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First record of a cavernicolous Kinnaridae from the Old World (Hemiptera, Auchenorrhyncha, Fulgoromorpha, Kinnaridae, Adolendini) provides testimony of an ancient fauna

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Abstract

A new obligately cavernicolous species in the planthopper family Kinnaridae is described from Spain. This is the first record of a cavernicolous kinnarid from the Old World, and the first record of a troglobitic fulgoromorphan hemipteran from mainland Spain, and also the 7th cavernicolous kinnarid species worldwide. Epigean Kinnaridae are not known from the present-day fauna of the Iberian Peninsula nor from Western Europe at large. The new species is regarded as a relict from an ancient fauna which is now extinct. The new cavernicolous species could not be assigned to any of the existing genera, thus a new genus is established. Molecular data (COI barcode sequence) for the new species are presented. For the first time, a detailed description of the nymphal morphology of a kinnarid is provided. Information on its ecology, behaviour, distribution and conservation status is given, and biogeographic implications are discussed.

Keywords

Caves, conservation, Iberian Peninsula, morphology, taxonomy, troglobite, troglomorphy

Introduction

During several years of biospeleological research in the cave ecosystems of the Valencian Community (Spain), the former team of biologists from the Museu Valencià d'Historia Natural (Torres Sala Foundation), collected several specimens of a highly troglomorphic species of the planthopper (Fulgoromorpha) taxon Kinnaridae, previously unknown in the Iberian Peninsula. Its discovery received considerable attention in the local media, as the tiny creature is a) morphologically stunning with glassy wings characterized by a shining blue rim in males, evoking images of a "fairy", and b) its existence in the dark subterranean spaces of the last remains of Mediterranean forests in Valencia. Thus, this remarkable taxon was named the "fairy of the forests" (see below, etymology). At the moment, the new species has been studied from two caves, and has been observed in seven other caves, all in the most eastern reliefs of the Iberian Mountain Range in the east of the Iberian Peninsula. The species is characterized by several troglomorphies, e.g., absence of compound eyes and ocelli, very pale body pigmentation and reduced tegmina and wings, and is accordingly assumed to be obligately cavernicolous (troglobitic). This species represents the first record of a troglobitic planthopper species in mainland Spain, the first record of the taxon Kinnaridae in mainland Spain, the 7th cavernicolous kinnarid species worldwide, and the 3rd record of an obligately cavernicolous planthopper in the Mediterranean.

With currently 115 species in 24 genera (Bourgoin 2019), Kinnaridae is one of the smallest families of the Fulgoromorpha. Kinnarids are distributed throughout the world (Bourgoin 2019), predominantly in the tropics and subtropics (Wilson 2010). From the Palearctic region, several genera are documented, with species known from Iran and Tadzhikistan (Emeljanov 1984), Afghanistan (Dlabola 1957), India (Himalaya, Simla) (Distant 1916), the United Arabian Emirates (Wilson 2010) and from the Canary Islands (Remane 1985).

The majority of Kinnaridae species are epigean, with well-developed compound eyes, vivid body coloration, fully developed tegmina and wings, enabling flight. Several lineages, however, are known to have colonized caves in various regions of the New World: the Caribbean (Jamaica: Fennah 1980), Central America (Mexico: Fennah 1973) and South America (Brazil: Hoch and Ferreira 2013, 2016, Xing et al. 2013) and accordingly, display varying degrees of troglomorphies, such as the reduction of eyes, wings and body pigmentation (see information in Hoch and Ferreira 2016).

Knowledge of the biology and ecology of Kinnaridae in general is scarce. Most species are apparently associated with dicots (Asteridae and Dillenidae: Fennah 1948), but there are also records from ferns, gymnosperms (Ephedraceae) and monocots (Agavaceae) (see information in Ai-Ping 2001). Adults of epigean species feed on the exposed parts of plants, while nymphs are subterranean, feeding on roots (Fennah 1948, 1980).

The current state of Kinnaridae classification has been summarized by Hoch and Ferreira (2016). No hypothesis to explain phylogenetic relationships within Kinnaridae has yet been provided. The characters on which the current tribal classification is based are of important diagnostic value; they have not been evaluated as potential synapomorphies yet. This also applies to the established genera, rendering the accommodation of the new species into any of the supraspecific taxa problematic. According to the key given by Emeljanov (2006) the new cavernicolous kinnarid from Spain can be classified as a member of the subfamily Prosotropinae Fennah, 1945, and – with some *caveat* – of the tribe Adolendini (see Discussion: suprageneric classification). In characters of the male genitalia, it does not share similarities with any species of the known kinnarid genera (in or outside the Adolendini) which could be interpreted as synapomorphies. Thus, a new genus is established to accommodate this new species described below. We also provide a description of the 5th instar nymph as the nymphal morphology of Kinnaridae in general is largely unknown.

Material and methods

Collecting, preservation, permanent storage

The specimens were discovered by visual search, collected by hand, and transferred into vials containing 70% and 96% ethanol. For permanent storage, after dissection and examination, genitalia were transferred to polyethylene vials, and individually associated with the specimen vial.

Morphological examination techniques, visualization

Measurements and examinations of external body features were made from the specimen in ethanol. To prepare male genitalia for dissection, the genital capsule was removed from the specimen, macerated for 24 h in 10% KOH at room temperature, washed in water, transferred to glycerine for storage or to glycerine-jelly for drawings. Examinations and drawings were made using a Leitz stereomicroscope with a *camera lucida* attachment.

Scanning electron microscopy

Specimens preserved in 96% Ethanol were critical point dried with a Leica EM CPD 300, and gold coated for 2, and 4 minutes, respectively. Morphological investigations were conducted with a Zeiss EVO LS 10 electron microscope.

Molecular data

DNA was purified individually from two whole nymphs with a Qiagen Blood & Tissue kit using the manufacturer's protocol. Polymerase chain reaction (PCR) was used to amplify a mitochondrial gene fragment, a 710 bp fragment of the Cytochrome Oxidase subunit I gene (COI) using primers LCO1490 and HCO2198 (Folmer et al. 1994), the so-called DNA Barcoding fragment. PCR was performed in 25 μ l volumes containing 1× Taq buffer, 1.5 mM MgCl2, 200 μ M each dNTP, 1 U Taq polymerase, ca. 50–100 ng DNA and ddH2O. After an initial denaturation step of 3 min at 94 °C, cycling conditions were 35 cycles at 94 °C for 35 s, 45 °C (COI) for 60 s, and 72 °C for 1 min, with a final elongation step of 5 min at 72 °C. The same primers were used in PCR and sequencing. PCR products were sent to Macrogen Europe for purification and cycle sequencing of both strands. The sequences were processed and corrected using CodonCode Aligner v. 5.1.5 (CodonCode Corporation), both nymphs had identical sequences (sharing a single haplotype). The haplotype sequence has been deposited in GenBank, access number MW323405.

Results

Taxonomy

Kinnaridae Muir, 1925: 158 Prosotropinae Fennah, 1945: 449 Adolendini Emeljanov, 1984: 470 (51)

Valenciolenda Hoch & Sendra, gen. nov. http://zoobank.org/87FFCB90-92D3-4CED-AAA2-DEDDD769C90E

Type species. *Valenciolenda fadaforesta* sp. nov. (type locality: Spain, València, Murciélagos cave).

Diagnosis. Small kinnarid (ca. 3–4 mm body length), strongly troglomorphic: compound eyes and ocelli absent, tegmina reduced in length but surpassing lateral body margins, wings vestigial, body whitish, pigmentation largely reduced (Fig. 1a). *Valenciolenda* gen. nov. can be distinguished from all other genera of the Kinnaridae by the unique combination of the following characters: narrow and short vertex; short and wide tegmina, in life held nearly horizontally over the body and, in dorsal view, forming a near circle; male genitalia with genital segment in caudal aspect longish ovate, not constricted; anal segment short, ventrocaudally with two arm-like processes, genital styles slender at base, apically strongly enlarged, medially concave; aedeagus tubular stout, distally widening, ventrocaudal margin with a short, acute tip.

Description. *Head* (Fig. 2). Vertex short, with a very obtuse median carina, area of vertex slightly tilted against area of frons, slightly wider posteriorly than anteriorly, anterior margin slightly concave or nearly straight, posterior margin shallowly concave. Frons narrow, ca. $1.45 \times \text{longer}$ than maximally wide (widest between level of antennae and frontoclypeal suture); ca. $2.1 \times \text{longer}$ than post- and anteclypeus combined; surface medially smooth, devoid of a median carina; lateral margins distinctly ridged and directed laterally. Frontoclypeal suture shallowly arched, in a furrow between frons and postclypeus. Post- and anteclypeus with a distinct median carina, carina gradually



Figure 1. *Valenciolenda fadaforesta* sp. nov., habitus, dorsal view **a** adult male, dorsal view **b** nymph (IV. instar) from 'Murciélagos' cave (Vilamarxant, València) (photos by: Sergio Montagud Alario) **c** morphological analogy in the troglobitic *Solonaima baylissa* Hoch & Howarth, 1989 (Cixiidae) from Australia: habitus, adult male, dorsal view. Body length 4.5 mm (photo by H. Reimer, Marburg, used with permission).

vanishing towards frontoclypeal suture. Rostrum elongate; in repose well surpassing caudal margin of hind coxae; third joint shorter than second. Compound eyes and ocelli absent. Antennae with short scape, subcylindrical; pedicel subcylindrical, ca. $1.8 \times as$ long as wide, with distinct sensory plate organs; sensory plate organs of the "flattened star-shaped plate" as reported for Kinnaridae (partim) by Bourgoin and Deiss (1994); arista ca. $3.5 \times as$ long as pedicel.

Thorax. Pronotum tricarinate, ca. $2.3 \times$ wider than head at level below antennae, short, ca. $5 \times$ wider than medially long, posterior margin shallowly concave; carinae distinct, median carina reaching, but not surpassing anterior margin of pronotum; lateral carinae very shallowly S-shaped, joining hind margin laterally; mesonotum distinctly tricarinate, slightly wider than medially long; tegulae vestigial. Hind tibiae laterally unarmed, distally with 6–7 slender, terete spines, indistinctly grouped (3+4), and forming a shallow arc. First metatarsal joint with 4–5, 2nd metatarsal joint with 3–5 sturdy denticles (bilaterally and individually variable). Pretarsal claws and arolia small, inconspicuous. 2nd and 3rd metatarsal joints together slightly shorter than 1st metatarsal joint. Tegmina (Fig. 3) in males short and wide, ca. 1.6 × longer than wide, with

terminal margin obliquely transversely truncate; in life held nearly flat over the body and forming a near circle, in the female narrower: ca. 2 × longer than wide, laterally considerably exceeding the lateral margins of thorax and abdomen. Costal vein strong, in life covered with conspicuous filamentous waxy exudations (so far only observed in males). Venation in proximal part as in epigean Kinnaridae with a large and wide subcostal cell, clavus cixioid (*sensu* Emeljanov 1984), i.e., common claval vein (Pcu and A1) reaching hind margin of clavus (vein A2); basal cell of forewing open, i.e., not closed by anastomosis of M and CuA, no arculus developed; tegmen distally of nodal line distinctly reduced, with 6–7 marginal cells (Fig. 3: vein terminology according to Bourgoin et al. 2015). Hindwings vestigial, ca. 1/6 the total length of tegmen; venation strongly reduced.

Male genitalia (Figs 4, 5). Genital segment, anal segment, genital styles and aedeagus bilaterally symmetrical. Genital segment in caudal aspect longish ovate, not constricted medially, anal segment short, ventrocaudally with two arm-like processes, and ventrobasally with a median blunt process; genital styles slender at base, apically strongly enlarged, medially concave, aedeagus tubular, stout, distally widening.

Females (Fig. 6). Females with abdominal tergites VI, VII, and VIII bearing wax fields. Female genitalia as in other Kinnaridae of the non-piercing type; sternite VII in ventral view trapezoidal, with lateral margins diverging caudally, caudal margin straight; gonocoxae VIII bilobate; anal segment tubular.

Etymology. The genus name is a combination of Valencia, the capital city of the Valencian Community, an autonomous region of Spain in the east of the Iberian Peninsula where the type locality is located, and the tribe of Kinnaridae, Adolendini, to which the type species is assigned. The gender is feminine.

Valenciolenda fadaforesta Hoch & Sendra, sp. nov.

http://zoobank.org/571CB15C-1A95-40F9-AB0C-FD438C342218 Figs 1–9, 11d

Diagnosis. Habitus (Fig. 1a). Strongly troglomorphic species, predominantly whitish colouration, compound eyes and ocelli absent, body dorsoventrally compressed, tegmina short and wide, in repose very shallowly tectiform, almost flat, caudally reaching or slightly surpassing tip of abdomen, laterally surpassing external body margin with about half of their width, together creating a nearly circular shape; with a light blue wax fringe – which in life is quite eye-catching – accompanying costal vein; hind wings vestigial.

Description. *Body length.* Measurements refer to distance between anterior margin of head to tip of abdomen (= caudal margin of genital styles in males, and tip of anal segment in the female).

Males. 2.8 (in a specimen with contracted abdominal segments) -3.8 mm (in the holotype which displays fully extended abdominal segments) (n = 4). Females. 4.1 mm (n = 1).

Colouration. Head, thorax and abdominal segments largely unpigmented, whitish except lateral carinae of frons and rostrum, legs and genitalia in both sexes (genital



Figure 2. *Valenciolenda fadaforesta* sp. nov. **a** head and thorax, dorsal view **b** head, ventral view **c** same, left lateral view. Scale bar: 0.5 mm.

segment, genital styles, gonocoxae VIII) which are light yellowish. Distal spines on hind tibiae, 1st and 2nd metatarsal joints sordid brown. Tegmina translucent, unpigmented, veins whitish.

Configuration, shape and proportions of head and thorax as described for the genus.

Male genitalia. Genital segment bilaterally symmetrical, in lateral aspect short, narrow in dorsal half, gradually widening caudoventrally; ventrally ca. 3.2 × longer than dorsally. Anterior margin of genital segment smooth, devoid of median apodemes. Genital segment in caudal aspect highly ovate, lateral margins in ventral portion more or less parallel, slightly diverging in dorsal third, dorsally gently arched medially, without conspicuous transverse bridge; caudal margin of genital segment ventrally smooth. Anal segment bilaterally symmetrical, short, stout, caudally on each side with a short, apically rounded, arm-like process directed laterocaudally. Paraproct short, stout, mushroom-shaped; epiproct broadly disc-shaped, laterally wider than paraproct, caudally not exceeding paraproct. Genital styles bilaterally symmetrical, slender at base, apically considerably enlarged; enlarged portion medially deeply concave, bearing 3



0.5 mm

Figure 3. *Valenciolenda fadaforesta* sp. nov. Right tegmen, male. Scale bar: 0.5 mm. Abbreviations: ScP+R+M+Cu, subcosta posterior + radius + media + cubitus; scc, subcostal cell; ScP+RA, subcosta posterior + radius anterior; RP, radius posterior; PCu, cubitus posterior; A1, first anal vein; A2, second anal vein; CuA, cubitus anterior; PCu+A1, cubitus posterior + first anal vein; CuP, cubitus posterior; MP, media posterior; C1-C5, nodal cells.

apically rounded processes: one arising from ventral margin, directed mediodorsally, the others arising from dorsal margin and directed dorsally and laterodorsally, respectively. Genital styles densely covered with strong setae; setae predominantly on dorsal processes. Connective straight, and narrow. Aedeagus bilaterally symmetrical, short, stout, tubular, ventrally narrow and slightly compressed, distally widening and with ventral margin of strongly sclerotized part produced into a median tip which in repose is pointing ventrocaudally. Periandrium without any spinose or lobate processes; near base laterally on each side with a short, wing-like process, which is connected to the genital segment; apically with a wide membranous portion exposed caudally. Phallotreme not visible. Proximal apodeme of aedeagus ("tectiform structure" *sensu* Bourgoin (1997), term coined for Meenoplidae) shorter than periandrium, with dorsal and ventral margins almost parallel, proximal margin truncate.

Females with abdominal tergites VI–VIII bearing wax fields. Genitalia with sternite VII in ventral view trapezoidal, with lateral margins diverging caudally, caudal margin smooth, straight; gonocoxae VIII wide at base, distally bilobate with dorsal lobe larger than ventral one, lobes medially converging, both lobes apically with setae; tergite IX in dorsal aspect short, expanding ventrally and forming a continuous sclerotized bridge surrounding the anal segment. Anal segment (segment X) tubular, in dorsal aspect with lateral margins more or less parallel; anal style (segment XI) with paraproct prominent.

Immatures (Figs 1b, 7–9).

V. instar nymph. Body length 2.5 mm (specimen with contracted abdomen) -3.1, resp. 3.2 mm. (specimens with extended abdomen) (n = 3).



Figure 4. Valenciolenda fadaforesta sp. nov. Male genitalia in situ, left lateral view; paratype. Scale bar: 0.1 mm.

Habitus. *Body* ca. 1.7 × longer than maximally wide; maximum width at lateroposterior margins of forewing pads. Vertex short, compound eyes absent; rostrum elongate, well surpassing hind coxae, with ca. half its total length; frons, thoracic nota and abdominal tergites IV–VIII with numerous sensory pits.

Colouration. Vertex, frons, thoracic and abdominal nota as well as distal parts of legs (tibiae, tarsi) light yellowish; head laterally, thorax ventrally as well as proximal parts of legs (coxae, femora) and abdomen ventrally white. Carinae of head and lateral carinae of pronotum yellowish brown; distal teeth of metatibia and metatarsomeres dark brown.

Head. Vertex short, ca. 4 × wider than medially long, medially divided by a narrow longitudinal membraneous furrow, separated from frons by a distinct ridged transverse carina which medially slightly arches anteriorly. Frons smooth, without median carina, but with submedian carinae present, arising from frontoclypeal suture, parallel to lateral carinae of frons, converging towards apex and uniting into a short common stem which connects to anterior margin of vertex. Lateral as well submedian carinae of frons and their common stem distinctly ridged; frontoclypeal suture nearly straight, only slightly arching towards frons. Frons ca. 1.2 × as long as maximally wide (widest at level of antennae), apically straight; frons ca. 2.4 × longer than post- and anteclypeus together. Frons between lateral and submedian carinae with two parallel rows of sensory pits, in upper portion with complementary sensory pits between the two rows. Setae of pits directed towards adjacent carinae and those of complementary pits directed towards lateral carina. Post- and anteclypeus smooth, without median carina. Tip of rostrum with dorsal and ventral sensory fields convex, as described by Brozek and Bourgoin (2013), covered with numerous sensilla; type, number, and arrangement of sensilla very similar to those of the Kinnaridae species studied by Brozek and Bourgoin (2013), Southia capnorhina Fennah, 1980, Atopocixius major Fennah,



Figure 5. *Valenciolenda fadaforesta* sp. nov. Male genitalia **a** genital segment, caudal view **b** anal segment, dorsal view **c** left genital style, left lateral view **d** same, ventral view **e** aedeagus, left latero-dorsal view **f** same, ventral view. Scale bars: 0.1 mm.

1945, and *Nesomicrixia insularis* Synave, 1958. Compound eyes absent, their former position recognizable as a slightly vaulted area dorsally of antennae. Antennae with scape short and ring-like, pedicel nearly cylindrical, ca. $1.5 \times$ longer than wide; arista ca. $3.6 \times$ longer than pedicel.

Thorax. Pronotum short, in dorsal aspect medially ca. $2 \times$ as long as vertex, and ca. $2 \times$ as wide as maximum width of head; lateral carinae of pronotum nearly straight,



Figure 6. *Valenciolenda fadaforesta* sp. nov. Female genitalia **a** left lateral view **b** same ventral view. Scale bar: 0.1 mm.

strongly diverging posteriorly; "additional carina" of pronotum (sensu Yang and Yeh 1994: 3, fig. 1H), dividing anterior portion of pronotum into a smaller median, and a larger lateral area. Pronotum dorsally on each side with two rows of sensory pits: one, consisting of 5 larger sensory pits, parallel to posterior, resp. median margin, the other, consisting of 8 smaller sensory pits, adjacent to lateral carina; anterior portion of pronotum in larger, lateral area with a row of 9-11 sensory pits adjacent to lateral carina; smaller, median area devoid of sensory pits. Mesonotum medially ca. 2 × longer than pronotum, with posterior margin laterally more or less angularly curved; forewing pads well developed, ca. 2 × longer than mesonotum medially, posteriorly slightly surpassing caudal margin of hind wing pads; lateral carinae of mesonotum (separating the nota from the wing pad) distinctly ridged, slightly diverging posteriorly, attaining hind margin of mesonotum; mesonotum with a short, but distinct furrow on anterior portion of forewing pad; forewing pad with two distinct longitudinal carinae. Mesonotum with numerous sensory pits arranged on each side as follows: medially of lateral carina - a row of 6 larger sensory pits parallel to carina and 2 smaller sensory pits closer to midline, on forewing pad, between median furrow and lateral carina in anterior part of mesonotum - a group of 6 sensory pits, and three rows of sensory pits between longitudinal carinae, along exterior carina and parallel to lateral margin, respectively. Metanotum medially about as long as mesonotum, hind margin nearly straight, laterally only slightly, expanding caudally; lateral carinae of metanotum (separating the nota from the hind wing pad) distinctly ridged, straight, slightly converging posteriorly, reaching hind margin of metanotum. Hind wings pads inconspicuous, vestigial, their posterior margin shorter than posterior margin of forewing pads, covered by forewing pad. Metanotum on each side with ca. 15 small sensory pits, seemingly irregularly arranged across notum, and on hind wing pad with a group of 3 larger sensory pits adjacent to



Figure 7. Valenciolenda fadaforesta sp. nov. V. instar nymph, habitus (distribution of sensory pits reconstructed from SEM); Cova de Murcielagos, 24.vi.2017, A. Sendra leg.

lateral carina. Legs. Hind trochanter as in most other Fulgoromorpha families (except Tettigometridae: Asche 1988) medially with cog-wheel-like opposing ledges, the "coupling apparatus" (Emeljanov 1979) which facilitate synchronization of the hind legs during jumping (Burrows and Sutton 2013). Metacoxae with meracanthus present, inconspicuous, surface with fine tubercles. Metatibiae laterally unarmed, distally with 7–8 (bilaterally and individually variable) slender teeth, arranged in a slightly concave row. Metabasitarsus distally with 5, 2nd metatarsomere with 4 small teeth. Metabasitarsus slightly shorter than 2nd and 3rd metatarsomeres together. Pretarsus with short, slender claws, not longer than arolium.

Abdomen as in other Fulgoromorpha 9-segmented (except for Tettigometridae: Yang and Yeh 1994), ovoid, in cross section roundish; first two abdominal segments narrow, thus creating a distinct separation between thorax and abdomen. Abdomen medially about as long as head and thorax together. Abdominal tergites medially smooth, without any crest or carina; tergites I–II short, their hind margins straight; tergites I–III devoid of sensory pits; tergites III–VI with hind margin medially incised. Tergites IV–VIII with numerous sensory pits, on each side arranged as follows: IV –



Figure 8. *Valenciolenda fadaforesta* sp. nov., V. instar nymph (SEM) **a** head and pronotum, dorsal view **b** head, ventral view **c** left antenna, dorsal view **d** head (partim) with antenna, left lateral aspect; arrow indicates the former position of the compound eye **e** tip of left antenna, as in Fig. 8e, enlarged **f** overview of body, right lateral view, arrow indicates meracanthus **g** meracanthus, as in Fig. 8f, enlarged.



Figure 9. *Valenciolenda fadaforesta* sp. nov., V. instar nymph (SEM) **a** tip of rostrum with sensilla, ventral aspect **b** metatarsus, ventral view **c** abdominal segments VI–IX (arrow – see explanation in text). Abbreviations: mx, md, mandible, maxillae; SF-D, dorsal sensory field; SF-V, ventral sensory field.

a row of 6 sensory pits laterally, parallel to hind margin; V - a row of 6 sensory pits laterally, parallel to hind margin, and a group of 3 sensory pits laterally, near anterior margin; VI - a row of 4 sensory pits parallel to hind margin, and a group of 3-4 sensory pits laterally, closer to anterior margin; VII – an irregular row of 4 large sensory pits accompanying hind and lateral margin of tergite, and 4 small sensory pits laterally, closer to anterior margin; VIII - in dorsal half with one small sensory pit laterally near caudal margin, and 4 (3 + 1) large sensory pits lateroventrally. Abdominal tergite IX (pertaining to the anlage of the genital segment) in dorsal view short, narrow, in caudal view bent ventrally in a horseshoe shape, with ventral margin broadly rounded, on each side with 1 sensory pit in dorsal half near caudal margin and a group of at least 3 sensory pits near lateroventral margin. Anlagen of abdominal segments X and XI small, triangular, tapering caudally, devoid of sensory pits. All nymphs examined display the same configuration of the pregenital abdomen and genital structures (segment IX). Abdominal tergites VI–VIII are devoid of wax-pore plates. The anlagen of the genitalia on the IX segment, however, are difficult to interpret. The dorsal unpaired process is likely the anlage of the anal style (segment XI). This structure is framed laterally and ventrally by narrow, elongated lobes (it is not recognizable whether or not they are

fused medially), which may or may not be homologues to what has been termed "anal combs" in the other Fulgoromorpha families, except Tettigometridae (Yang and Yeh 1994). The two short conical processes located medially at the level of the posterioventral corner of tergite IX could be interpreted as *anlagen* of either the genital styles (of the male), or of the gonocoxae VIII (of the female). The high degree of reduction of the ovipositor in adults within the Meenoplidae-Kinnaridae clade apparently impedes unambiguous identification of the sex of the nymphs as already observed by Wilson (1983) for the meenoplid *Nisia nervosa* ("In *Nisia nervosa* it was not possible to find obvious differences in nymphs which separate the sexes": Wilson, 1983: 123).

Remarks. Hitherto, no information on nymphal morphology of Kinnaridae has been available – they are not covered in the seminal works on Fulgoromorphan nymphal morphology, Yang and Yeh (1994) and Emeljanov (2001), apparently due to lack of material. Thus, the description of *Valenciolenda fadaforesta* nymphs represents the first example of a kinnarid nymph. As such, it shares several characters with other Fulgoromorpha taxa which are not explicitly mentioned above. According to Yang and Yeh (1994) and Emeljanov (2001) these include: ocelli absent, second antennal segment with sensory organs, thoracic nota separated along median line by membraneous area, with numerous sensory pits on tergal parts of head, thorax and abdominal tergites III–VIII (for morphology of sensory pits, their disposition and orientation see Liebenberg 1956, Emeljanov 2001, Bräunig et al. 2012), Pro- and mesotarsi with 2 joints, metatarsi with 3 joints.

Molecular data. A blast search in GenBank and BOLD data bases for most similar COI sequence data revealed that *Valenciolenda fadaforesta* shows 15% divergence to all other Auchenorrhyncha. A molecular phylogeny of Kinnaridae, however, did not seem feasible due to insufficient taxon sampling: all other kinnarid taxa represented in Genbank and BOLD are from the New World (USA, Honduras, Mexico, Costa Rica).

Etymology. The species name is a combination of the Valencian word for "fairy" (fada) and forest, thus meaning "fairy of the forest". The gender is feminine.

Material examined. Type-locality: Spain, Valencia, Vilamarxant, ,Murcielagos' cave, 39.537095, -0.624732, 5th April 2016, L. Beltran and A. Sendra leg.; in coll. MfN (Museum für Naturkunde, Berlin, Germany).

Type-specimen: *Holotype* male, preserved in 96% ETOH, polyethylene vial. Original label: "Spain, València, Vilamarxant, ,Murcielagos' cave, (30SYJ0410579181 (UTM/MGRS Datum EUR50), 5th April 2016, L. Beltran and A. Sendra leg."; printed label (red): "*Valenciolenda fadaforesta* Hoch & Sendra, holotype male".

Paratypes. 1 male, same data as holotype. 1 male, 1 female, same locality as holotype, 30th April 2017, S. Teruel and A. Sendra leg; 1 male, same locality as holotype, 24.VI. 2017. 1 male, Spain, Castelló, ,Coves de Sant Josep'cave, 4th June 2016, S. Teruel leg.

Paratypes in coll. **NAT** (Museu de Cièncias Naturals de Barcelona, Spain), **MUVHN** (Museu de la Universitat de València d'Història Natural, Burjassot, València, Spain) and **ES** (Laboratório de Ecologia Subterránea/ISLA: Coleção de Invertebrados Subterráneos da UFLA – Universidade Federal de Lavras, Brazil).

Additional material. 1 nymph, V. instar, same data as holotype. 4 nymphs, V. instar, same locality as holotype, 24.VI. 2017; MfN.

Distribution, ecology and behaviour. Specimens of Valenciolenda fadaforesta have been studied in two caves ("Murciélagos' cave and "Coves de Sant Josep' caves) in two karstic areas of Triassic dolomite separated by 45 kilometers and located in the eastern reliefs of the Iberian Mountain Range, from eleven to twenty-seven kilometers inland from the Mediterranean coast (Fig. 10). ,Cueva de los Murcielagos' was excavated in a dolomitic outcrop on a small isolated mountain of the Rodanes Municipal Park, in Vilamarxant (València) (Sendra et al. 2015) and represents the best known and most abundant population of V. fadaforesta. In the other three caves from the same small karst rocky outcrop nymphs presumably belonging to *V. fadaforesta* have been observed. These are the caves of ,Pedrizas, Llentiscle' and Sima del Perot' that occupy an area of less than one square kilometer in the Rodanes (Sendra et al. 2015). The other cave studied is the well-known tourist subterranean river cave ,Coves de Sant Josep', which descends three thousands meters with explored galleries under the surface of the western slopes of the karstic region of ,Serra Espadà' Mountains, in Vall d'Uixó (Castelló) (Garay, 2003, Sendra et al. 2017). In addition, specimens presumably belonging to V. fadaforesta have also been observed and also photographed in four other caves located geographically not far from the studied caves. They are the caves of ,Soterranya', a tectonic cave with over one kilometer of narrow passages and ,Sima Plà dels Llomes' a chasm 42 meters deep, both caves located in a large karstic area within ,Calderona Natural Park' in Serra, València. The third one is the small ,Cova del Cavall" cave, isolated in a limited karstic area called Buitreras' hill in Llíria, València. The fourth cave colonized is "Cueva de las Raices", the southernmost locality, an epithelial cave situated in a large karstic area in the Caroig Platform in Millares, València. In summary, the presumed range of distribution of *V. fadaforesta* seems to occupy the large karstic dolomitic and limestone outcrops in the eastern reliefs of the Iberian Mountain Range, under the Mediterranean climate in the thermo-mediterranean zone characterized by scarce precipitation at low altitudes, below 570 m.asl in the case of the highest located cave, Sima Plà dels Llomes".

V. fadaforesta displays a configuration of external characters which are certainly troglomorphic traits, such as the absence of compound eyes and ocelli, and reduced body pigmentation as well as tegmina and wings. The species is known exclusively from caves, and it can be assumed that it is restricted to subterranean environments. According to the ecological classification concepts proposed by Sket (2008) and more recently, by Howarth and Moldovan (2018) it is regarded as a troglobiont. Specimens were found from the twilight to the deep zone, from a few meters up to twenty meters below the surface, however, always in humid conditions. In two of the cited caves, V. fadaforesta has been observed as a single male specimen probably coming from the ceiling of the gallery ("Sant Josep' and "Plà dels Llomes' caves) and in the "Soterranya' and "Cavall' caves a few nymphs have been seen near to roots although juveniles were more abundant in `Raíces' cave. The only cave that has allowed ecological and behavioral observations was ,Murciélagos' cave. Uniquely to this cave, nymphs are abundant throughout the year but male and female adults are very scarce, one or two adults were seen on four of the twelve biospeleological visits into the cave. In "Murciélagos' cave, V. fadaforesta is found after the entrance zone, very scarce in the twilight zone and more abundant in the deep humid spots of the deep zone of the cave, but only where roots are present at least



Figure 10. Distribution map of *Valenciolenda fadaforesta* gen. nov., sp. nov. Localities: 1, Raíces' cave, Millares, València 2, Murciélagos' cave (type locality), Pedrizas' cave, , Llentiscle' cave and ,Sima del Perot, cave in Vilamarxant, València 3, Cavall' cave, Lliria, València 4, Soterranya' cave, Serra, València 5, Sima Plà dels Llomes', Serra, València 6, Coves de Sant Josep' caves, la Vall d'Uixó, Castelló. Dark blue areas mark karst regions. (map modified after Ayala et al. 1986)

nearby. This deep zone is characterized by high humidity with slight variation of 1.8 °C in temperature from 16.5–16.6 °C during February to May up to 18.1–18.3 °C during September to November (Sendra et al. 2015). In some spots, numerous nymphs wander around on the surface, where extremely rarely adults are seen. Roots are represented by a few short sections hanging from the ceiling or the walls. In a few places, these roots produce a small pile, elevated from the soil surface three to five centimeters due to water dripping from the ceiling. Although no analysis has been made to identify the plant species to which the roots pertain, pine (*Pinus halepensis*), carob (*Ceratonia siliqua*) or mastic trees (*Pistacia lentiscus*) are likely candidates, being abundant outside the cave entrance. In ,Cueva de las Raíces' juveniles can be seen in a few hanging roots from the ceiling, but they are not abundant (Fig. 11a–c). *V. fadaforesta* also occupies a different habitat in other spots in the cave in the interstitial spaces of the fragmented or excavated rock where roots are present too although very scarce. We assume that *V. fadaforesta* could live

among the cracks and crevices of the mesocavernous rock system, that could be considered as an epikarst of the karst wherever sufficient food resources (roots) are available.

Although there is no information on the mating behaviour of any kinnarid species, *Valenciolenda fadaforesta* may utilize the same communication system to locate potential mating partners, as has been documented for other (epigean and cavernicolous) planthoppers, i.e., surface-borne vibrations (Hoch and Howarth 1993, Hoch and Wessel 2006, Hoch et al. 2013, Soulier-Perkins et al. 2015) which have been shown to carry effectively over several meters via living plant material such as roots (Hoch and Howarth 1993).

An amazing similarity in behaviour has been observed in Valenciolenda fadaforesta and an obligate cave species of the family Cixiidae from Australia: Solonaima baylissa Hoch & Howarth, 1989, from Bayliss Cave, a lava tube of Undara lava flow, Queensland (Fig. 1c), which also displays a similar degree of tegmina reduction as well as the prominent blueish-white wax fringe along the costal vein (Hoch and Howarth 1989). Both species hold their tegmina nearly flat over the abdomen and - when disturbed exercise escape jumps with the tegmina resembling tiny parachutes obviously slowing down the jumping individual (personal observation). This behavior - observed in two totally unrelated species, on two continents - is an excellent example of convergent evolution. Its context has not been studied vet, but it is conceivable that in an environment where roots may be few and far between, escape from approaching predators, such as spiders; the "parachuting" could be a means to avoid predaters as well as ensuring the jumping planthopper is not catapulted too far from its host root. Adults and nymphs have been observed in "Murciélagos' cave jumping several centimeters to avoid predetors, such as Dysdera spiders and the carabid beetles (Laemostenus terricola (Herbst, 1784) or Porotachys bisulcatus (Nicolai, 1822)) with V. fadaforesta (Sendra et al. 2015). In addition, the tegmen morphology (strong costal vein, covered with waxy exudation, and tegmina exceeding lateral body margins) may aid to avoid predation too.

Another striking behavior has been observed in the nymphs and adults of *V. fadaforesta*. When they wander around and also when they remain in the same spot, a quick lateral movement of the abdomen has been observed. Such movement is usually followed by a change in the walking direction which is consistent with that of the lateral abdominal deflection. It could be interpreted as a signal to change the direction of movements, perhaps in response to yet unidentified stimuli.

Conservation status. In order to settle the conservation status of this remarkable endemic genus, two interesting aspects might be considered. Firstly, conservation of the general habitat of *Valenciolenda fadaforesta*. All caves in the Valencian Community are protected by law (11/94 Law of Natural Protected Spaces and Legal decree 65/2006, of 12th May) devoted to caves with special protection for 150 notable caves, among them there are all the cavities of the 'Pedrizas' in the Rodanes karstic area, 'Soterranya' and 'Sant Josep' caves inhabited by *V. fadaforesta*. Also, the Rodanes caves are within a natural protected park including the Turia Natural Park. Secondly, *V. fadaforesta*, according to the IUCN Red Data Book categories ought to be regarded as *vulnerable*, or even *endangered* (IUCN 2019), based on its small distribution, specialized habitat and presumed small population size. If the criteria given in Sánchez et al. (2004) are applied, which are more suitable for arthropod taxa, it can be considered as a 'highly



Figure 11. Root habitat in 'Raices' cave (Millares, València) **a** overview main room **b** roots along cracks in the cave ceiling **c** roots dangling from the ceiling **d** *Valenciolenda fadaforesta* sp. nov., adult, on cave floor in 'Murciélagos' cave (photos **a–c** by Teresa Molina Jiménez and Ricardo Giménez Mezquita, used with permission of UEE Fotogrup; photo **d** by Sergio Montagud Alario).

vulnerable taxon' according to its degree of endemicity, small distribution area, rarity and threat to its habitat.

There are real threats to the sustained occurrence of *V. fadaforesta*. Most notably, the species shows a low population density: in almost all caves where it has been reported, only one or a few specimens have been observed. Only the 'Murcielagos' cave contains a stable population all year round, but even this population apparently diminished during the extended 2013–2016 drought which affected the flora, with a particular impact on the pine trees, *Pinus halepensis*. This drought period also impacted the roots that appear inside the cave. Fortunately, after the end of the drought period at the end of 2017 there was an apparent recuperation of *V. fadaforesta* of the 'Murcielagos' cave.

Discussion

Suprageneric classification

According to the classification of Kinnaridae suggested by Emeljanov (2006), *Valenciolenda* belongs to the subfamily Prosotropinae Fennah, 1945, as it displays 1) costal vein of fore wing strong from base up to nodus, 2) branches of RP and M free, 3) a cixioid clavus, i.e., the common claval vein reaches the hind margin of the clavus.

The placement of *Valenciolenda* into Adolendini follows the concept of tribal division of Kinnaridae by Emeljanov 2006. According to this, the Adolendini are characterized by a combination of the following characters:

- 1) *Metope* (= frons) *without median carina, narrow, with high lateral carinae.* According to Emeljanov (personal communication, used with permission) this is an apomorphy, however, with low weight because of high potential for homoplasy.
- 2) Median carina of pronotum reaching fore carina but not prolonged in front of it.
- 3) Basal cell of fore wing closed by anastomosis of M and CuA (Emeljanov 2006: 1). According to Emeljanov (personal communication, used with permission) the anastomosis replaces the arculus, and is considered a likely apomorphy for Adolendini.

However, at least one of these characters (frons smooth, without median carina), is often observed in obligately cavernicolous planthoppers (Hoch 1994) as the reduction of the compound eyes strongly alters head morphology and may lead to a broadening of frons (and vertex), along with reduction of carinae (Hoch and Howarth 1989). It can thus not be excluded that the closest epigean relative of *Valenciolenda fadaforesta* featured or features a median frontal carina. The pronotum configuration postulated for Adolendini by Emeljanov (2006) does apply to *Valenciolenda fadaforesta*, however, the fore wing character does not: there is no anastomosis of M and CuA, and there is no distinct basal cell recognizable (Fig. 3). The configuration of the fore wing, or tegmen, observed in *V. fadaforesta* may or may not be a consequence of the troglomorphic fore wing reduction. It should be noted, though, that none of the characters mentioned have been discussed as potential synapomorphies for the pertaining taxa.

Biogeographical implications

Given the background of the current state of knowledge on the phylogeny of Kinnaridae, it is difficult to make conclusions as to which taxa may be the closest living relatives of *Valenciolenda fadaforesta*. The geographically closest Kinnaridae are species from 2 genera (*Kinnacana* Remane, 1985 and *Kinnoccia* Remane, 1985) (tribe Kinnocciini Emeljanov 2006) recorded from the Canary Islands (Remane 1985). These display – like *V. fadaforesta* – wax fields in the female on abdominal segments VI, VII and VIII (Emeljanov 2006), but – unlike *V. fadaforesta* – the basal cell of the forewing is closed by an anastomosis of M and CuA (Emeljanov 2006).

Except for the Kinnocciini, Kinnaridae have not been documented from Western Europe. Several species are known from Iran, Tadzhikistan (Emeljanov 1984), Afghanistan (Dlabola 1957), India (Distant 1916) and the United Arabian Emirates (Wilson 2010). However, none of those taxa display character configurations which could be interpreted as synapomorphies with *Valenciolenda fadaforesta*. No close epigean relatives could thus be identified for *Valenciolenda fadaforesta* neither in Spain, nor elsewhere. Consequently, *Valenciolenda fadaforesta* must currently be regarded as a relict species which has long been isolated. This assumption is corroborated by the high divergence of its COI sequence from all other Auchenorrhyncha.

Although it cannot be determined on the basis of our current knowledge whether initial cave adaptation was driven by allopatry (extinction of closely related epigean populations: see *climatic relict hypothesis*, as postulated by e.g., Vandel 1964, or Barr 1968) or parapatry (adaptive shift of troglophilic populations in order to exploit novel food resources, as suggested by Howarth 1981, see also Howarth et al. 2019), it is clear that at some point, Kinnaridae must have been represented in the epigean fauna of Spain. The Iberian Fulgoromorpha fauna can be regarded as well investigated (Bourgoin 2019). Thus, it is unlikely that epigean Kinnaridae are still extant, but remain undiscovered. It is rather more likely that Valenciolenda fadaforesta provides testimony of an ancient fauna which is now extinct. The fossil record of Kinnaridae is scarce and not informative in regard to any putative epigean relatives of Valenciolenda fadaforesta, as there are only few species documented, exclusively from Oligocene/Miocene deposits of Dominican amber (Szwedo et al. 2004). It is conceivable that the epigean Kinnaridae which eventually gave rise to Valenciolenda migrated into the Western Mediterranean not from Europe, but from Asia through Northern Africa, perhaps in the context of the late Miocene Messianian salinity crisis. This southern migration route was hypothesized for other animal taxa, e.g., several genera of Muroidea (mammalia) of Eastern Spain, which show African or Asian affinities (Agustí 1989).

A similar case of a relict distribution has been documented from the Canary Islands: there, obligately cavernicolous species of the Fulgoromorpha taxon Meenoplidae are known from La Palma (Hoch and Asche 1993), El Hierro (Remane and Hoch 1988, Hoch and Asche 1993), and Gran Canaria (Hoch et al. 2012), while epigean Meenoplidae are not part of the present-day fauna of the Canary Islands.

The unexpected discovery of this planthopper of the Kinnaridae family, *Valenciolenda fadaforesta* gen. nov., sp. nov., in a relatively well-known Iberian cave highlights the importance of subterranean biodiversity, and leads us to conclude that there are still many amazing discoveries awaiting us in cave environments. The study of cave faunas may yield valuable information on evolutionary and biogeographic history, and thus provide veritable windows to the past.

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References

- Agustí J (1989) On the peculiar distribution of some muroid taxa in the Western Mediterranean. Bolletino della Società Paleontologica Italiana 28(2–3): 147–154.
- Ai-Ping L (2001) First record of the genus Adolenda Distant (Hemiptera: Fulgoroidea: Kinnaridae) from China, with description of one new species. Zoological Studies 40(4): 365–370. https://www.sinica.edu.tw/zool/zoolstud/40.4/365.pdf
- Asche M (1988) Preliminary thoughts on the phylogeny of Fulgoromorpha (Homoptera Auchenorrhyncha). In: Proceedings of the 6th Auchenorrhyncha Meeting, Turin, Italy, 7–11 Sept. 1987, 47–53.
- Ayala FJ, Rodriguez JM, Prieto C, Duran JJ, Del Val Melus J, Rubio J (1986) Memoria del Mapa del Karst de España. Instituto Geológico y Minero de España. Madrid.
- Barr Jr TC (1968) Cave ecology and the evolution of troglobites. Evolutionary Biology 2: 35–102. https://doi.org/10.1007/978-1-4684-8094-8_2
- Bourgoin T, Deiss V (1994) Sensory plate organs of the antenna in the Meenoplidae-Kinnaridae group (Hemiptera: Fulgoromorpha). International Journal of Insect Morphology and Embryology 23(2): 159–168. https://doi.org/10.1016/0020-7322(94)90008-6

- Bourgoin T (1997) The Meenoplidae (Hemiptera, Fulgoromorpha) of New Caledonia, with a revision of the genus *Eponisia* Matsumura, 1914, and new morphological data on forewing venation and wax plate areas. In: Najt J, Matile L (Eds) Zoologia Neocaledonica, Vol. 4. Mémoires du Musée national d'Histoire naturelle, 171, Paris, 197–249.
- Bourgoin T (2019) FLOW (Fulgoromorpha Lists on The Web): a world knowledge base dedicated to Fulgoromorpha (Insecta: Hemiptera: Fulgoromorpha). Version 8. https://www. hemiptera-databases.org/flow/ [last accessed July 2020]
- Bourgoin T, Wang R-R, Asche M, Hoch H, Soulier-Perkins A, Stroinski A, Yap S, Szwedo J (2015) From micropterism to hypopterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). Zoomorphology 134(1): 63–77. https://doi.org/10.1007/s00435-014-0243-6
- Bräunig P, Krumpholz K, Baumgartner W (2012) Sensory pits Enigmatic sense organs of the nymphs of the planthopper *Issus coleoptratus* (Auchenorrhyncha, Fulgoromorpha). Arthropod Structure and Development 41: 443–458. https://doi.org/10.1016/j.asd.2012.06.001
- Brozek J, Bourgoin T (2013) Morphology and distribution of the external labial sensilla in Fulgoromorpha (Insecta: Hemiptera). Zoomorphology 132(1): 33–65. https://doi. org/10.1007/s00435-012-0174-z [Published on-line 2012]
- Burrows M, Sutton GP (2013) Interacting gears synchronise propulsive leg movements in a jumping insect. Science 341: 1254–1256. https://doi.org/10.1126/science.1240284
- Distant WL (1916) Homoptera: Appendix The Fauna of British India including Ceylon and Burma, Rhynchota. Vol. 6: 1–248.
- Dlabola J (1957) Die Zikaden Afghanistans (Homoptera Auchenorrhyncha). Mitteilungen der Münchner Entomologischen Gesellschaft 47: 265–303. [Taf. 1–7]
- Emeljanov AF (1979) The problem of family distinction between the Fulgoridae and Dictyopharidae (Homoptera Auchenorrhyncha). Academy of Sciences of the USSR, Proceedings of the Zoological Institute, vol. 82: Phylogeny and Systematics of Insects: 3–22. [in Russian]
- Emeljanov AF (1984) To the knowledge of the families Kinnaridae and Meenoplidae (Homoptera, Fulgoroidea). Entomologicheskoye Obozreniye 3: 468–483. [in Russian] [English translation: Entomological Review, 1985: 49–65.]
- Emeljanov AF (2001) Larval characters and their ontogenetic development in Fulgoroidea (Homoptera, Cicadina). Zoosystematica Rossica 9: 101–121.
- Emeljanov AF (2006) Subdivision of the family Kinnaridae into subfamilies and tribes (Homoptera, Fulgoroidea). Zoosystematica Rossica 15: 77–78.
- Fennah RG (1945) The Fulgoroidea, or lanternflies, of Trinidad and adjacent parts of South America. Proceedings of the United States National Museum 95(3184): 411–520. [7–17 pls] https://doi.org/10.5479/si.00963801.95-3184.411
- Fennah RG (1948) New Pintaliinae, Cixiidae, Kinnaridae and Tropiduchidae from the Lesser Antilles (Homoptera: Fulgoroidea). Annals and Magazine of Natural History Ser. 12(1): 417–437. https://doi.org/10.1080/00222934808653922
- Fennah RG (1973) Three new cavernicolous species of Fulgoroidea (Homoptera) from Mexico and Western Australia. Proceedings of the Biological Society, Washington 86(38): 439–446.

- Fennah RG (1980) New and little-known neotropical Kinnaridae (Homoptera Fulgoroidea). Proceedings of the Biological Society, Washington 93: 674–696.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitocondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3(5): 294–299.
- Garay P (2003) Ensayo sobre la anisotropía del sistema kárstico drenado por el manantial de Sant Josep (La Vall d'Uixó, Provincia de Castellón de la Plana). Boletin de la Sociedad Española de Espeleología y Ciencias del Karst 7: 70–79.
- Hoch H (1994) Homoptera (Auchenorrhyncha Fulgoroidea). In: Juberthie C, Decu V (Eds) Encyclopedia Biospeologica, Société de Biospéologie, Moulis-Bucarest, 313–325.
- Hoch H, Asche M (1993) Evolution and speciation of cave-dwelling Fulgoroidea in the Canary Islands (Homoptera: Cixiidae and Meenoplidae). Zoological Journal of the Linnean Society 109: 53–101. https://doi.org/10.1111/j.1096-3642.1993.tb01259.x
- Hoch H, Ferreira RL (2013) Potiguara troglobia gen. n., sp. n. first record of a troglobitic Kinnaridae from Brazil (Hemiptera: Fulgoromorpha). Deutsche Entomologische Zeitschrift 60(1): 33–40.
- Hoch H, Ferreira RL (2016) *Iuiuia caeca* gen. n., sp. n., a new troglobitic planthopper in the family Kinnaridae (Hemiptera, Fulgoromorpha) from Brazil. Deutsche Entomologische Zeitschrift 63(2): 171–181. https://doi.org/10.3897/dez.63.8432
- Hoch, H, Howarth FG (1989) Six new cavernicolous cixiid planthoppers in the genus Solonaima from Australia (Homoptera Fulgoroidea). Systematic Entomology 14: 377–402. https://doi.org/10.1111/j.1365-3113.1989.tb00291.x
- Hoch H, Wessel A (2006) Communication by substrate-borne vibrations in cave planthoppers (Auchenorrhyncha: Homoptera: Fulgoromorpha: Cixiidae). In: Drosopoulos S, Claridge MF (Eds) Insect sounds and communication: physiology, behaviour, ecology and evolution. CRC-Taylor & Francis, Boca Raton, London, New York, 187–197. https://doi. org/10.1201/9781420039337
- Hoch H, Mühlethaler R, Wessel A (2013) Acoustic communication in the subtroglophile planthopper Trigonocranus emmeae Fieber, 1876 (Hemiptera: Fulgoromorpha: Cixiidae: Oecleini). Acta Musei Moraviae Scientiae biologicae 98(2): 155–162.
- Hoch H, Naranjo M, Oromi P (2012) Witness of a lost world: *Meenoplus roddenberryi* sp. nov., a new cavernicolous planthopper species (Hemiptera, Fulgoromorpha, Meenoplidae) from Gran Canaria. Deutsche Entomologische Zeitschrift 59(2): 207–215.
- Howarth FG (1981) Non-relictual terrestrial troglobites in the tropical Hawaiian caves. In: Proceedings of the 8th International Congress of Speleology, Huntsville, AL (USA), 1981. National Speleological Society, 539–541.
- Howarth FG, Moldovan OT (2018) The ecological classification of cave animals and their adaptations. In: Moldovan OT, Kovács L, Halse S (Eds) Cave Ecology, Ecological Studies 235, Springer Nature Switzerland, 41–67. https://doi.org/10.1007/978-3-319-98852-8_4
- Howarth FG, Hoch H, Wessel A (2019) Adaptive Shifts. In: Culver DC, White WB (Eds) Encyclopedia of Caves. Elsevier Academic Press, 47–55. https://doi.org/10.1016/B978-0-12-814124-3.00007-8

- IUCN [International Union for the Conservation of Nature] (2019) International Union for the Conservation of Nature. http://www.newworldencyclopedia.org/entry/IUCN_Red_List
- Liebenberg K (1956) Die Borstengruben ein wenig bekanntes larvales Haarsinnesorgan von *Calligypona pellucida* F. (Homoptera Cicadina). Zoologische Beiträge 2: 441–446.
- Muir FAG (1925) On the genera of Cixiidae, Meenoplidae and Kinnaridae (Fulgoroidea, Hemiptera). Pan-Pacific Entomologist 1(4): 156–163.
- Remane R (1985) Kinnaridae in der SW-Paläarktis: zwei neue Taxa von den Kanaren (Homoptera Fulgoromorpha). Marburger Entomologische Publikationen 1(10): 241–264.
- Remane R, Hoch H (1988) Cave-dwelling Fulgoroidea (Homoptera: Auchenorrhyncha) from the Canary Islands. Journal of Natural History 22: 403–412. https://doi. org/10.1080/00222938800770291
- Sánchez-Fernández D, Abellán P, Barahona J, Velasco J, Millán A (2004) Propuesta para la elaboración de la lista roja de invertebrados de la Región de Murcia: el case de los coleópteros acuáticos. In: Actas III congreso de la naturaleza de la Región de Murcia. Octubre 2004, 83–88.
- Sendra A, Ballester A, Alcocer A, Aura E, Azkárraga JM, Castelló AJ, Fernández J, Garay P, Herrero-Borgoñón JJ, Monsalve MA, Pascual JL, Ponce JI, Sanchís A, Sarrión I, Sendra C, Teruel S, Tiffagom M, Vila S (2015) Les Rodanes, un paraje de cuevas y simas. Vilamarxant, València. Generalitat Valenciana, Federació d'Espeleologia de la Comunitat Valenciana, 139 pp.
- Sendra A, Escrig J, Teruel S, Urios G, Beltrán MD (2017) El barquero de Les Coves de Sant Josep de la Vall d'Uixó: descubriendo el ecosistema subterráneo. Berig 17: 62–72.
- Sket B (2008) Can we agree on an ecological classification of subterranean animals? Journal of Natural History 42(21–22): 1549–1563. https://doi.org/10.1080/00222930801995762
- Soulier-Perkins A, Ouvrard D, Hoch H, Bourgoin T (2015) Singing in Namoroka Caves, First record in situ for a cave dwelling insect: *Typhlobrixia namorokensis* (Hemiptera, Fulgoromorpha, Cixiidae). Journal of Insect Behavior 28(6): 704–721. https://doi.org/10.1007/ s10905-015-9531-3
- Vandel A (1964) La biologie des animaux cavernicoles. Gauthier-Villars, Paris, 619 pp. https:// doi.org/10.1126/science.144.3626.1563-a
- Szwedo J, Bourgoin T, Lefebvre F (2004) Fossil Planthoppers (Hemiptera: Fulgoromorpha) of the World. Jacek Szwedo, Warsaw, 199 pp.
- Wilson MR (1983) The nymphal stages of some Auchenorrhyncha associated with rice in South East Asia. In: Knight WJ, Pant NC, Robertson TS, Wilson MR (Eds) Proceedings of the 1st International Workshop on Leafhoppers and Planthoppers of Economic Importance. Commonwealth Institute of Entomology, London, 121–134.
- Wilson MR (2010) Order Hemiptera, families Meenoplidae and Kinnaridae. Arthropod fauna of the UAE 3: 126–131.
- Xing J-C, Hoch H, Chen X-S (2013) New replacement name for the planthopper genus *Potiguara* Hoch et Ferreira, 2013 (Hemiptera: Fulgoromorpha: Kinnaridae). Zootaxa 3734(3): 400–400. https://doi.org/10.11646/zootaxa.3734.3.11
- Yang C-T, YehW-B (1994) Nymphs of Fulgoroidea (Homoptera: Auchenorrhyncha). Chinese Journal of Entomology, Special Publiations 8: 1–189.

Supplementary material I

Video sequence

Authors: Sergio Montagud Alario

Data type: Video sequence

Explanation note: Video sequence documenting *Valenciolenda fadaforesta* sp. nov. (adult male) in its natural environment (video by Sergio Montagud Alario).

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