightly curved dorsad, distinctly surpassing the anal segment; ninth tergite caudally truncate; wax-secreting field comparatively small and indistinctly defined, medially separated by a membranous area.

Etymology. The species is named after its type locality, Cueva de Tacande, on the island of La Palma.

Holotype. Male: Canary Islands, La Palma, S. El Paso, Cueva de Tacande, 24.x.1988, M. Asche & H. Hoch leg. (ULL).

Paratypes. Four females, same data as holotype except 9.ii.1988, 14.ii.1988, 16.x.1988, 17.iv.1990, M. Asche & H. Hoch leg. (ULL, AH).

Additional material. Nymphs, same locality as holotype: 1 III (♂), 1 IV (♂), 16.xi.1986, J. L. Martin leg. 6 V (♂), 2 IV (♂), 9.ii.1988; 4 V (♂), 2 IV (♂), 10.ii.1988; 1 V (♂), 14.ii.1988; 1 II, 16.x.1988; 2 V (♂), 1 IV (♂), 17.iv.1990, M. Asche & H. Hoch leg. (ULL, AH).

Diagnosis. *Cixius tacandus* displays a similar degree of troglomorphy as the other cavernicolous *Cixius* species of La Palma; it is similar in size to *C. ratonicus*, but differs considerably from this and the other cave-dwelling species with respect to the male genitalia: base of shaft ventrally with a single solid spine arising from a socle-shaped projection, aedeagus with both subapical spinose processes very long, their tips in repose pointing to the left.

Distribution and ecology. *Cixius tacandus* is found only in Cueva de Tacande, S. El Paso, La Palma (Fig. 38). The cave is 111 m long and is located in a prehistoric lava flow, at an altitude of 650 m a.s.l. The temperature measured in the dark zone of the cave in February, April and October was around 21°C. The entrance is located in a cultivated area with remnants of native vegetation. Roots, presumably of *Rumex lunaria* and/or *Schizogyne sericea*, are distributed sporadically on the floor, on washed-in soil deposits, in the central part as well as in the end chamber (rear part) of the cave. The troglomorphies displayed by *C. tacandus* and its ecology suggest that the species is troglobitic.

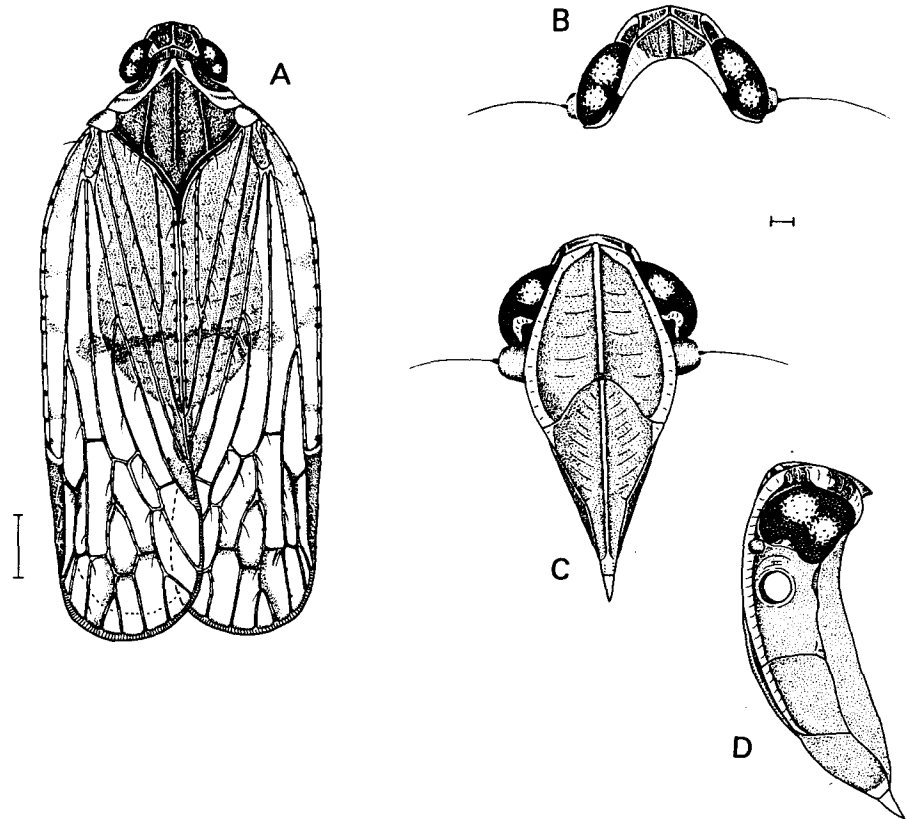


Figure 12. *Cixius palmensis* Lindberg, male from S. Jedey, La Palma, male no. 1. A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, left lateral aspect. Scale bar: A 0.5 mm, B-D 0.1 mm.

Cixius palmensis Lindberg 1960
(Figs 12-14)

Lindberg H. 1960 *Soc. Sci. Fenn. Comm. Biol.* **22**: 14 (Fig. 6, p. 15).

Supplementary description. Habitus is characteristic for epigeic *Cixius* species with well-developed compound eyes, tegmina and bodily pigmentation (Fig. 12A).

Total length. Male 4.9-5.5 mm ($n=15$). Female 5.5-6.0 mm ($n=9$).

Head (Fig. 12). Area of vertex and areolets concave, with lateral carinae sharply ridged and converging anteriorly, vertex at posterior corners about 2.2 times wider than it is medially long; areolets small, separated from frons by an obtuse transverse carina. Area of frons slightly concave, ascending to median carina; only slightly wider than it is medially high, lateral carinae foliately ridged and moderately produced anterolaterad, lateral carinae continuing on postclypeus without sharp interruption. Median carina of frons and clypeus distinctly ridged. Lateral ocelli distinct, median frontal ocellus obsolete. Second antennal segment subglobose.

Thorax (Fig. 12A). Pronotum tricarnate, median carina obtuse, lateral carinae distinctly ridged and diverging posterolaterad. Pronotum medially about one-third the length of the vertex, posterior margin deeply excavate. Mesonotum

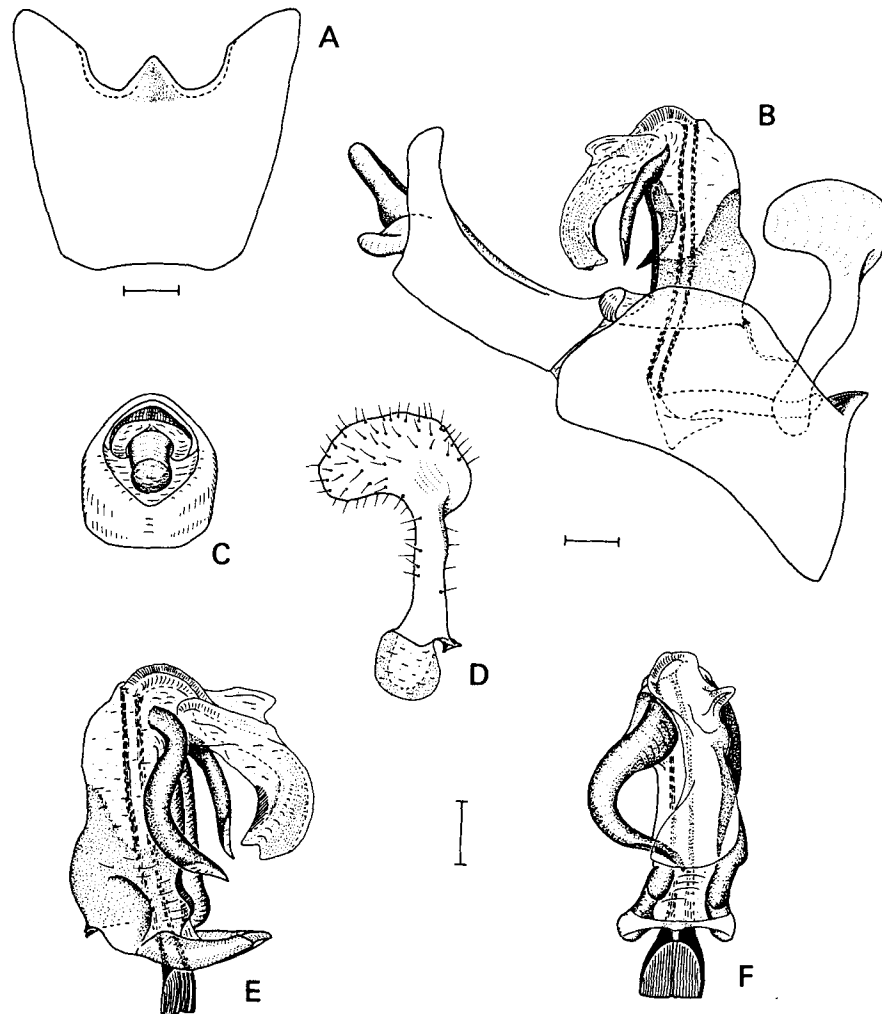


Figure 13. *Cixius palmensis* Lindberg, male genitalia, male from S. Jedey, La Palma, male no. 2. A, genital segment, ventral aspect; B, male genitalia *in situ*, left lateral aspect; C, anal segment, caudal aspect; D, left paramere, maximum view; E, aedeagus, right lateral aspect; F, aedeagus, dorsal aspect. Scale bar: 0.1 mm.

distinctly tricarinate, with lateral portions tectiform, median portion almost planate, in midline about 14 times the length of the pronotum. Tegulae well developed. Tegmina surpassing tip of abdomen by about one-third of their total length; numerous bristles in callous bases along all veins except for apical margin, pterostigma conspicuous. Wings well developed. Metatibiae laterally with three minute spines, apically with six teeth. First metatarsal segment slightly longer than second and third together. First metatarsus apically with seven to nine teeth, second with three teeth and seven macrochaetae (platelli).

Male genitalia (Fig. 13). Genital segment similar in general configuration to that of the troglobitic *Cixius* species of La Palma. Anal segment about twice as long as it is wide, distal portion slightly bent ventrad, caudal margin rounded.

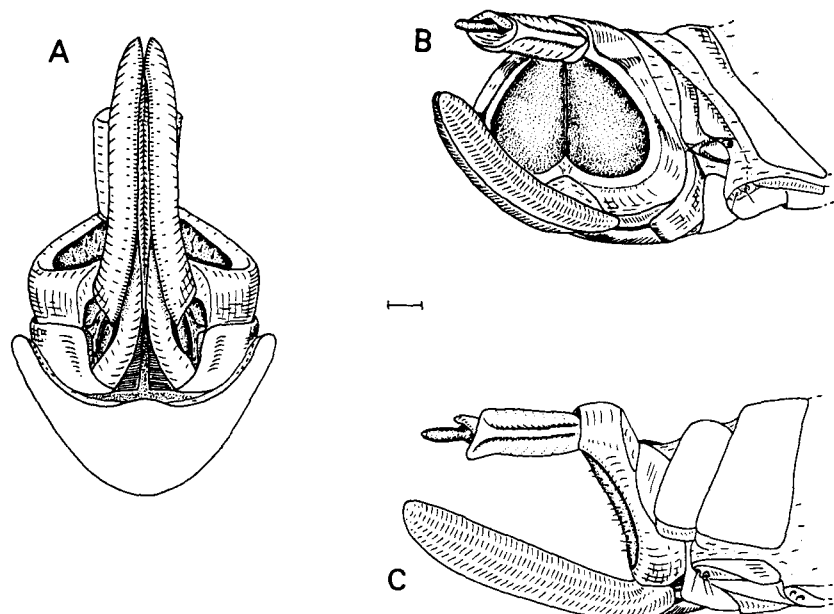


Figure 14. *Cixius palmensis* Lindberg, female genitalia, female from S. Jedey, La Palma. A, ventral aspect; B, laterocaudal aspect; C, right lateral aspect. Scale bar: 0.1 mm.

Parameres distally with caudodorsal margin convex. Basal part of aedeagus stout, compressed, ventrally ridged, with two small, rigid spines directed ventrad. Shaft in basal half with enhanced sclerotization; subapically with two movable spinose processes: left lateral one almost straight, in repose slightly curved dorsomedial; right lateral one very strongly developed, hook-shaped, in repose pointing dorsomedial. Distal part of aedeagus in repose reaching basal third of shaft, apically without spine, in its proximal half with a triangular membranous velum on its left side. Slight variation was observed in the ventral silhouette of the shaft in lateral aspect and in the length and degree of bending of the two movable spinose processes.

Female genitalia (Fig. 14). Seventh sternite subtriangular; ovipositor ensiform, slightly surpassing the anal segment, anal segment comparatively long; ninth tergite caudally truncate, wax-secreting field distinctly limited, concave, inversely heart-shaped, medially not separated but with a distinct ridge.

Material examined. Canary Island, La Palma: 6 ♂♂, 2 ♀♀, S. Jedey, road to Fuencaliente, approximately 800 m, 9.iv.1990, on *Pinus canariensis*, M. Asche & H. Hoch leg. (AH); 10 ♂♂, 3 ♀♀, approximately 4 km N. E. Fuencaliente, road to Montes de Luna, approximately 800 m, 15.iv.1990, on *Pinus canariensis*, M. Asche & H. Hoch leg. (AH); 6 ♂♂, 8 ♀♀, supra El Paso, road to Refugio de El Pilar (W. of Cumbre Vieja), approximately 1300 m, 17.iv.1990, on *Pinus canariensis*; M. Asche & H. Hoch leg. (AH).

Diagnosis and remarks. *Cixius palmensis* is the only known epigean representative of the genus *Cixius* on La Palma and on the other Canarian Islands. It displays well-developed compound eyes and is fully flighted. In the male genitalia the aedeagus bears two movable spinose processes as is the case in several European

and African *Cixius* species, but also in the three species of the Madeira Islands, *C. verticalis* Noualhier, *C. madeirensis* China, and *C. chaoensis* China. Whether this spinose configuration of the aedeagus indicates phylogenetic relationships to any of these extra-Canarian species cannot be decided yet. It also appears doubtful to assign *C. palmensis* to any of the (rather weakly defined) subgenera of *Cixius* mainly established by Wagner (1939), e.g. to *Paracixius* Wagner or *Ceratocixius* Wagner as discussed by Lindberg (1960).

Cixius palmensis differs from the cavernicolous *Cixius* species from La Palma in the configuration of the male and female genitalia: in males the shape and direction of bending of the two subapical aedeagal processes is different, and, in particular, there is a membranous velum in the upper portion of the distal part of the aedeagus; in females the difference lies in the shape of the concave wax-bearing field of the ninth tergite with its conspicuous median ridge. Whether *C. palmensis* represents a close relative of any of the cavernicolous *Cixius* species from La Palma cannot be determined on a merely morphological basis. It is equally conceivable that the distinct differences in male and female genital structures between *C. palmensis* and the cavernicolous *Cixius* species were either acquired in the course of cave adaptation, or instead reflect the morphological display of ancestral epigean species other than *C. palmensis* (which today are not known from La Palma). In the latter case, *C. palmensis* would represent an epigean survivor of an older set of *Cixius* species that may have colonized the Canary Islands in the past.

Distribution and ecology. *Cixius palmensis* is an epigean *Cixius* species endemic to La Palma. On the island, it is apparently widely distributed within the Pinar, on *Pinus canariensis*, in altitudes between 800 and 1300 m. Populations are known from the northern (Los Tilos: Lindberg, 1960), western (Jedey), southern/southeastern (around Fuencaliente) and central part (supra El Paso) of the island.

***Cixius ariadne* sp. nov.**

(Figs 15–17)

Description. In general appearance it is similar to the troglotic *Cixius* species of La Palma.

Total length. Male 2.7–3.0 mm ($n=4$). Female 3.2–3.95 mm ($n=6$).

Colouration. Body and legs generally pallid, antennae white, tegmina translucent with venation pale yellow, bristles on tegmina dark brown.

Head (Fig. 15). Vertex short, about 3 times wider at its base than it is long in the midline, basal cell obtusely triangular, areolets small, shallowly concave; vertex faintly separated from frons by an obsolete transverse carina. Frons convex, about 1.5 times wider than medially high, lateral carinae moderately produced laterad, faintly continuing on upper postclypeus, median carina absent. Anterior portion of frons feebly pustulate. Compound eyes and ocelli absent, their former position recognizable by a slightly vaulted area. Second antennal segment ovoid, 1.2 times longer than wide.

Thorax (Fig. 15A). Pronotum delicately tricarinate, lateral carinae diverging posteriorly, medially about 1.4–1.5 times the length of the vertex, posterior margin obtuse, angulately concave. Mesonotum nearly planate, weakly tricarinate, in midline about 3.2 times the length of the pronotum. Tegulae

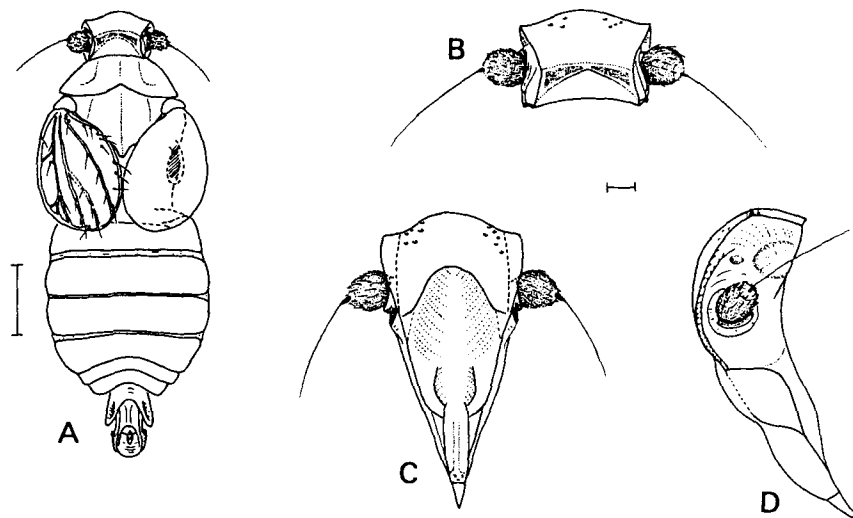


Figure 15. *Cixius ariadne* sp. nov., holotype. A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, left lateral aspect. Scale bar: A 0.5 mm, B–D 0.1 mm.

small. Tegmina strongly reduced, but variable among individuals in total length, venation rudimentary, with numerous conspicuous bristles along veins. Wings vestigial. Metatibiae laterally with minute spines: one to two in males and two to three in females, apically with six teeth. First metatarsal segment about 1.2 times longer than the second and third together. First metatarsus apically in both sexes with four apical teeth, second metatarsus in males with five, and in females with four to six; macrochaetae absent.

Male genitalia (Fig. 16). Genital segment in caudal aspect slightly higher than it is wide. Anal segment about twice as long as it is wide, distal portion slightly bent ventrad, caudal margin rounded. Parameres with dilated distal part strongly expanding dorsad. Aedeagus with basal part slender, compressed, ventrally with a massive bifurcate projection directed basad. Shaft subapically on its right side with a single long, slender, movable spinose process, in repose slightly curved dorsad. Distal part of aedeagus in repose reaching basal half or shaft, without spine at apex and velum.

Female genitalia (Fig. 17). Seventh sternite short, with anterior margin rounded, posterior margin almost straight; ovipositor ensiform, slightly curved dorsad, exceeding the anal tube with more than a third of its length; ninth tergite caudally truncate, wax-secreting field distinctly limited, slightly concave, with a distinct median ridge, medioventral excavation obtusely angulate, inversely heart-shaped (as in *C. palmensis*).

Etymology. The species is named after Ariadne, daughter of King Minos of Crete.

Holotype. Male: Canary Islands, El Hierro, infra El Pinar (Taibique), road to La Restinga, Cueva de La Curva, approximately 600 m, 21.ii.1988, M. Asche & H. Hoch leg. (ULL).

Paratypes. Two females, same data as holotype. Three males, four females, same data as holotype except 29.x.1988, 29.iv.1990, 30.iv.1990, M. Asche & H. Hoch leg. (ULL, AH).

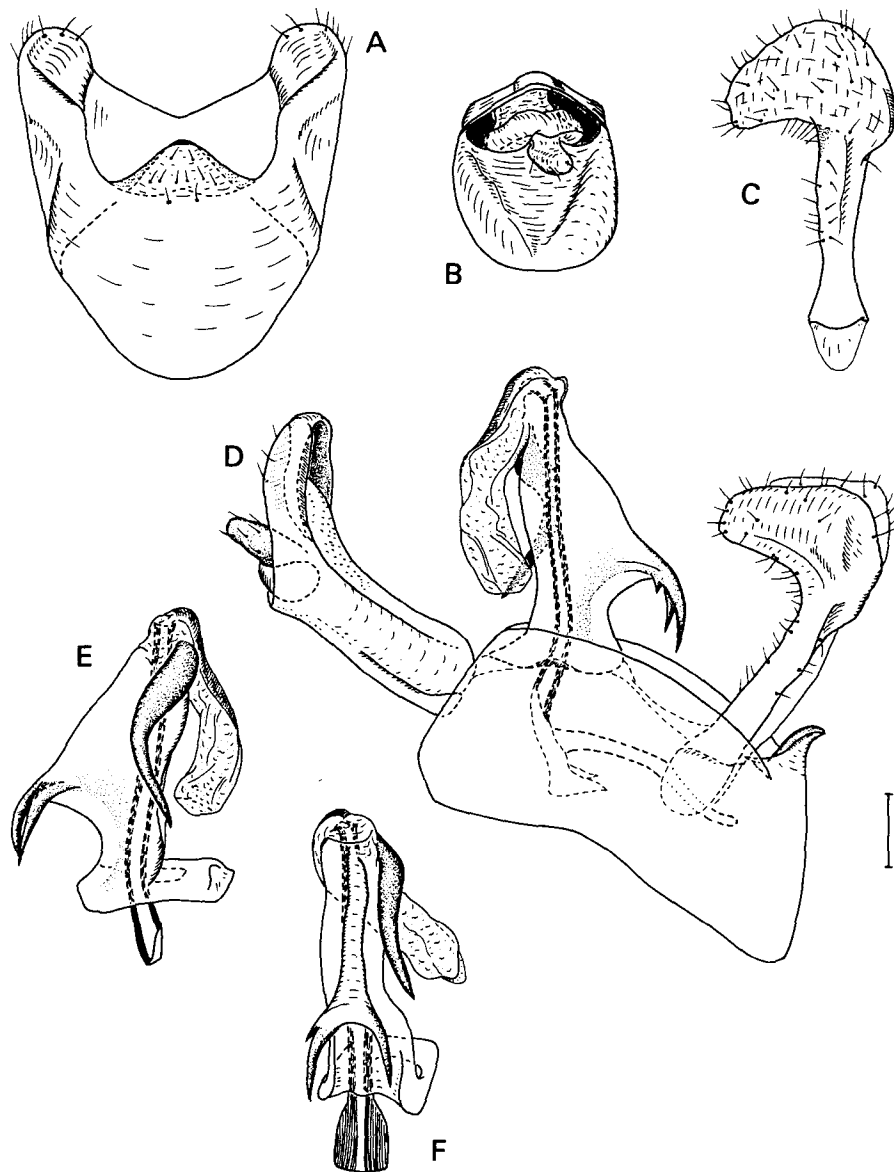


Figure 16. *Cixius ariadne* sp. nov., male genitalia, holotype. A, genital segment, ventrocaudal aspect; B, anal segment, caudal aspect; C, left paramere, maximum view; D, male genitalia *in situ*, left lateral aspect; E, aedeagus, right lateral aspect; F, same, ventral aspect. Scale bar: 0.1 mm.

Additional material. Nymphs, same locality as holotype; 1 V, 1 III, 20.ii.1988; 1 III, 21.ii.1988; 1 III, 3 IV, 3 V (♀), 5 V (♂), 3.xi.1988; 4 V (♀), 30.iv.1990; M. Asche & H. Hoch leg. (ULL, AH).

Diagnosis and remarks. This species displays a similar degree of troglomorphy as the cave-dwelling *Cixius* species of La Palma, but differs considerably in characters of the male genitalia: aedeagus at ventral base with a solid bifurcate projection, subapically only a single spinose process on right side, distal part of

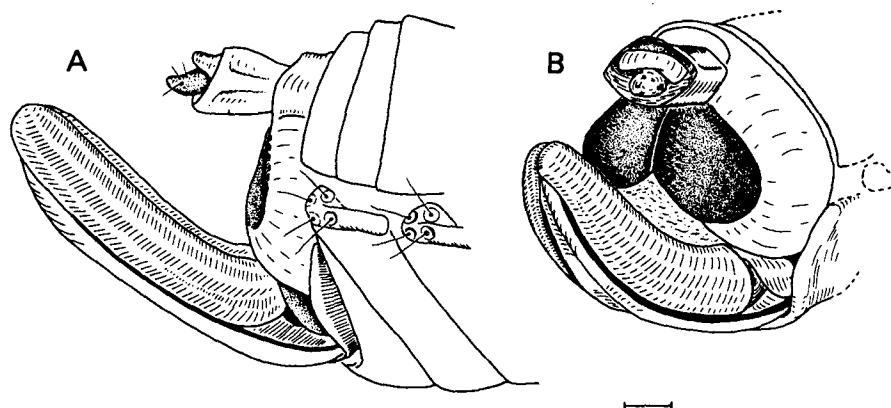


Figure 17. *Cixius ariadne* sp. nov., female genitalia, paratype. A, right lateral aspect; B, laterocaudal aspect. Scale bar: 0.1 mm.

aedeagus devoid of spines. In the female genitalia the truncate wax-secreting field, unlike that in the cavernicolous *Cixius* species of La Palma, is not medially separated by a membranous area. This species appears morphologically isolated from all other Cixiidae known from the Canary Islands. A close relationship can only be determined with the other new cavernicolous cixiid species from El Hierro, *Cixius nycticolus* sp. nov., which is described below. The carination of the mesonotum and the general configuration of the male and female genitalia place this species in the tribe Cixiini. The generic placement in *Cixius*, however, is tentative because of the morphological alterations of external features evolved during the process of cave adaptation (troglomorphies). There are no representatives of *Cixius* known in the epigeal fauna of El Hierro.

Distribution and ecology. *Cixius ariadne* is known only from Cueva de La Curva, El Hierro (Fig. 38). This lava tube is located in a prehistoric lava flow at an altitude of 600 m a.s.l. The cave consists of an upper passage of about 40 m and a lower passage of about 141 m. The temperature in February, April and October was approximately 19.5°C in the lower, and 21.5°C in the upper passage. A high relative humidity prevails in both passages, and roots, presumably of *Rumex lunaria*, are comparatively abundant. Additionally, various washed-in, germinating seeds of unidentified plant species were found at the rear end of the upper passage. Considering its high degree of troglomorphy, *C. ariadne* is presumed to be restricted to subterranean habitats, and is therefore regarded as troglotic.

In Cueva de La Curva *C. ariadne* occurs syntopically with a new troglotic species of the family Meenoplidae which is described below. This is the only known cave on El Hierro where two troglotic Fulgoroidea species occur. A potential predator is the troglotic Emesine *Collartida anophthalma* Español & Ribes (Heteroptera).

***Cixius nycticolus* sp. nov.**

(Figs 18, 19)

Description. In habitus and size closely resembling *C. ariadne*.

Total length. Female 3.8 mm ($n=2$).

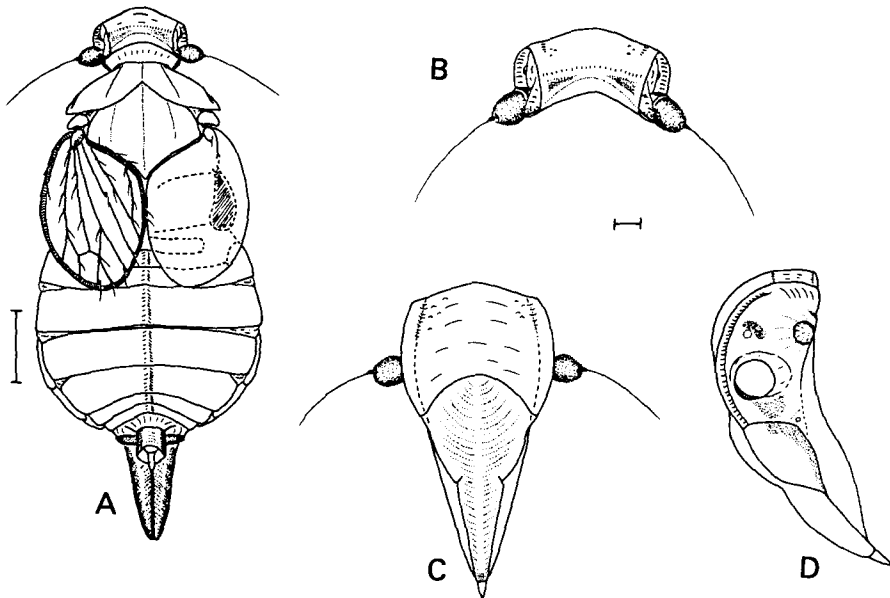


Figure 18. *Cixius nycticolus* sp. nov., holotype (female). A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, same, left lateral aspect. Scale bar: A 0.5 mm, B-D 0.1 mm.

Colouration. Body and legs generally yellow, head laterally, i.e. around blemmata, below antennae and hind margin of lamina maxillaris with dilute brownish marks, antennae white, tegmina translucent, veins hyaline, distal margin yellowish, bristles on tegmina fuscous.

Head (Fig. 18). Vertex short, about 2.5 times wider at its base than it is long in the midline, basal cell obtusely triangular, areolet small, indistinct, very shallowly concave; vertex anteriorly continuously rounded into frons. Frons convex, about 1.7 times wider than it is medially high, lateral carinae ridged and directed laterad, median carina absent. Anterior portion of frons as in *C. ariadne* feebly pustulate. Compound eyes and median frontal ocellus absent, former position of compound eyes marked by a slightly vaulted area; lateral ocelli present although very small, with about three blemmata above each ocellus. Antennae as in *C. ariadne*.

Thorax (Fig. 18A). Pronotum delicately tricarinate, lateral carinae diverging posteriorly, in midline about as long as the vertex, posterior margin obtuse angulately excavated. Mesonotum nearly planate, tricarinate, carinae weakly defined, medially about 4 times the length of the pronotum. Tegulae small. Tegmina strongly reduced; venation rudimentary, with numerous conspicuous bristles along veins but not between veins on apical margin. Wings vestigial. Metatibiae laterally with two minute spines, apically with six teeth. First metatarsal segment about 1.2 times longer than the second and third together. First metatarsus with four apical teeth, second with four to five, devoid of macrochaetae.

Female genitalia (Fig. 19). Seventh sternite short, with anterior margin rounded, posterior margin medially expanding caudally; ovipositor ensiform, slightly curved dorsad, surpassing the anal segment with almost half its length;

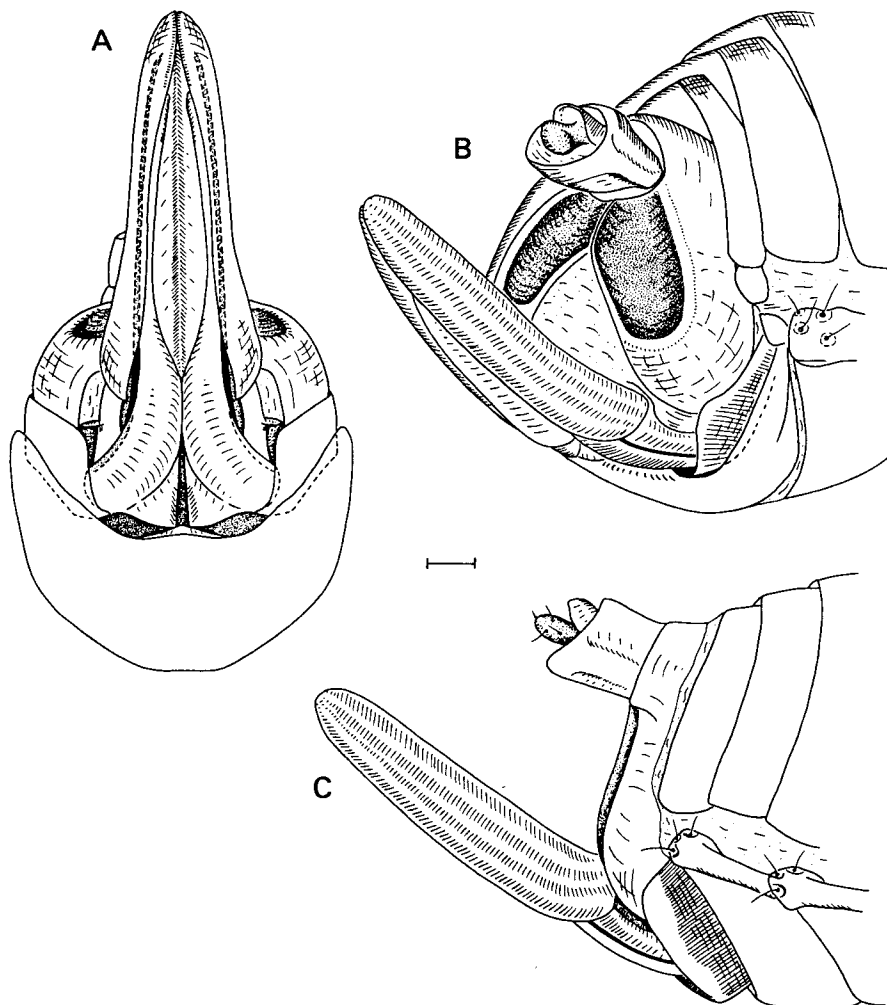


Figure 19. *Cixius nycticolus* sp. nov., female genitalia, holotype. A, vental aspect; B, laterocaudal aspect; C, right lateral aspect. Scale bar: 0.1 mm.

anal segment comparatively short; ninth tergite caudally truncate, wax-secreting field distinctly limited, shallowly concave, with a short but distinct median ridge, membranous medioventral excavation comparatively deep, acutely angulate.

Etymology. The name of the species refers to its life in a permanently dark environment.

Holotype. Female: Canary Islands, El Hierro, N. La Restinga, Montaña Roja, Cueva Roja, 22.iv.1990, M. Asche & H. Hoch leg. (ULL).

Paratype. One female, same data as holotype (AH).

Additional material. Nymphs: 1 V, same data as holotype; 1 IV, same data as holotype except 17.ii.1988, M. Asche & H. Hoch leg. (AH); 1 V (♀), same data as holotype except 20.iv.1985, J. L. Martín leg. (ULL).

Diagnosis. Although this species is very similar to *C. ariadne* in habitus and general character configuration, there are clear differences which separate *C. nycticolus* from *C. ariadne*: the presence of lateral ocelli and blemmata, a longer

rostrum, shallower posterior margin of vertex and pronotum, less highly arched frontoclypeal suture. In the female genitalia the posterior margin of the seventh sternite is expanded medially, the wax-secreting field is distinctly more deeply excavated medioventrally resulting in a shorter median ridge, and the anal segment is shorter in lateral aspect.

Distribution and ecology. *Cixius nycticolus* is only known from Cueva Roja on El Hierro (Fig. 38). The entrance of the prehistoric Cueva Roja lava tube is located within the crater of Montaña Roja volcano, at an altitude of about 350 m a.s.l. The two-storey cave has approximately 300 m of explored passage. The upper passage is wide and tunnel-like, the lower passage is narrower, ending in a flat chamber. Sparse roots (presumably of *Rumex lunaria*) are found in most parts of the cave, being more abundant in the end chamber of the upper passage. The temperature in the end chamber of the upper passage in February and April was 14.2–14.8°C. The entrance, twilight and transition zones experience strong air drafts corresponding to outside weather conditions. This effect is apparently enhanced by the steep entrance descent of the upper passage (chimney effect), *Cixius nycticolus* displays a similarly high degree of troglomorphy as *C. ariadne* and is also considered a troglobitic species.

Family Cixiidae

Genus *Tachycixius* Wagner

***Tachycixius crypticus* sp. nov.**

(Figs 20, 22)

Description. In general appearance it resembles epigean *Tachycixius* species with diffusely spotted tegmina; only slightly troglomorphic.

Total length. Male 5.5 mm. Female 6.1 mm.

Coloration. Body testaceous with yellow and fuscous portions of head and thorax. Tegmina translucent, slightly yellow, veins hyaline, bases of bristles centred in dark brown callouses, with dilute brown marks enclosed by Y-veins and in distal third, numerous faint fuscous transverse bars spotted over the entire tegmen. Wings translucent, veins hyaline to light brown. Legs stramineous, pro- and mesotibiae with brown ring-like marks at base, distally suffusely brown.

Head (Fig. 20). Vertex short, about 2.2 times wider at its base than it is long in the midline, basal cell concave, anteriorly rounded; areolets small, slightly concave, medially separated by a faint longitudinal carina; vertex separated from frons by an obsolete transverse carina. Area of frons slightly concave, frons about 1.3 times wider than it is medially high, lateral carinae foliately produced laterad; median carina of frons and clypeus obtuse. Compound eyes present, in comparison to epigean taxa slightly reduced in size, lateral ocelli distinct, median frontal ocellus rudimentary. Second antennal segment subglobose, about 1.2 times longer than it is wide.

Thorax (Fig. 20A, E). Pronotum tricarinate, lateral carinae ridged and diverging posteriorly around posterior margin of compound eyes, in middle line about half as long as the vertex, posterior margin rectangularly excavated. Mesonotum tricarnate, lateral carinae softly sinuate, lateral portions shallowly tectiform, median portion planate, medially 6.5 times the length of the pronotum. Tegulae well developed. Tegmina distally slightly reduced, in both

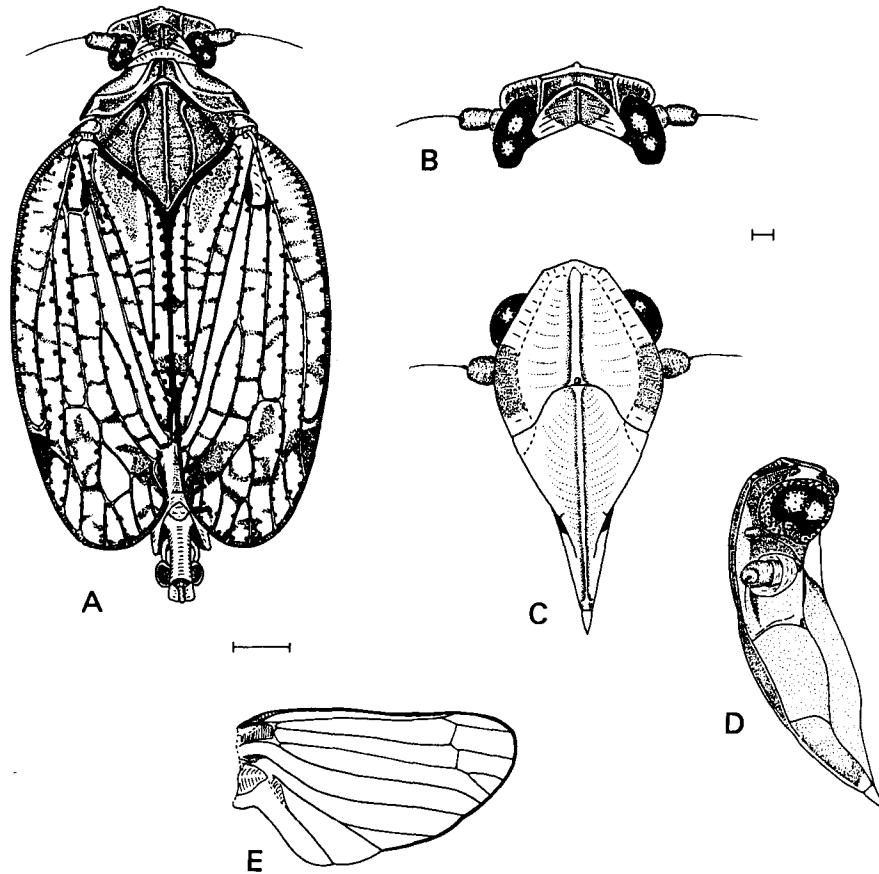


Figure 20. *Tachycixius crypticus* sp. nov., holotype. A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, same, left lateral aspect; E, tegmen. Scale bar: A, E 0.5 mm, B-D 0.1 mm.

sexes distally reaching genital segments, venation well developed, numerous conspicuous bristles along veins and on apical margin between veins. Wings distally and in anal area conspicuously reduced. Metatibiae laterally with three to four small spines, apically with six teeth. First metatarsal segment about 1.2 times longer than the second and third together. First and second metatarsus each with eight apical teeth, the median four teeth of the second metatarsus each with a macrochaete.

Male genitalia (Fig. 21). Genital segment in caudal aspect slightly higher than it is wide, laterodorsally on each side with an obtuse projection, medioventral process in ventral aspect tongue-shaped, with a sharp median ridge on its dorsal side. Anal segment long and slender, about 3 times as long as it is wide, distal third abruptly bent ventrad, caudal margin medially shallowly concave. Parameres (Fig. 21F) as in other *Tachycixius*. Basal part of aedeagus slightly depressed, ventrally with a longitudinal ridge right of middle line, a strongly developed ear-shaped projection on its left side, and a socle-shaped projection near its base on the right side. Shaft subapically on its right side with two slender movable spinose processes: dorsal one almost semicircular, in repose curved dorsomedial; ventral one more straight, in repose curved basolateral. Shaft

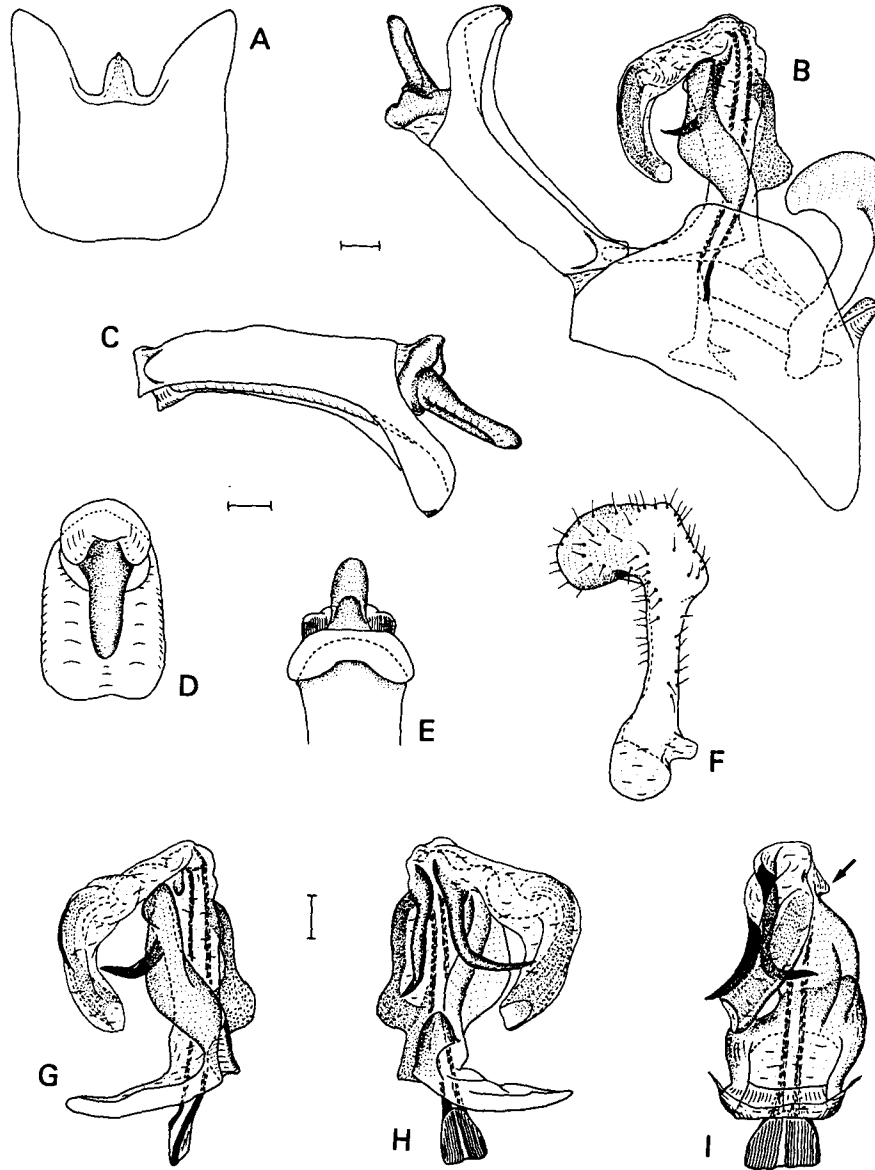


Figure 21. *Tachycixius crypticus* sp. nov., male genitalia, holotype. A, genital segment, ventral aspect; B, male genitalia *in situ*, left lateral aspect; C, anal segment, left lateral aspect; D, same, caudal aspect; E, same, ventral aspect; F, left paramere, maximum view; G, aedeagus, left lateral aspect; H, same, right lateral aspect; I, same, dorsal aspect. Scale bar: 0.1 mm.

subapically on its left side with a small membranous velum (Fig. 21I, arrow). Distal part of aedeagus medially almost rectangularly bent, in repose reaching to basal third of shaft, without spine at apex and velum, on its left side with a conspicuous, ridge-like sclerite slightly below bending.

Female genitalia (Fig. 22). Seventh sternite subtriangular, with distal margin medially straight; ovipositor ensiform, slightly curved dorsad, surpassing the anal

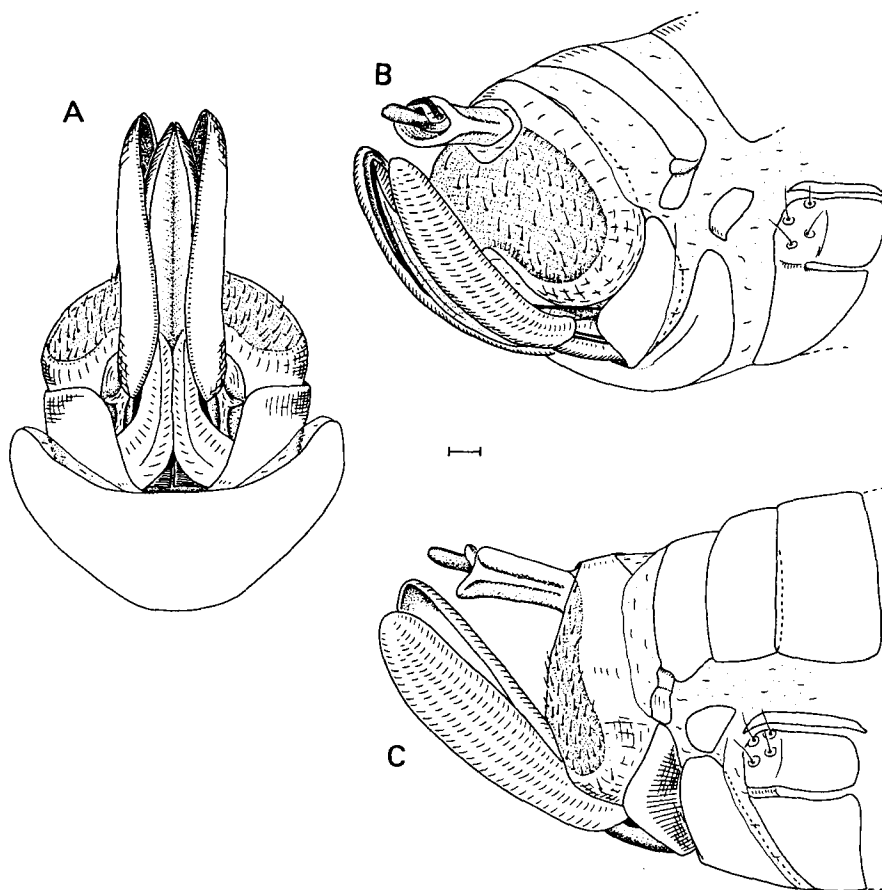


Figure 22. *Tachycixius crypticus* sp. nov., female genitalia, paratype. A, ventral aspect; B, laterocaudal aspect; C, right lateral aspect. Scale bar: 0.1 mm.

segment; anal segment comparatively long, depressed, laterally ridged; ninth tergite caudally truncate, wax-secreting field indistinctly limited, transition to margins smooth, slightly convex, beset with numerous fine hairs, medioventral excavation shallow.

Etymology. The name of this species refers to its concealed underground habitat.

Holotype. Male: Canary Islands, Tenerife, S.E. Tigaiga, Palo Blanco, 25.x.1986, A. Aguiar leg. (MSC).

Paratype. One female: same locality as holotype, 3.ix.1986, A. Aguiar leg. (AH).

Additional material. Nymphs, same locality as holotype: 1 V (♀), 4.vii.1986; 1 V, 25.x.1986; 1 V (♀), 13.xii.1986; 1 IV, 7.ii.1987; A. Aguiar leg. (MSC, AH).

Diagnosis. *Tachycixius crypticus* resembles *T. canariensis* (see below) in general appearance and in the shape of the genital structure, but differs with respect to the following characters: tegmina in distal part and wings more strongly reduced (flight capacity doubtful), compound eyes relatively small; in male genitalia distal part of parameres more strongly expanded dorsad, subapically on the left

side of aedeagus shaft with a small lobe, but devoid of a spine; the ventral one of the two right subapical spinose processes longer and more straight, the dorsal right spine more strongly curved dorsad.

Distribution and ecology. *Tachycixius crypticus* is known from its type locality in the central north of Tenerife only, a relictual laurel forest patch in the western cliffs of La Orotava Valley, S.E. Tigaiga, Palo Blanco (Fig. 38). It has been collected in pitfall traps at a depth of 50 cm below the surface. Since the precise habitat requirements of this species are not yet known, it cannot be decided whether *T. crypticus* which displays only a mild degree of troglomorphy, is ecologically classifiable as endogean, MSS-dwelling, or troglobitic.

***Tachycixius retrusus* sp. nov.**

(Figs 23–26)

Description. In habitus and size very similar to *T. crypticus*, but with more strongly pronounced troglomorphies.

Total length. Male 4.4–5.8 mm ($n=6$). Female 4.8–6.3 mm ($n=6$).

Colouration. Body generally stramineous with pale yellow and brown portions of head and thorax. Tegmina translucent, pale yellow, veins hyaline, bases of bristles centred in brown callouses; tegmen with a large longitudinal brown mark in anterior part of clavus and irregularly distributed conspicuous brown marks (for individual variation see Fig. 23A, E). Wings translucent, veins hyaline to pale brown. Legs stramineous, pro- and mesotibiae with brown ring-like marks at base, distally with brown suffusion.

Head (Fig. 23). Vertex short, about 1.9 times wider at its base than it is long in the midline, basal cell concave, anteriorly rounded; areolet small, slightly concave, separated from frons by an obsolete transverse carina. Area of frons slightly concave, frons about 1.3 times wider than it is medially high, lateral carinae foliately ridged and directed anterolaterad. Median facial carina obtuse on frons and obsolete on clypeus. Compound eyes present, in comparison to epigeal *Tachycixius* species and to *T. crypticus* slightly reduced in size, lateral ocelli distinct, surrounded by one to four irregular blemmata, median frontal ocellus absent. Second antennal segment about 1.5 times longer than it is wide.

Thorax (Fig. 23A, E, F). Pronotum tricarinate, lateral carinae ridged and diverging posteriorly, medially slightly shorter than vertex, posterior margin deeply rectangularly excavate. Mesonotum tricarinate, lateral carinae diverging posteriorly, lateral areas shallowly tectiform, median area planate, in midline about 5 times the length of the pronotum. Tegulae small. Tegmina distally reduced, venation well developed, individually variable in distal part, with numerous conspicuous bristles along veins as well as on apical margin. Distal part and anal area of wings strongly reduced. Metatibiae laterally with three small spines, apically with six teeth. First metatarsal segment about 1.2 times longer than the second and third together. First metatarsus with seven apical teeth, second with eight (in the second metatarsus the median four teeth each have a macrochaete).

Male genitalia (Figs 24, 25). Genital segment similar to that of *T. crypticus*, medioventral process in ventral aspect tongue-shaped, with a distinct median ridge on its dorsal side. Anal segment about 3 times longer than it is wide, distal third almost abruptly bent ventrad, caudal margin convexly rounded.

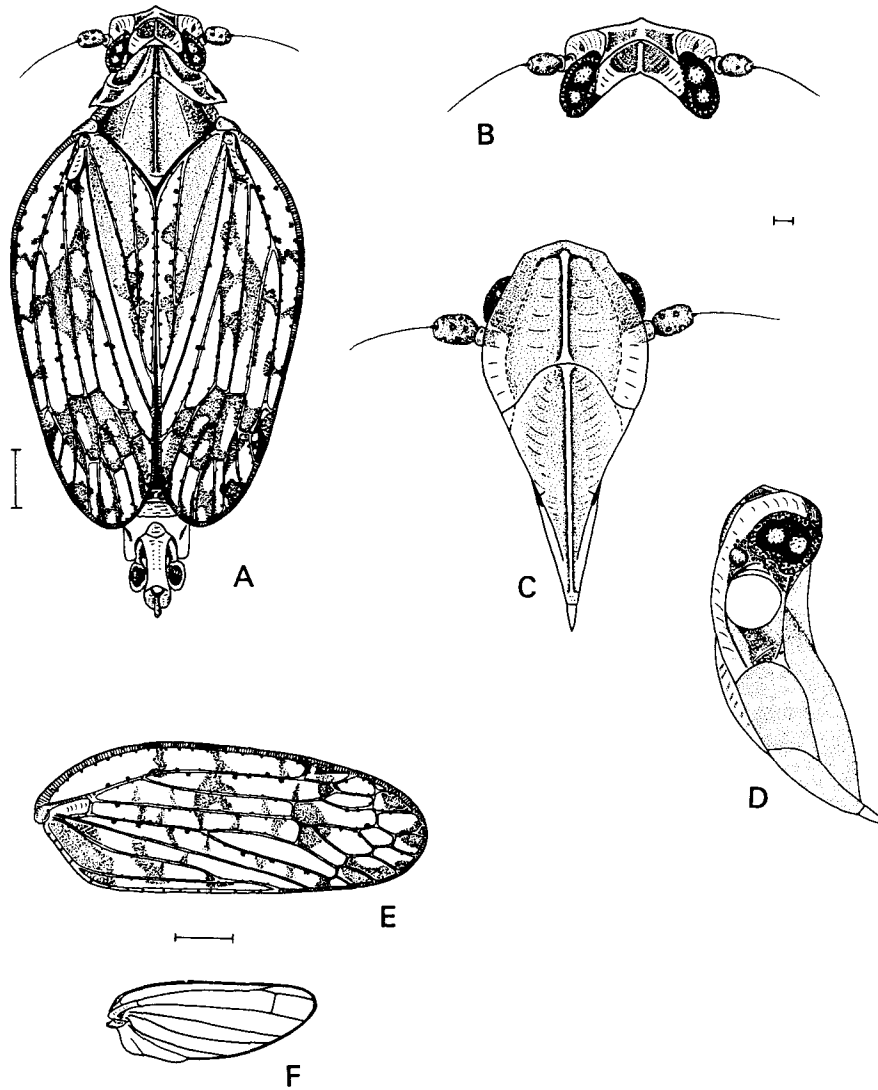


Figure 23. *Tachycixius retrusus* sp. nov. A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, left lateral aspect (all holotype male); E, tegmen; F, wing (all paratype male). Scale bar: A, E, F 0.5 mm, B-D 0.1 mm.

Compared with *T. crypticus*, distal dilated third of parameres less expanding dorsad, caudal margin convex, dorsal margin subtruncate. Basal part of aedeagus depressed, ventrally with a median longitudinal ridge and a socle-like projection near its base on the right side. Dorsal portion of shaft on each side produced into a strongly developed bulbous projection directed laterad. Shaft subapically on its right side with two slender movable spinose processes: dorsal one hook-shaped, in repose curved nearly basolaterad, ventral one basally almost straight, in repose with tip pointing ventrad; absolute length and degree of bending of the two spines individually variable. Shaft subapically on its left side with a small ear-shaped projection (Fig. 24I, arrow). Distal part of aedeagus

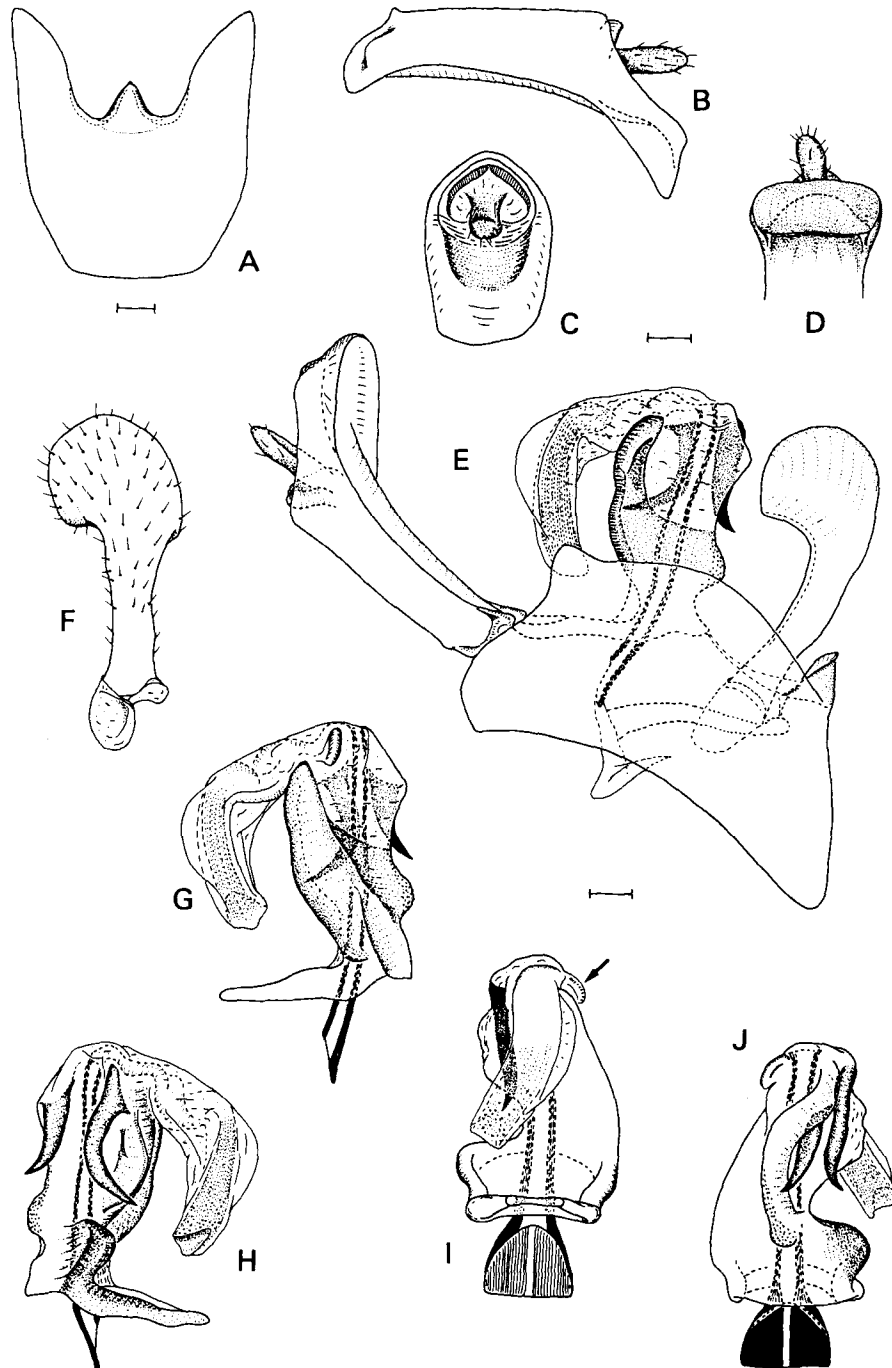


Figure 24. *Tachycixius retrusus* sp. nov., male genitalia, paratype. A, genital segment, ventral aspect; B, anal segment, lateral aspect; C, same, caudal aspect; D, same, ventral aspect; E, male genitalia *in situ*, left lateral aspect; F, left paramere, maximum view; G, aedeagus, left lateral aspect; H, same, right lateral aspect; I, same, dorsal aspect; J, same, ventral aspect. Scale bar: 0.1 mm.

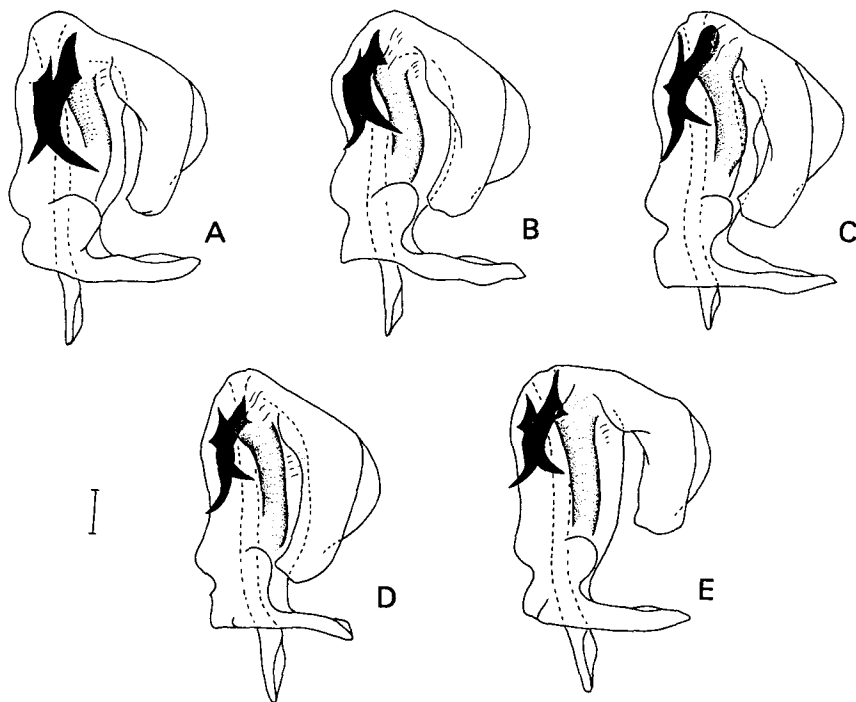


Figure 25. *Tachycixius retrusus* sp. nov., paratypes; A-E, aedeagus, right lateral aspect, intraspecific variation. Scale bar: 0.1 mm.

medially bent rectangularly, in repose reaching basal third of shaft, in distal half with a conspicuous membranous velum, without apical spine.

Female genitalia (Fig. 26). Seventh sternite subtriangular, with distal margin medially slightly expanded caudad; ovipositor ensiform, distinctly curved dorsad, slightly surpassing the length of the anal segment; anal segment laterally distinctly ridged; ninth tergite caudally truncate, wax-secreting field distinctly limited, margins smooth, shallowly concave, medioventral excavation shallow.

Etymology. The name of this species refers to its assumed secluded habitat.

Holotype. Male: Canary Islands, Tenerife, Anaga, Barranco de Ijuana, 2.iii.1986, A. Aguiar leg. (MSC).

Paratypes. Six males, same data as holotype except 20.v.1986, 11.vii.1986, 29.ix.1986, 25.xi.1986; one female, same data as holotype; seven females, same data as holotype except 20.v.1986, 11.vii.1986, 29.ix.1986, 25.xi.1986, A. Aguiar leg. (AH, MSC).

Additional material. Nymphs, same locality as holotype, 1 III, 1 IV, 3 V (♀), 28.xi.1985; 2 IV, 9 V (5 ♂, 4 ♀), 21.i.1986; 1 IV, 21.i.1986; 7 V (5 ♂, 2 ♀), 2.iii.1986; 1 V (♀), 21.iii.1986; 5 V (2 ♂, 3 ♀), 11.vii.1986; 3 V (1 ♂, 2 ♀), 29.ix.1986; 2 V (1 ♂, 1 ♀), 25.xi.1986, A. Aguiar leg. (MSC, AH).

Diagnosis. In general appearance similar to *T. crypticus* and *T. canariensis* (see below) but differing in its higher degree of troglomorphy (median ocellus absent, compound eyes smaller) and in characters of the male genitalia (e.g. aedeagus with subapical membranous lobe on left side of shaft more distinctly developed, both subapical spinose processes on right side of shaft relatively shorter).

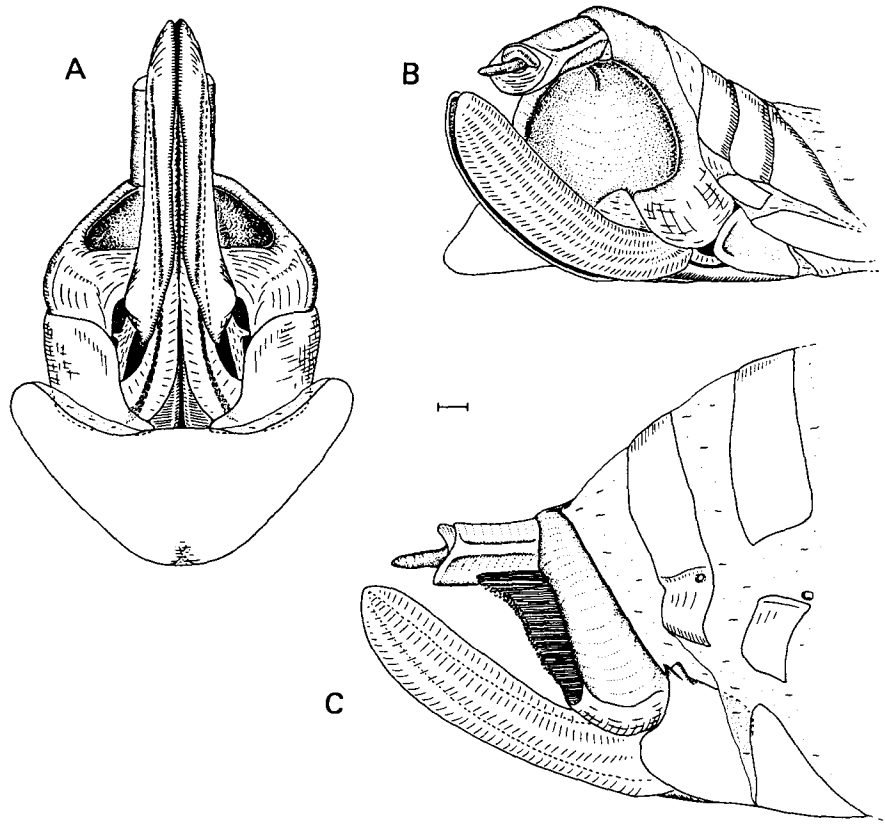


Figure 26. *Tachycixius retrusus* sp. nov., female genitalia, paratype. A, ventral aspect; B, latero-caudal aspect; C, right lateral aspect (wax filaments not removed).

Tachycixius retrusus differs from *T. canariensis* by the development of troglomorphic characters and in characteristics of the male genitalia, mainly by the absence of a subapical short spine on the left side of the aedeagus shaft.

Distribution and ecology. *Tachycixius retrusus* is known from its type locality only, Barranco de Ijuana, in the Anaga Mountains of Tenerife (Fig. 38). Like *T. crypticus* it has been collected in pitfall traps at a depth of up to 50 cm below the surface. It is unknown whether its natural habitat is the deeper soil strata or the mesocavernous rock system. Although *T. retrusus* displays a slightly stronger degree of troglomorphy than *T. crypticus* (slightly reduced eyes, reduced wings, presumably flightless), it cannot be classified with certainty as endogean, MSS-dwelling, or troglobitic.

Tachycixius canariensis Lindberg
(Figs 27, 28)

Lindberg H. 1954. *Soc. Sci. Fenn. Comm. Biol.* **14**: 159 (Fig. 34, p. 159)

Supplementary description of the holotype. Epigeal species. In general appearance similar to *T. crypticus* and *T. retrusus*, but lacking the troglomorphic characters of these species.

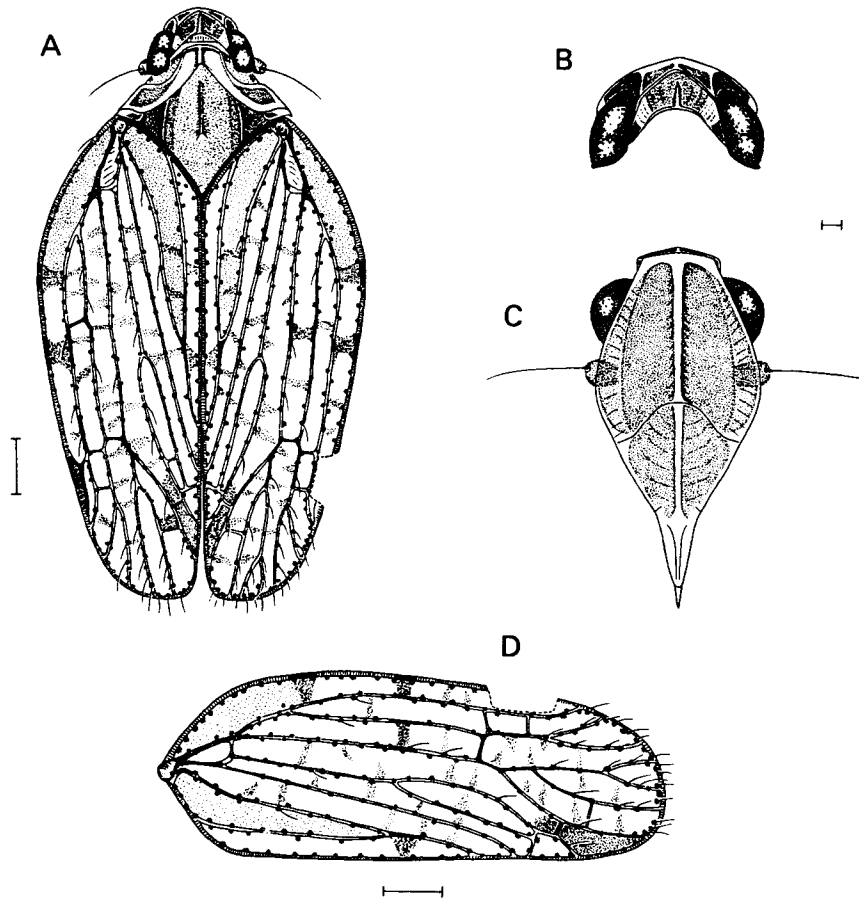


Figure 27. *Tachycixius canariensis* Lindberg, holotype. A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, tegmen. Scale bar: A, D 0.5 mm, B, C 0.1 mm.

Total length. Male 5.7 mm.

Colouration. Body generally chestnut-brown to testaceous with dark fuscous and yellow portions on head and thorax. Tegmina slightly opaque, venation yellow to light brown, with dark brown stretches in areas of indistinct brown transversal bands; numerous irregular transverse brown bars between the veins. Numerous long brown bristles centred in conspicuous dark brown callouses along veins. Wings hyaline, veins brown. Legs stramineous to brown.

Head (Fig. 27). Vertex short, about 2.2 times wider at its base than it is long in the midline; basal cell concave, areolets small, slightly concave, separated from frons by an obtuse transverse carina. Frons almost planate, slightly ascending to median carina, slightly wider than medially high, lateral carinae foliately ridged and directed laterad, median carina obtuse on frons, and obsolete on clypeus. Compound eyes and lateral ocelli well developed, three blemmata around each ocellus, median frontal ocellus reduced. Second antennal segment slightly longer than wide.

Thorax (Fig. 27A, D). Pronotum tricarinate, carinae ridged, lateral carinae diverging posterolaterad; pronotum in midline about half as long as the vertex,

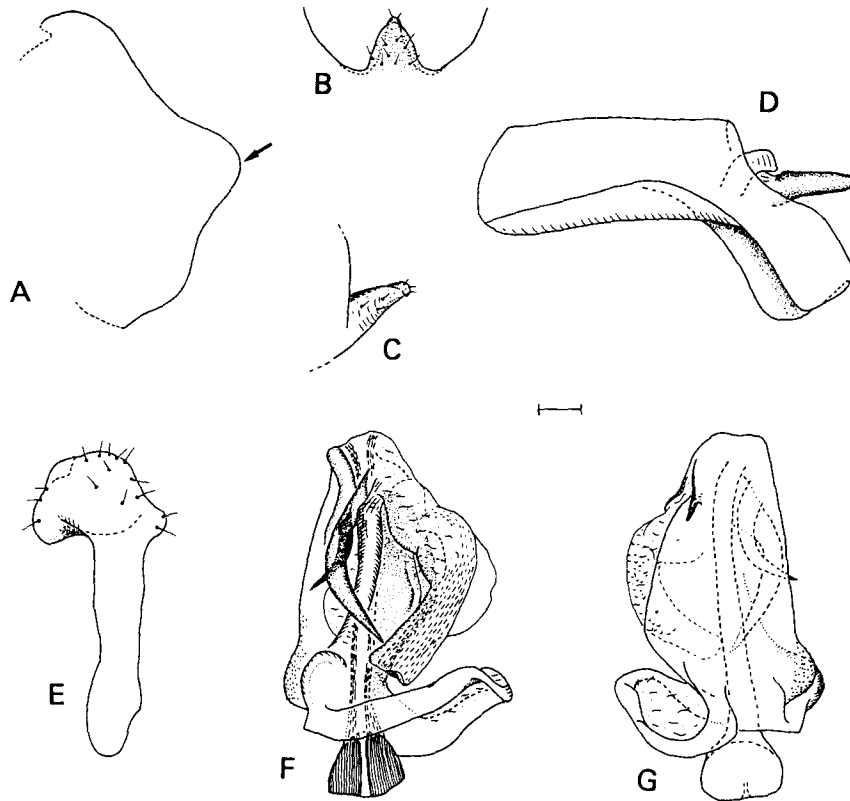


Figure 28. *Tachycixius canariensis* Lindberg, male genitalia, holotype. A, genital segment (fragment), left lateral aspect; B, medioventral process of genital segment, ventral aspect; C, same, left lateral aspect; D, anal segment, left lateral aspect; E, left paramere, maximum view; F, aedeagus, right lateral aspect; G, same, ventral aspect. Scale bar: 0.1 mm.

posterior margin acutely angulately excavate. Mesonotum distinctly tricarinate, with lateral portions shallowly tectiform, median portion planate, in midline about 8 times the length of the pronotum. Tegulae, tegmina and wings well developed. Tegmen with numerous conspicuous bristles along veins and on apical margin, pterostigma distinct, bearing bristles; apical part of tegmina short and narrowed.

Male genitalia (Fig. 28). Genital segment dorsolaterally with an obtuse projection (Fig. 28A, arrow), medioventral process tongue-shaped with a distinct median ridge on its dorsal side. Anal segment with distal portion bent ventrad, distal margin almost straight. Dilated distal part of parameres with irregular caudal margin. Basal part of aedeagus ventrally with a longitudinal ridge, and on its right side with a socle-like projection near base. Shaft dorsally on each side with an ear-shaped projection directed laterad and forming a groove to receive the reflected distal part of the aedeagus. Shaft subapically with three spinose processes: one on its left side, two on its right; left lateral spine short and stout, presumably rigid; right lateral spinose processes apparently movable, slender, dorsal one in repose (presumably) curved dorsad, ventral one in repose (presumably) directed ventrad or laterad. Distal part of aedeagus medially

almost bent rectangularly, in repose reaching basal third of shaft, without apical spine, but with a distinct membranous velum distad of bending.

Material examined. Holotype male: 'Tenerife, Agua Mansa, 15.v.47, Lindberg' (ZMU, No. 10938). Allotype female: 'Gran Canaria, Tamadabe, 30.iii.49, Lindberg' (ZMU, No. 10939).

Diagnosis and remarks. *Tachycixius canariensis* resembles *T. crypticus* and *T. retrusus* in habitus and general configuration of the male genitalia. It differs from these two species mainly in the presence of a distinct rigid subapical spine on the left side of the aedeagus shaft (instead of a membranous lobe). Its tegmina and wings are much less reduced, and the species is likely to be able to fly. Because of the extent of morphological congruence in apparently derived characters (e.g. the tendency to reduce the left subapical spinose process of the aedeagus) these three species are likely to be closely related.

The genitalia of the holotype, the only known male of the species, had been dissected and slide-mounted in caedax by Lindberg. For re-examination, the remaining parts of the genitalia (the genital segment is strongly damaged) were recovered from caedax (4 weeks in xylol, 1 day in 100% ethanol). However, they remain (artificially) compressed. They are now stored in a glass vial containing glycerine.

Distribution and ecology. On Tenerife, *T. canariensis* is known only from the type locality, Agua Mansa in the north of the island. Due to different proportions of the vertex, it is uncertain whether a single female from Gran Canaria assigned to *T. canariensis* as allotype by Lindberg (1954) is conspecific. The ecology of *T. canariensis* is unknown. Although Agua Mansa is located adjacent to the Pine zone, the *Pinar*, the possibility that the holotype is a specimen flown in from a different vegetation zone cannot be excluded.

Tachycixius lavatubus Remane & Hoch
(Fig. 29)

Remane R., Hoch H. 1988. *J. Nat. Hist.* **22:** 404 (figs 1–8, pp. 407, 408).

Diagnosis. In general appearance (Fig. 29A) and degree of troglomorphy *T. lavatubus* resembles the troglobitic *Cixius* species of La Palma and El Hierro, but differs considerably in features of the tegmina (bristles on apical margin between the veins) and the genital characters.

Total length. Male 3.2–4.7 mm. Female 3.7–4.7 mm (Remane & Hoch, 1988).

Male genitalia (Fig. 29B, C). In general configuration resembling those of *T. crypticus* and *T. retrusus*, but differing in the following details: caudal margin of anal segment produced into two distinct lateral lobes. Parameres with caudal margin of dilated distal third more distinctly triangular. Shaft of aedeagus subapically with three slender, movable spinose processes (*T. crypticus* and *T. retrusus* have two processes): one on its left, and two on its right side. Distal part of aedeagus mediodorsally with a distinct, bill-shaped tooth.

Female genitalia. Wax-secreting field of ninth tergite distinctly limited, shallowly concave, in contrast to *T. crypticus* and *T. retrusus* medially separated by a membranous area.

The type material is preserved at ULL.

Remarks. *Tachycixius lavatubus* differs externally from the group of species comprising *T. crypticus*, *T. retrusus* and *T. canariensis* by its high degree of

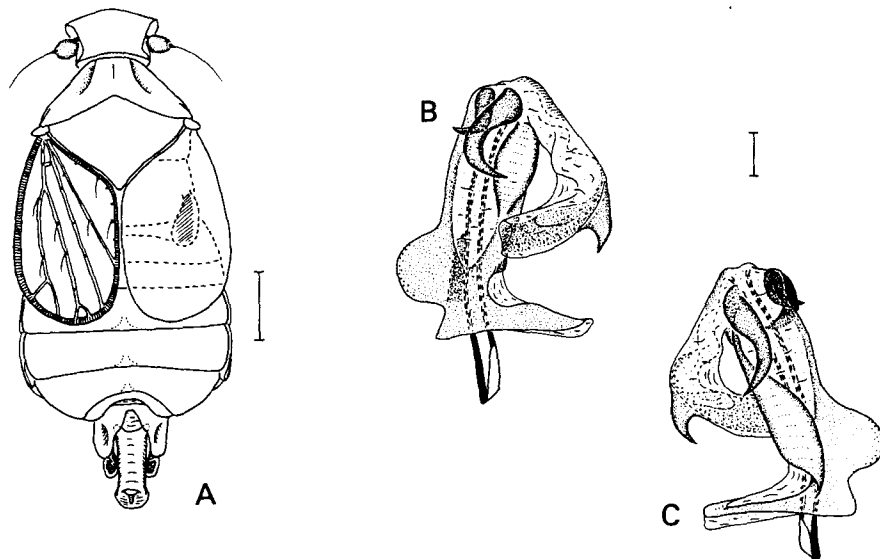


Figure 29. *Tachycixius lavatubus* Rémame & Hoch, male from Cueva Grande de Chío (non-type). A, habitus; B, aedeagus, right lateral aspect; C, same, left lateral aspect. Scale bar: A 0.5 mm, B, C 0.1 mm.

troglomorphy (complete loss of compound eyes and ocelli, strong reduction of tegmina and wings, reduction of bodily pigmentation) and in the configuration of male and female genitalia: aedeagus subapically on the left side with a well-developed movable spinose process, distal part of aedeagus devoid of a membranous velum but displaying a strong tooth instead, wax-secreting field of the female's ninth tergite medially separated by a membranous area.

The presence of a movable, left lateral spinose aedeagal process in *T. lavatubus* (which is also found in many epigeic *Tachycixius* species) can be interpreted as plesiomorphic in comparison with the corresponding situation in *T. canariensis*, *T. retrusus* and *T. crypticus*, which show varying degrees of reduction of this spine. Thus we postulate the presence of such a movable aedeagal spine in the hypothetical ancestral species of *T. lavatubus*. Consequently, neither *T. canariensis*, nor *T. crypticus* and *T. retrusus* can be regarded as potential ancestral species of *T. lavatubus*.

Distribution and ecology. This troglotic species was originally described from Cueva Grande de Chío lava tube from Western Tenerife. Populations of morphologically similar troglotic cixiids preliminarily assigned to *T. lavatubus* are known from caves in other parts of Tenerife (Fig. 38): Cueva de Felipe Reventón, supra Icod de Los Viños, in the North, and Cueva Labrada, near La Laguna, in the north-east (Rémame & Hoch, 1988).

Family Meenoplidae
Genus Meenoplus Fieber
***Meenoplus claustrophilus* sp. nov.**
 (Figs 30–32)

Description. Troglomorphies weakly defined except for eyes and pigmentation, in general appearance resembling an epigeic *Meenoplus* species.

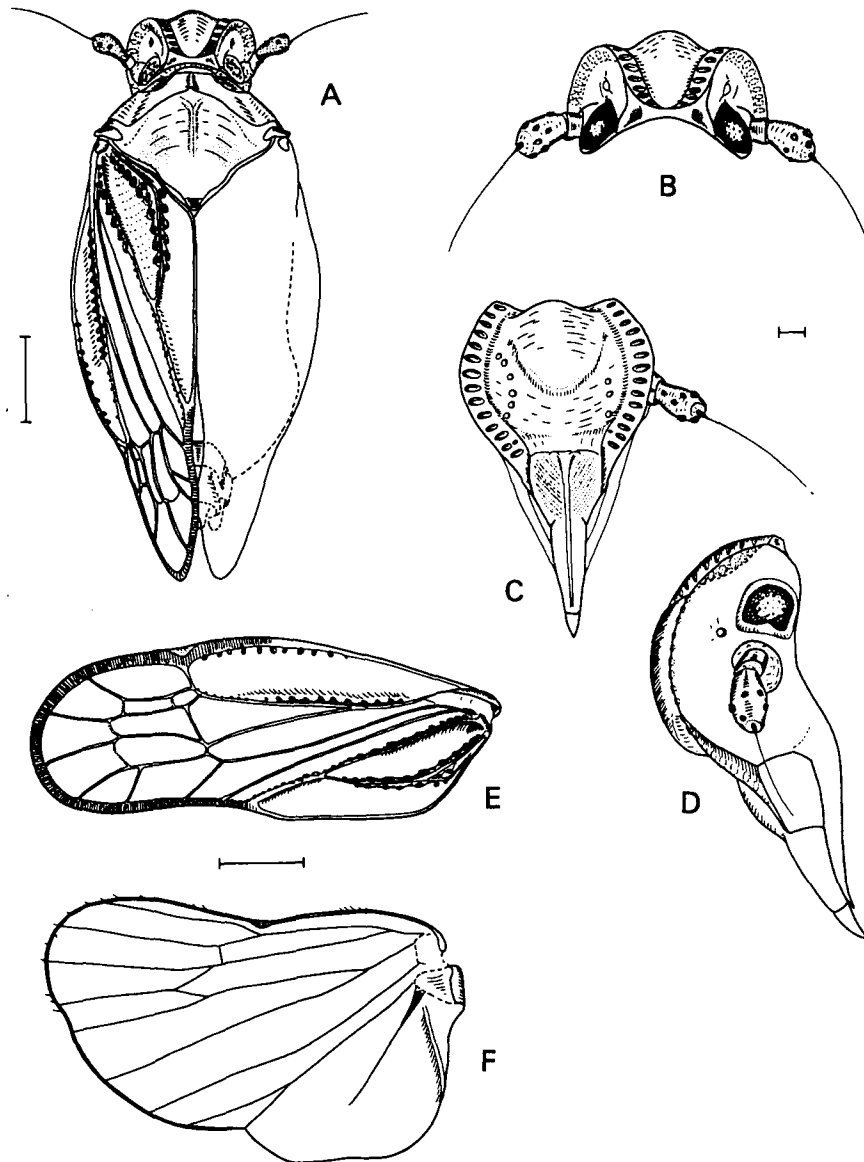


Figure 30. *Meenoplus claustrophilus* sp. nov. A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, same, left lateral aspect (all holotype male); E, tegmen; F, wing (all paratype male). Scale bar: A, E, F 0.5 mm, B-D 0.1 mm.

Total length. Male 3.1–3.3 mm ($n=3$). Female 3.3–3.8 mm ($n=5$).

Colouration. Body generally light stramineous with infuscate areas on frons, lateral portions of mesonotum, tegulae and on tegmen. Compound eyes red. Tegmina translucent, pale stramineous; venation as well as areas along veins and between sensory pits light brown. Wings hyaline, venation brown.

Head (Fig. 30). Vertex very short, about 9 times wider at its base than it is long in the midline, distinctly separated from frons by a ridged transverse carina. Frons strongly convex, anterior portion bulbous, about 1.2 times wider than it is

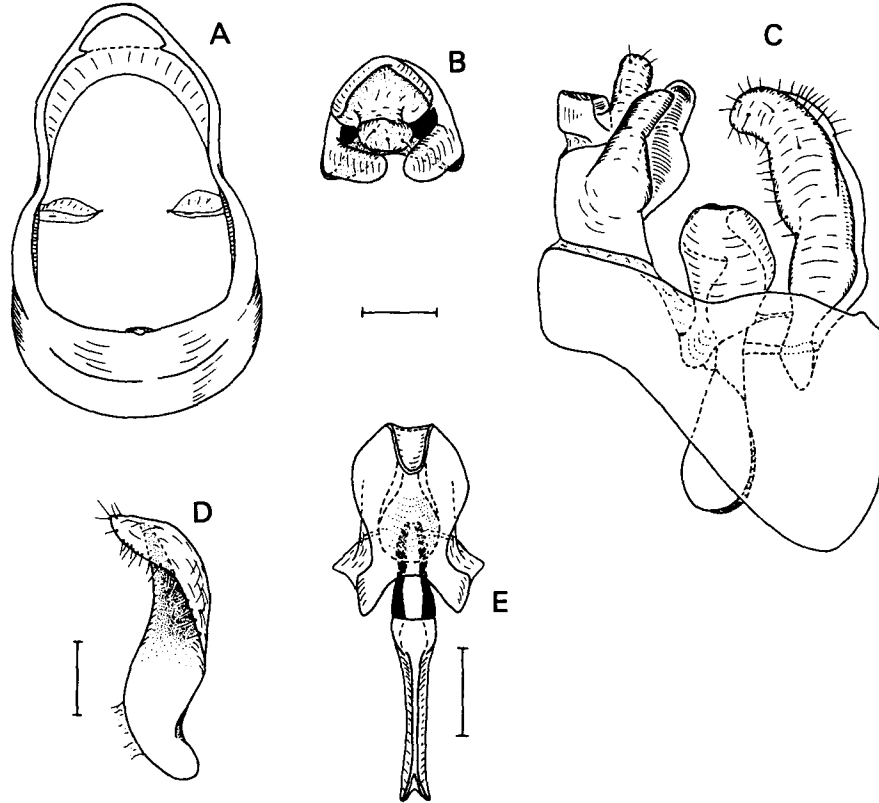


Figure 31. *Meenoplus claustrophilus* sp. nov., male genitalia, paratype. A, genital segment, caudal aspect; B, anal segment, caudal aspect; C, male genitalia *in situ*, left lateral aspect; D, left paramere, dorsal aspect; E, aedeagus, dorsal aspect. Scale bar: 0.1 mm.

medially high, in inferior part on each side with a short row of sensory pits irregular in number (three to six). Lateral carinae of frons foliately ridged and directed anterolaterad, anteriorly bearing a row of densely packed oval sensory pits; lateral lamelliformous carinae continuing onto postclypeus. Median facial carina absent on frons, indistinct on postclypeus and sharply ridged on anteclypeus. Compound eyes small, lateral ocelli rudimentary, median frontal ocellus absent. Second antennal segment cylindrical, about 1.6 times longer than it is wide.

Thorax (Fig. 30A, E, F). Pronotum feebly tricarinate, medially about twice the length of the vertex, posterior margin obtusely angulate. Mesonotum slightly vaulted, mediodorsally nearly planate, median carina rudimentary, lateral carinae absent, in midline about 10 times the length of the pronotum. Tegulae, tegmina and wings well developed; tegmina distally surpassing tip of abdomen, with rows of sensory pits along distal half of costal vein, along RSc and Y-shaped anal veins in clavus. Metatibiae laterally unarmed, with eight apical teeth. First metatarsal segment about as long as the second and third together. First metatarsus with seven apical teeth, second with six.

Male genitalia (Fig. 31). Genital segment ventrally about 3 times as long as it is dorsally. Anal segment distally produced into two ventrocaudal lobes directed

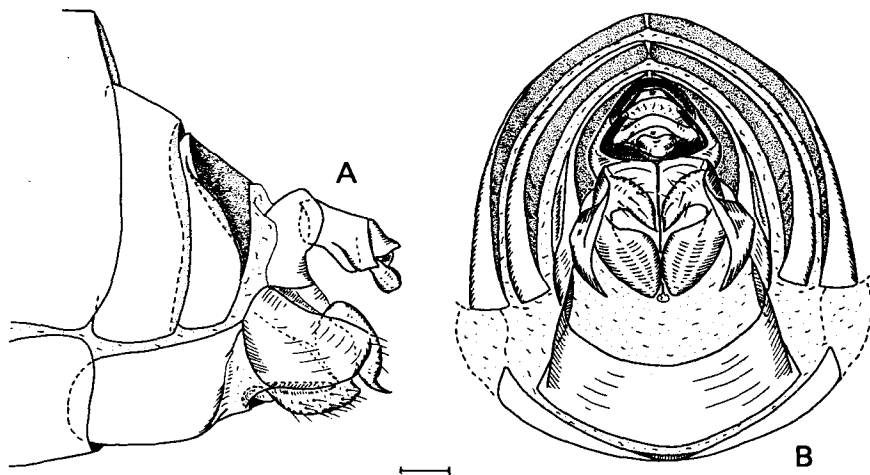


Figure 32. *Meenoplus claustrophilus* sp. nov., female paratype. A, left lateral aspect; B, caudal aspect. Scale bar: 0.1 mm.

mediad. Parameres slender, narrow, not dilated, in lateral aspect slightly curved dorsad, in ventral aspect inner margin concave, distally pointing mediad, apical margin rounded. Aedeagus tubular, short, stout, with phallotrema apical and dorsocaudally exposed, without any spinose processes.

Female genitalia (Fig. 32) [terminology after Woodward (1957)]. As in other Meenoplidae strongly reduced; laterocaudal margin of ventral valvifer produced into a rounded lobe; ventral valvula bearing a minute tip apically pointing mediocaudad.

Etymology. This species is named after the physical conditions of the type locality, Cueva del Ratón, which has some rather narrow passages.

Holotype. Male: Canary Islands, La Palma, S.E. Fuencaliente, Cueva del Ratón, 8.ii.1988, M. Asche, H. Hoch & J. L. Martín leg. (ULL).

Paratypes. One male, same data as holotype (AH); three females, same data as holotype (ULL, AH); two females, same data as holotype except 9.iv.1990 (AH); one male, same data as holotype except 19.iv.1990 (AH).

Additional material. Nymphs: 3 V, same data as holotype (AH); 2 V, same data as holotype except 12.vii.1986, J. L. Martín leg. (ULL); 1 V, same data as holotype except 17.viii.1986, J. L. Martín leg. (ULL); 1 IV, same data as holotype except 21.viii.1986, J. L. Martín leg. (ULL).

Diagnosis and remarks. This species displays a mild degree of troglomorphy, as indicated by its comparatively small compound eyes and weak pigmentation. Tegmina and wings, however, are well developed and individuals of the species have been observed flying. Its genital morphology in both males and females strongly resembles *M. cancavus* Remane & Hoch from El Hierro (see below). It is therefore conceivable that both species derive from a common stock of epigeic ancestral species. Remarkably, Meenoplidae are not known in the present-day epigeic fauna of the Canary Islands.

Distribution and ecology. *Meenoplus claustrophilus* is known from Cueva del Ratón, S.E. of Fuencaliente, La Palma (Fig. 38). Individuals were found exclusively in the deep cave zone, both nymphs and adults on sporadic roots of presumably

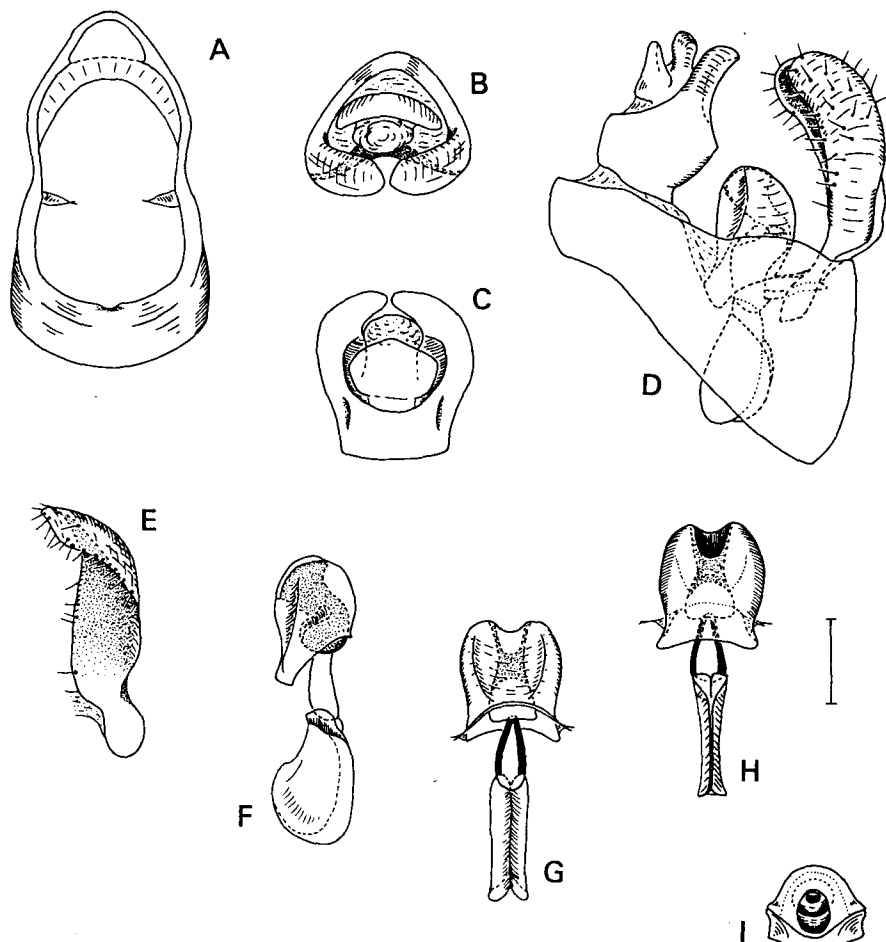


Figure 33. *Meenoplus concavus* Remane & Hoch, male genitalia, male from Cueva del Lajial (non-type). A, genital segment, caudal aspect; B, anal segment, caudal aspect; C, same, dorsal aspect; D, male genitalia *in situ*, left lateral aspect; E, left paramere, dorsal aspect; F, aedeagus, left lateral aspect; G, same, ventral aspect; H, same, dorsal aspect; I, same, caudal aspect (view on phallotrema) Scale bar: 0.1 mm.

Rumex lunaria and/or *Schizogyne sericea*, while adults have also been observed away from roots on cave walls. Despite its comparatively mild degree of troglomorphy, *M. claustrophilus* is assumed to be restricted to underground habitats and is thus regarded as troglotic. In Cueva del Ratón, *M. claustrophilus* occurs syntopically with *Cixius raticus*.

Meenoplus concavus Remane & Hoch
(Figs 33–34)

Remane R., Hoch H. 1988. *J. Nat. Hist.* **22**: 406 (figs 9–12, p. 409).

Description of male.

Total length. 1.9–2.1 mm ($n=2$).

Male genitalia (Fig. 33). In general configuration very similar to *M. claustrophilus*. Genital segment ventrally about 2.8 times long as it is dorsally.

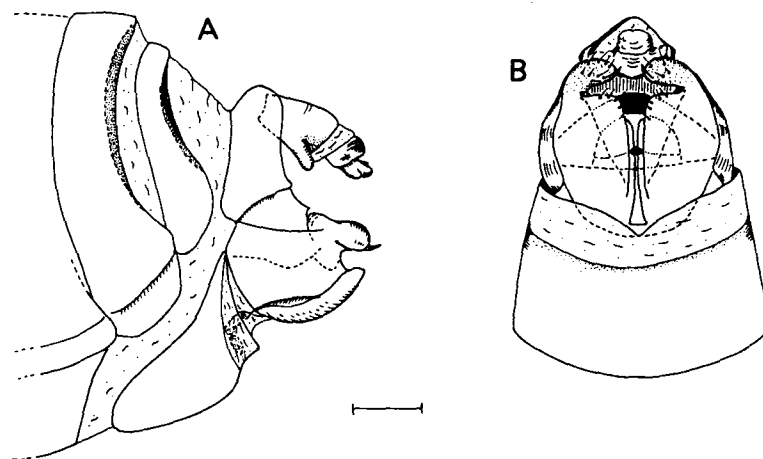


Figure 34. *Meenoplus cancavus* Remane & Hoch, female genitalia, female from Cueva del Lajjal (non-type). A, left lateral aspect; B, ventral aspect. Scale bar: 0.1 mm.

Anal segment in dorsal aspect rounded, distally slightly expanding, in middle line about 1.6 times longer than it is wide at the base, distally produced into two ventrocaudal lobes directed mediad. Parameres slender, narrow throughout, dorsal side slightly concave, distal half bent mediad, apically rounded. Aedeagus short, stout, in lateral aspect ovoid, in dorsal aspect about 1.16 times as long as it is wide, medioventrally slightly concave, phallotrema apical and dorsocaudally exposed, without any spinose processes.

Female genitalia (Fig. 34). In general configuration very similar to *M. claustrophilus*.

Material examined. Holotype female, Canary Islands: El Hierro, Cueva de Don Justo, 18.x.1984, J.L. Martín, GIET (ULL). Four males, seven females and 10 nymphs from Cueva del Lajjal, N. La Restinga, S.E. Montana de Julian: 4 ♂♂, 30.x.1988, 3.xi.1988, 28.iv.1990; 7 ♀♀, 16.ii.1988, 30.x.1988; nymphs: 5 V, 16.ii.1988; 3 V, 30.x.1988; 2 V, 3.xi.1988; M. Asche & H. Hoch leg. (ULL, AH).

Diagnosis and remarks. *Meenoplus cancavus* was previously known by a single female from Cueva de Don Justo, supra La Restinga, El Hierro. Apparently conspecific specimens were found in Cueva del Lajjal, north of La Restinga, south-east of Montana de Julian. *Meenoplus cancavus* displays a much higher degree of troglomorphy than *M. claustrophilus* (loss of compound eyes, tegmina reduced, wings vestigial). The male and female genitalia are very similar to those of *M. claustrophilus*, but differ in the shape of the aedeagus which is much shorter in *M. cancavus*.

Distribution and ecology. This troglotic species is known from two caves on El Hierro: Cueva de Don Justo and Cueva del Lajjal, north of La Restinga (Fig. 38). Both caves are presumably located in the same (prehistoric) lava flow (= El Lajjal), and have a similar ecology and surface vegetation: extended deep cave zone passages with ample roots, presumably of *Rumex lunaria* and/or *Schizogyne sericea*. Cueva del Lajjal is at an altitude of 250 m a.s.l., and the temperature measured in February, April and October/November was 23°C. Cueva de Don Justo is at an altitude of 150 m a.s.l., and the temperature in April was also 23°C.

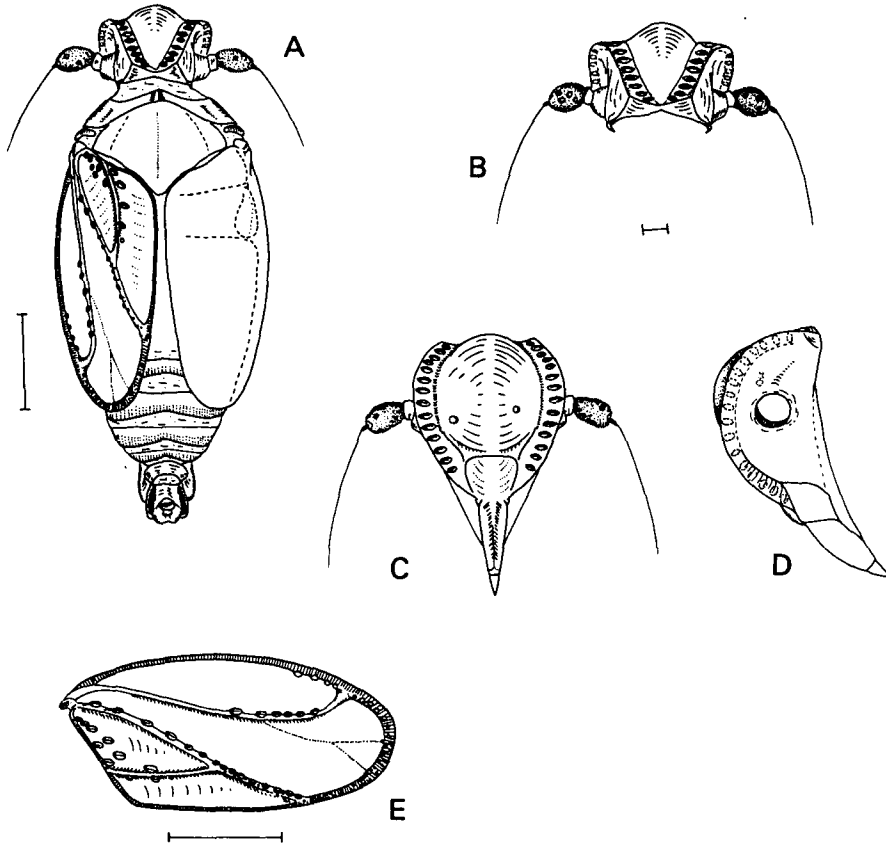


Figure 35. *Meenoplus charon* sp. nov., paratype male. A, habitus; B, head, dorsal aspect; C, same, ventral aspect; D, same, left lateral aspect; E, tegmen. Scale bar: A, E 0.5 mm, B-D 0.1 mm.

In both caves *M. cancavus* occurs syntopically with the troglotic Emesine *Collartida anophthalma*.

***Meenoplus charon* sp. nov.**

(Figs 35-37)

Description. Habitus, degree of troglomorphy, colouration, proportions and carination of head and thorax as well as venation of tegmina (Fig. 35) are as in *M. cancavus*.

Total length. Male 2.4-2.9 mm ($n=2$). Female 2.3-3.1 mm ($n=8$).

Male genitalia (Fig. 36). Very similar to *M. claustrophilus* and *M. cancavus*. Genital segment ventrally about 2.6 times as long as it is dorsally. Anal segment in dorsal aspect rounded, distally expanding, in midline about 1.8 times longer than it is wide at the base, distally produced into two ventrocaudal lobes directed mediad. Parameres as in *M. cancavus*. Aedeagus short, stout, in lateral aspect tube-shaped, in dorsal aspect about 1.56 times as long as it is wide, medioventrally slightly concave, phallotreme apical and dorsocaudally exposed, without any spinose processes.

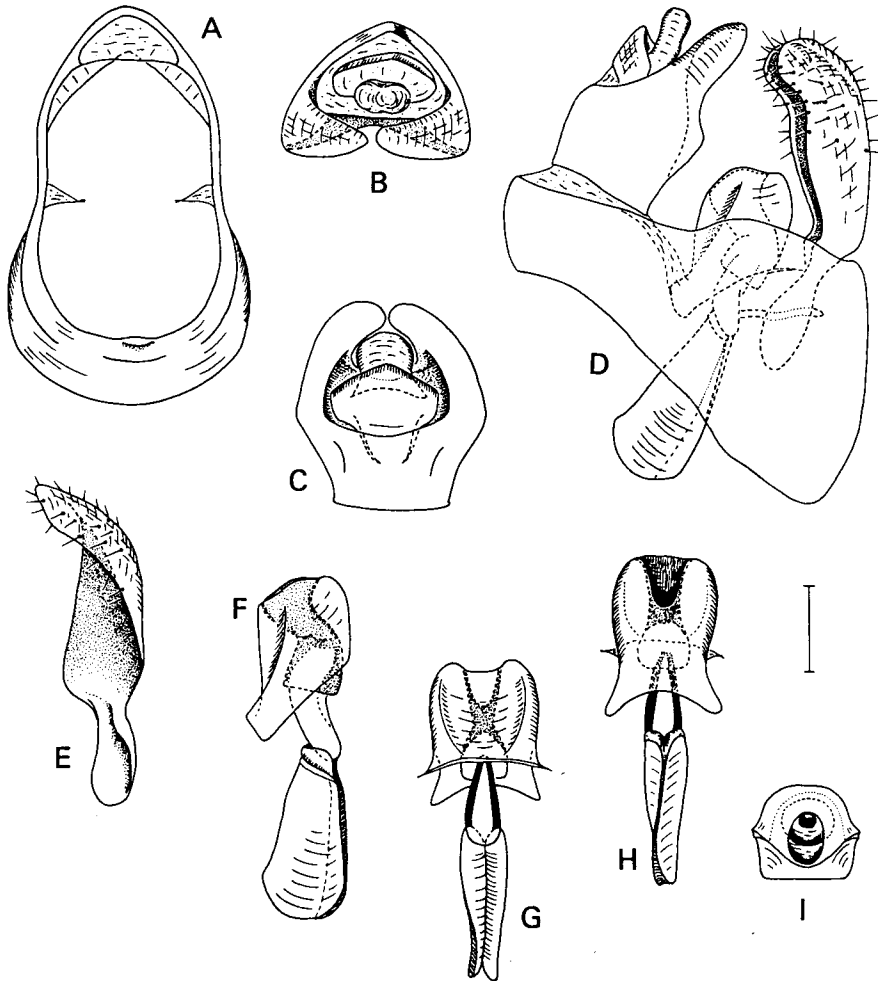


Figure 36. *Meenoplus charon* sp. nov., male genitalia, holotype. A, genital segment, caudal aspect; B, anal segment, caudal aspect; C, same, dorsal aspect; D, male genitalia *in situ*, left lateral aspect; E, left paramere, dorsal aspect; F, aedeagus, left lateral aspect; G, same, ventral aspect; H, same, dorsal aspect; I, same, caudal aspect (view on phallotrema). Scale bar: 0.1 mm.

Female genitalia (Fig. 37). As in *M. cancavus*.

Etymology. This species is named after *Charon*, a god of the Underworld in classical mythology.

Holotype. Male: Canary Islands, El Hierro, infra El Pinar (Taibique), road to La Restinga, Cueva de La Curva, 24.iv.1990, M. Asche & H. Hoch leg. (ULL).

Paratypes. One male, one female, same data as holotype; eight females, same data as holotype except 20.ii.1988, 21.ii.1988, 29.x.1988, 3.xi.1988; M. Asche & H. Hoch leg. (ULL, AH).

Additional material. Nymphs, same locality as holotype: 2 V, 20.ii.1988; 4 V, 21.ii.1988; 2 V, 30.iv.1990; M. Asche & H. Hoch leg. (AH).

Diagnosis and remarks. *Meenoplus charon* shows a similar degree of troglomorphy as *M. cancavus*, but can be distinguished from this species by its larger body size

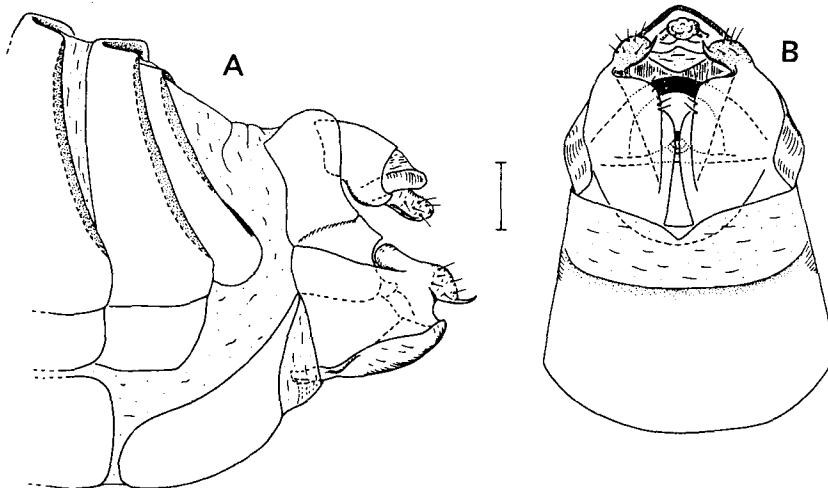


Figure 37. *Meenoplus charon* sp. nov., female genitalia, paratype. A, left lateral; B, ventral aspect. Scale bar: 0.1 mm.

(in spite of its occurrence at a higher altitude) and especially in the shape of its male genitalia: the aedeagus is more elongate and in lateral aspect apically almost truncate, not evenly rounded as in *M. cancavus*; in lateral view the dorsal margin of the aedeagus is straight, not curved as in *M. cancavus*. The high general morphological conformity in external and genital characters of *M. charon* and *M. cancavus* is difficult to judge: it is possible that these two species evolved from a single ancestral epigeic species which became adapted to subterranean environments and subsequently diverged. It is equally conceivable that the two species are the result of parallel evolution, i.e. they may have derived from separate, although morphologically similar epigeic species.

Distribution and ecology. *Meenoplus charon* is known from Cueva de La Curva, infra El Pinar (Taibique), El Hierro (Fig. 38), which is in a different lava flow than Cueva de Don Justo and Cueva del Lajial. Specimens were collected mainly in the upper passage of the lava tube, preferably on washed-in germinating seeds spread over gravel (for ecological conditions of the cave see *Distribution and ecology* of *C. ariadne* which occurs syntopically with *M. charon*). Because of its high degree of troglomorphy, *M. charon* is presumably restricted to underground habitats and regarded as troglobitic.

DISCUSSION

On the Canary Islands the cavernicolous Fulgoroidea show the following distribution pattern: four troglobitic species of Cixiidae from La Palma (*Cixius palmeros*, *C. tacandus*, *C. ratonicus*, *C. pinarcoladus*), two troglobitic species from El Hierro (*Cixius ariadne*, *C. nycticolus*) as well as one troglobitic (*Tachycixius lavatubus*) and two (ecologically yet unclassified) species (*T. crypticus*, *T. retrusus*) from Tenerife. In the Meenoplidae there is one troglobitic species known from La Palma (*Meenoplus claustrophilus*) and two troglobitic species from El Hierro (*M. cancavus*, *M. charon*).

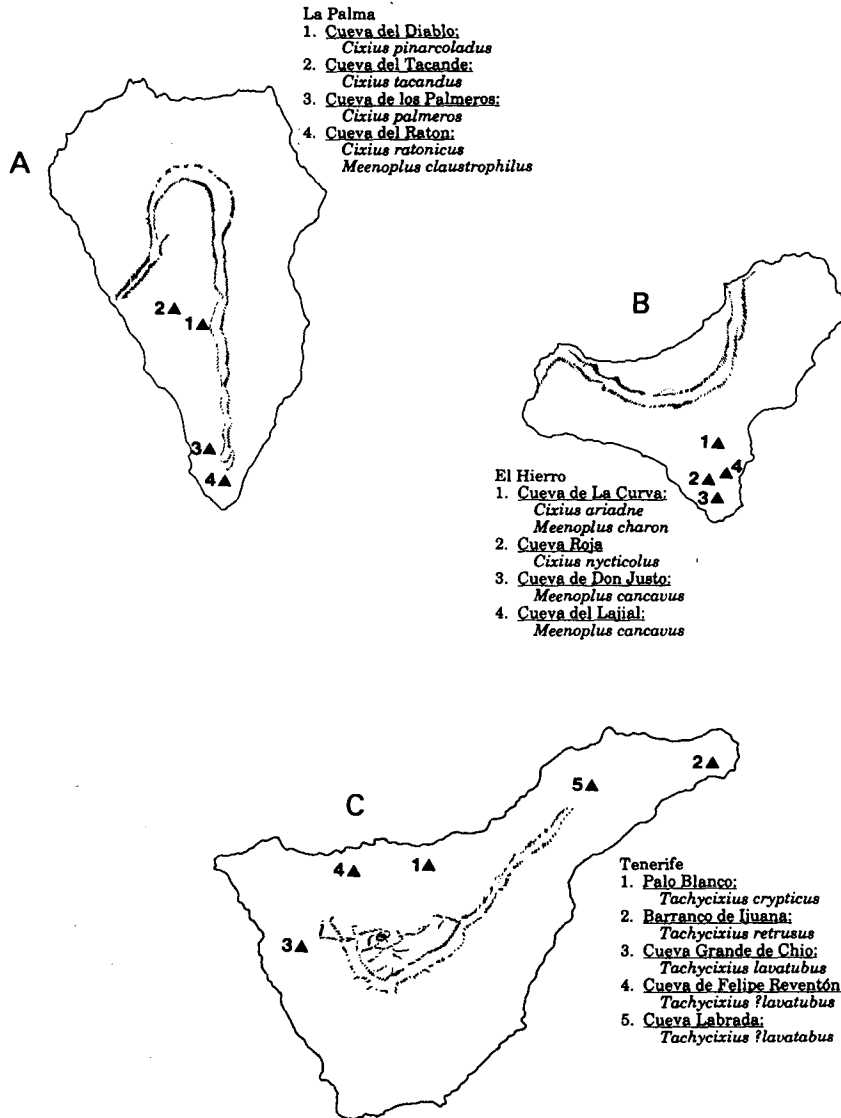


Figure 38. Distribution of cavernicolous Fulgoroidea in the Canary Islands.

It seems remarkable that La Palma, El Hierro and Tenerife (Table 1) contain more species of the families Cixiidae and Meenoplidae in subterranean habitats (Cixiidae: nine spp., Meenoplidae: three spp.) than in surface habitats (Cixiidae: five spp.). Out of the five epigean cixiid species, only two (*Cixius palmensis* on La Palma, and *Tachycixius canariensis* on Tenerife) belong to the same tribe as the cavernicolous species, the Cixiini, while the remaining three species belong to the genus *Hyalesthes* Signoret in the tribe Oliarini (see Hoch & Remane, 1985).

For the troglotic Cixiidae of El Hierro and for all cavernicolous Meenoplidae, potential epigean ancestral species are entirely missing in the

present-day fauna of the corresponding island. Since obligate cavernicolous species are restricted to their underground habitat, dispersal on the surface and between islands can be excluded. Thus we can assume that the cave species evolved autochthonously, i.e. on the same island where they occur today. The higher diversity of cavernicolous Cixiidae and Meenoplidae compared to their extant epigeal relatives indicates that the epigeal fauna in these families must have been richer in the past. Reasons for the apparent impoverishment observed today may either lie in faunal succession phenomena characteristic of oceanic islands (Ashmole *et al.*, 1992) or in climatic changes.

Those cave species without any close relatives living in surface habitats on the same island (or elsewhere) are now relicts, i.e. "persistent remnants of formerly widespread faunas...existing in certain isolated areas or habitats" (Lincoln, Boxshall & Clark, 1982). Whether their present relict status, however, is the consequence of the disappearance of epigeal ancestral species prior or subsequent to the evolution of the cavernicolous species, i.e. whether cave adaptation occurred allopatrically (isolation hypothesis: Vandel, 1964; Barr, 1968, 1973) or parapatrically (adaptive shift hypothesis: Howarth, 1981a) cannot be deduced from the absence of close epigeal relatives alone.

It is remarkable that in the Canary Islands, obligate cavernicolous Fulgoroidea are today found only on the geologically comparatively young islands in the archipelago with historic or recent volcanism: La Palma (approximately 1.6 Myr), El Hierro (approximately 0.8 Myr), and Tenerife (maximum of 15 Myr) (Mitchell-Thomé, 1985). In the older and volcanically inactive islands, such as Gran Canaria and La Gomera (where despite intensive faunistic surveys of underground environments by members of the GIET no cavernicolous Homoptera have been found) progressive soil formation and erosion have presumably filled in the mesocaverns and dissected the cave passages causing much of the primary habitat of rhizophagous troglobites to disappear. Similar phenomena have been observed in the Hawaiian Islands (Howarth, 1981b).

TABLE 1. Geographic distribution of epigeal and cavernicolous Cixiidae and Meenoplidae of La Palma, El Hierro, and Tenerife

	La Palma		El Hierro		Tenerife	
	Cixiidae	Meenoplidae	Cixiidae	Meenoplidae	Cixiidae	Meenoplidae
Epigeal	<i>Hyalesthes angustulus</i> <i>Cixius palmensis</i>		<i>Hyalesthes angustulus</i>		<i>Hyalesthes angustulus</i> <i>H. flavipennis</i> <i>H. teno</i> <i>Tachycixius canariensis</i>	
Troglobitic	<i>Cixius palmeros</i> <i>C. pinarcoladus</i> <i>C. raticus</i> <i>C. tacandus</i>	<i>Meenoplus claustrorophilus</i>	<i>Cixius ariadne</i> <i>C. nycticolus</i>	<i>Meenoplus canavus</i> <i>M. charon</i>	<i>Tachycixius crypticus</i> (?) <i>T. retrusus</i> (?) <i>T. lavatubus</i>	

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