Description of a new hypogean species of the genus *Trechus* Clairville, 1806 from eastern Spain and comments on the *Trechus martinezi*-lineage (Coleoptera: Adephaga: Carabidae)

V. M. ORTUÑO¹ & A. ARILLO²

¹Departamento de Zoología y Antropología Física, Facultad de Biología, Universidad de Alcalá, Alcalá de Henares, Madrid, Spain, and ²Departamento de Zoología (Entomología), Facultad de Biología, Universidad Complutense de Madrid, Madrid, Spain

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Abstract
*Trechus torressalai* new species, a cave-dwelling ground beetle from eastern Spain is described. Ecological data are also included. Diverse morphological characters suggest they belong in the *Trechus fulvus*-group. Detailed study of the aedeagus suggests taxonomic affinities with *Trechus martinezi* Jeannel, *Trechus alicantinus* Español, and *Trechus beltrani* Toribio. The close relationship among these species reveals an adelphotaxon-complex that constitutes the *T. martinezi*-lineage, exclusive to the north-eastern Betic Mountains. An identification key to the species and biogeographical comments on the *T. martinezi*-lineage are also included.

Se describe *Trechus torressalai* nueva especie, carábido cavernícola del Este de España. Se incluyen datos sobre su ecología. Diversos caracteres morfológicos aconsejan su inclusión dentro del amplio grupo de *Trechus fulvus*. El estudio detallado de la genitalia masculina sugiere su proximidad taxonómica a *Trechus martinezi* Jeannel, *Trechus alicantinus* Español y *Trechus beltrani* Toribio. Las estrechas afinidades entre estas cuatro especies desvela un complejo de adelotaxones que constituyen el linaje de *T. martinezi*, exclusivo del extremo nororiental de las montañas Béticas. Se aportan claves de identificación para estas especies. Se incluyen comentarios sobre la biogeografía del linaje de *T. martinezi*.

Keywords: Biogeography, Carabidae, caves, Coleoptera, ecology, Iberian Peninsula, key, systematics, *T. martinezi*-lineage, taxonomy, Trechus torressalai new species

Introduction
In the Iberian Peninsula several hypogean ground beetle species are known, which exhibit a broad range of levels of adaptation to the subterranean environment. Some species belonging to the genus *Trechus* Clairville are among those with minor adaptations.

This is a large genus, including more than 500 species (Casale et al. 1998), with new ones being discovered every year, that currently is only well known from the Holarctic
region and East Africa. In the Iberian Peninsula 49 species belonging to this genus are known (Serrano 2003); among them, 17 have a hypogean life and some species show features that may be considered as adaptive to the subterranean environment, but only 13 of these species are known exclusively from caves (Table I).

In the east of Spain six species of *Trechus* are known, all of them occur in the northeastern Betic Mountains (Alicante province), while four of them are absent in Valencia and Castellón provinces. These six species belong to three different groups. The “*T. fulvus*-group” includes three endemic species: *T. martinezi* Jeannel, *T. alicantinus* Español, and *T. beltrani* Toribio. The “*T. austriacus*-group” only includes one endemic species: *T. barratxinai* Español (see Ortúñoh 2004). The “*T. quadristriatus*-group” includes two widely distributed eurytopic species: *T. quadristriatus* (Schrank) and *T. obtusus* Erichson.

In this region, the three species belonging to the “*T. fulvus*-group” are exclusively hypogean and they are closely related as their body morphology and their genitalia are similar. As these species have close geographical ranges, they probably have a recent, common origin.

We recently found a second record of the species *T. martinezi* (Torres Sala 1962, p 73) that was overlooked in recent Iberian catalogues (Jeannel and Zaballos 1986; Zaballos and Jeannel 1994; Serrano 2003). These specimens (one male and two females) were stored in the collection of the Museum Torres Sala from Valencia and they were identified and labelled by F. Español. As it was a long distance between this new locality (Punta de Benimaquia cave, from La Jara-Dénia, Alicante) and the type locality of *T. martinezi* (Maravillas cave from Cocentaina, Alicante) we guessed that a misidentification could be

Table I. *Trechus* species known exclusively from the hypogean environment in the Iberian Peninsula.

| Species | Only caves | Only mesocavernous shallow substratum and endogeous environment |
|---------|------------|---------------------------------------------------------------|
| *Trechus alicantinus* Español, 1971 | + | |
| *Trechus apoduvalipenis* Salgado and Ortúñoh, 1998 | + | |
| *Trechus arribasi* Jeannel, 1988 | | + |
| *Trechus bastanensis* Dupré, 1991 | + | |
| *Trechus beltrani* Toribio, 1990 | | + |
| *Trechus beusti* Schaufuss, 1862 | + | |
| *Trechus breului* Jeannel, 1913 | + | |
| *Trechus carrilloi* Toribio and Rodríguez, 1997 | + | |
| *Trechus comasi* Hernando, 2002 | + | |
| *Trechus escallerae* Abeille, 1903 | + | |
| *Trechus gloriosiensis* Jeannel, 1970 | | + |
| *Trechus machadoi* Jeannel, 1941 | + | |
| *Trechus martinezi* Jeannel, 1927 | + | |
| *Trechus navaricus* (Vuillefroy, 1869) | + | |
| *Trechus ortizi* Español, 1970* | + | |
| *Trechus pecignai* Toribio, 1992 | + | |
| *Trechus pieltaini* Jeannel, 1920 | + | |

Note: *T. barratxinai* Español, 1971 was described as cave-dwelling, but in fact it has geophilic, lucifugous, and hygrophilous habits, therefore, it is not a cavernicolous (troglobiont) species (Ortúñoh 2004). *This species has not been collected since its discovery in the Cueva de Ojo Guareña (Burgos). T. ortizi is possibly not a cave-dwelling species; this idea is supported when studying the morphology of the imagoes.
possible. We made a detailed study of this new material and we found that it belongs to a
new species closely related to *T. martinezi* (the new species is less related to *T. beltrani* and
*T. alicantinus*). However, some details remain obscure. When Españañol (1971) described *T.
alicantinus* he made a drawing of the aedeagus (in lateral vision) of *T. martinezi* for the
comparison between both species. In his drawing of the aedeagus no locality was indicated
and it is doubtful if the described aedeagus belongs to *T. martinezi* or to the new species. So
we include in this work a detailed description of the aedeagus of *T. martinezi* for
comparison with the new species. We also include the redescription of the male genitalia of
*T. alicantinus* and *T. beltrani* and new information about the female genitalia of this group of
species.

**Material and methods**

**Examined specimens**

*T. torressalai* new species. See type series.

*T. martinezi*. Seven males, 12 females, Cueva de las Maravillas, Cocentaina (Alicante, Spain), 19 March 2003, V. M. Ortùñol and J. A. Zaragoza leg. (deposited in the collection of V. M. Ortùñol/Department of Animal Biology, Alcalá University, Spain).

*T. alicantinus*. Four males, eight females, Cueva del Somo, Castell de Castells (Alicante, Spain), 7 July 1992, V. M. Ortùñol leg.; three females, idem, 23 March 1996, V. M. Ortùñol leg. (deposited in the collection of V. M. Ortùñol/Department of Animal Biology, Alcalá University, Spain).

*T. beltrani*. One male (holotype), Sierra de Bernia, Pinós (Alicante, Spain), 20 January 1990, J. M. Beltrán leg. (deposited in the collection of M. Toribio in Tres Cantos, Madrid, Spain). Two females, idem, 7 July 1992, V. M. Ortùñol leg. (deposited in the collection of V. M. Ortùñol/Department of Animal Biology, Alcalá University, Spain).

**Methods**

The aedeagus was extracted from the abdomen and separated from the tergal apodemal
ring; the parameres were separated from the associated membranes in the surface of the
median lobe. It was then immersed for 24 h in lactic acid for the maceration of soft tissues.
After examination, genital preparations were put in dimethyl hydantoin formaldehyde
(DMHF) and put on an acetate sheet.

A routine procedure was followed to prepare the female reproductive appendages for
scanning microscopy. The terminal abdominal segments of the female were gently
squeezed with forceps and placed in a saturated solution of KOH for 8 h. They then were
washed in Scheerpelz’s solution (see Ortùñol et al. 1992, p 148) and opened dorsally to
check the alkaline digestion. Staining was carried out with Chlorazol black E® in aqueous
solution for 1 min under visual control. The excess dye was removed by washing in KOH
and the structures washed again in Scheerpelz’s solution. The dissected structures were
placed in a watchglass with Scheerpelz’s solution under a stereomicroscope with a drawing
tube for observation and drawing. The female genital preparations were included in
DMHF and put on an acetate sheet.
All measurements of the specimens were made using a calibrated ocular grid set in a stereomicroscope, and all data are given in Table II.

*Trechus torressalai* Ortuno and Arillo, new species  
(Figures 1–5, 7b, 8a, 12a)

**Diagnosis**

Without developed wings. Microphthalmic, depigmented with microreticulate integument (Figure 2). Pronotum transverse and slightly cordate: hind angles sharp and sides slightly sinuous in basal margin. Elytra convex, slightly protruding shoulders with eight

| Species                  | Sex       | Length (mm) | Width (mm) |
|--------------------------|-----------|-------------|------------|
| *T. torressalai* new species | Male      | 5.972       | 2.326      |
|                          | Female    | 5.902       | 2.152      |
|                          | Female    | 5.451       | 2.048      |
| *T. martinezi* Jeannel, 1927 | Male     | 6.180       | 2.395      |
|                          | Male      | 6.388       | 2.361      |
|                          | Male      | 6.180       | 2.256      |
|                          | Male      | 6.423       | 2.361      |
|                          | Male      | 6.215       | 2.256      |
|                          | Male      | 5.902       | 2.152      |
|                          | Male      | 5.972       | 2.291      |
|                          | Female    | 5.972       | 2.152      |
|                          | Female    | 6.041       | 2.222      |
|                          | Female    | 6.145       | 2.152      |
|                          | Female    | 5.763       | 2.083      |
|                          | Female    | 6.354       | 2.395      |
|                          | Female    | 6.111       | 2.222      |
|                          | Female    | 6.145       | 2.256      |
|                          | Female    | 5.520       | 2.013      |
|                          | Female    | 5.833       | 2.152      |
|                          | Female    | 5.868       | 2.118      |
|                          | Female    | 6.145       | 2.222      |
|                          | Female    | 6.215       | 2.291      |
| *T. alicantinus* Español, 1971 | Male     | 5.416       | 2.013      |
|                          | Male      | 5.972       | 2.152      |
|                          | Male      | 5.312       | 1.944      |
|                          | Male      | 5.416       | 1.979      |
|                          | Female    | 5.625       | 2.048      |
|                          | Female    | 5.729       | 2.038      |
|                          | Female    | 5.312       | 1.979      |
|                          | Female    | 4.965       | 1.909      |
|                          | Female    | 5.486       | 2.013      |
|                          | Female    | 5.104       | 1.805      |
|                          | Female    | 5.486       | 1.979      |
|                          | Female    | 5.208       | 2.013      |
|                          | Female    | 5.277       | 1.909      |
|                          | Female    | 5.659       | 2.013      |
|                          | Female    | 5.277       | 1.909      |
| *T. beltrani* Toribio, 1990 | Male (holotype) | 5.833       | 2.118      |
|                          | Female    | 5.729       | 2.222      |
|                          | Female    | 5.451       | 2.048      |

Table II. Values for two quantitative characters used in the analysis of the *Trechus martinezi*-lineage.
Figure 1. Habitus of *Trechus torressalai* n. sp. Scale bar: 1 mm.
well-defined striae. Both sexes show similar external morphology, except for the first two
segments of anterior tarsus, which are dilated in males. Median lobe of the aedeagus almost
straight; long apical lamina curved to the left and sword-shaped (Figure 3a–d); inner piece
of median lobe simple. Female genitalia: genital shield with a line of thorn-shape setae on
gonosubcoxite; spermatheca sacciform lacking spermathecal gland (Figures 4, 5).

**Type series**

Holotype: one male with printed data labels, Cueva de la Punta de Benimaquia, Dénia
(Alicante, Spain), col. J. Torres Sala. Paratypes: two females, same locality (and printed
data) as holotype.

**Note.** Two specimens (holotype and paratype) are deposited in the collection of Museu
Valencià d’Història Natural (Fundación Entomológica Torres Sala) and one paratype in
the collection of V. M. Ortuño (Department of Animal Biology, Alcalá University, Spain).

**Description**

**Length.** Length of holotype (from tip of mandible to elytron-apex) 6.0 mm (Figure 1);
length of paratypes 5.4–5.9 mm.

**Head.** Head (to anterior end of clypeus) slightly wider than long; in dorsal view two deep
frontal sulci border ocular areas on both sides and fronto-clypeal area towards the centre.
Medium-sized eyes, slightly convex. Swollen tempora almost as long as the eyes
(Figures 7b, 8a). Antennae filiform, densely setulose, in particular from 2nd to 11th
antennomeres. Mandible prominent, sharp. Labial and maxillary palps as typical in the
genus.

**Cephalic chaetotaxy (Figures 1, 7b).** Two pairs of supraocular setae (anterior and posterior);
two setae at both sides of clypeus (outer one largest); six setae on labrum, lateral setae more
elongate; one seta in the sulcus of each mandible.
Pronotum. Pronotum one-third wider than long, with the sides slightly sinuous in basal third; maximum width in the middle; basal margin rectilinear and smoothly prominent toward the rear angles; basal foveae smooth and deep; hind angles almost right. Disk convex, divided longitudinally by central sulcus branching off towards anterior and posterior angles. Lateral channel of regular width.

Pronotal chaetotaxy (Figure 1). One anterior seta on each side (almost in the first third) and one posterior seta next to hind angle.

Elytra. Elytra slightly pyriform, approximately three times longer than wide (from the lateral margin until the elytral suture); humeral margin weakly defined, basally oblique.

Figure 3. Trechus torressalai n. sp., aedeagus. (a) Median lobe in left lateral view; (b) median lobe in right lateral view; (c) median lobe in dorsal view; (d) median lobe in ventral view; (e) left paramere; (f) right paramere. Scale bar: 0.3 mm.
Disk convex with transverse microsculpture (Figure 2); eight well-defined striae clearly stippled.

Elytral chaetotaxy (Figure 1). Marginal umbilical series typical of Trechus (humeral area with four equidistant setae; subapical area with four setae, two anterior and two posterior). Each elytron with one setigerous pore beginning at 2nd stria (scutellar pore), two discal setae in the 3rd stria (anterior seta in anterior fifth and posterior setae in the half), similarly subapical seta present at end of 2nd to 3rd stria, two smaller ones near apical margin. Rudimentary wings.

Legs. Legs long and slender, without special characteristics; foretibia with a longitudinal sulcus; first two tarsal segments of male foreleg dilated.

Aedeagus. Aedeagus 1.4 mm long, with the median lobe almost straight (not arched); long and narrowed apex; apical lamina asymmetrical curved to the left and sword-shaped.
(Figure 3a–d). Inner sac very simple with a small lamina; there is wrapped up a field of spines in the wall of the praeputial tube (Figure 3a–d). Parameres subsymmetrical (of different lengths), the left heptasetulose and the right pentasetulose in distal extreme (Figure 3e, f).

Female genitalia (Figures 4, 5). External genitalia (Figure 5) formed by dimerous IX gonopods (gonocoxites and gonosubcoxites) and IX laterotergites. Both gonocoxite are unguiform, with two (or three) thorn-shaped setae of considerable size on its dorsal surface (the largest located near the external edge). Small groove near apex and above ventral surface, with two fine, sensorial setae. Gonocoxite as long as wide, approximately with 10 large, thorn-shaped setae in the internal margin. Wing-shaped, slightly sclerotized IX laterotergite with one group of setae over basal margin (approximately 20) and one more internal group (approximately six). Internal genitalia (Figure 4) completely membranous; short and large tubular-shaped vagina-bursa ending in spermatheca sacciform with densely folded walls. The spermatheca is located from an oblique way to the sagittal plane. The odd oviduct makes a contact with the spermathecal complex at the base of the spermatheca (on

Figure 5. *Trechus torressalai* n. sp., right external genitalia (=genital shield). Scale bar: 0.1 mm.
the right side in ventral view), displaying some longitudinal folds; interior densely covered in microfringes.

**Variability.** Among the only three known specimens distinct morphological variability is not present.

**Etymology.** The name of the species is after Mr Juan Torres Salas, the great Spanish entomologist, who stored the studied material of *Trechus* used in this description in his collection.

**Ecological features**

Punta de Benimaquia is a eutrophic cave, very rich in guano because it is the subterranean roost of a huge number of bats belonging to the species *Myotis nattereri* (Kuhl) and *Miniopterus schreibersii* (Kuhl). Thick strata of guano widely cover the floor of the cave producing a great quantity of ammonia, making some parts of the cave highly adverse to life. However, other parts of the cave, with a lower quantity of guano, are propitious for the invertebrate fauna, with a high humidity (close to 90%) and a good temperature (around 18°C). The previously known fauna from the cave were obtained from Sendra and Zaragoza (1982), Zaragoza and Sendra (1988), and some recent studies with unpublished records. This fauna is as follows: *Dicranolasma soerenseni* Thorell [Opilionida]; *Brachyanillus liocraninus* Simon, *Pallidumphantes lorifer* (Simon), *Eidmannella pallida* (Emerton), and *Cybaeodes* sp. [Araneae]; *Polydesmus dismilus* (Berlese) [Diplopoda]; *Nesiotoniscus dianae* (Vandel) and *Cristarmadillidium muricatum* (Budde-Lund) [Isopoda]; *Heteromurus nitidus* (Templeton) [Collembola]; *Porotachys bisulcatus* (Nicolaï), *Laemostenus* (Pristonychus) *terricta* (Herbst), *Anillochlamys bueni* Jeannel, *Conosoma* sp., *Aglenus brunneus* (Gyllenhal) [Coleoptera]; *Oxychilus* (Ortizius) *mercadali* Gasull [Mollusca Stylommathophora].

Figure 6. Body size of *Trechus martinezi*-lineage species.
Taxonomic position and discussion

Following morphological features proposed by Jeannel (1927), *Trechus torressalai* n. sp. must be included in the *T. fulvus*-group. Although this group has a rather morphological
homogeneity, several sub-groups can be distinguished. One of these sub-groups is the *T. martinezi*-lineage, only present in the north-eastern Betic Mountains (“Levante” biospeleological district *sensu* Bellés 1987 or Betic biospeleological region *sensu* Galán 1993). Four closely related species belonging to this lineage are known: *T. martinezi*, *T. alicantinus*, *T. beltrani*, and *T. torressalai* n. sp.

The species belonging to this lineage have a particular aedeagus, with a long apical lamina, curved to the left and sword-shaped. This feature is unknown among species belonging to the *T. fulvus*-group and it could represent a synapomorphy already present in the common ancestor of these species. The spermathecal complex is very similar in the four species and it is even similar to other species like *T. fulvus* and perhaps to the rest of the group.

If only qualitative features are studied, differentiation among species belonging to the *T. martinezi*-lineage is difficult. However, the size of the eyes is a useful feature: *T. beltrani* (this is a species that lives in fissures and the mesocavernous shallow substratum) and *T. alicantinus* (troglobitic) have smaller eyes than the other species (*T. martinezi* and *T. torressalai* n. sp.) (Figures 7, 8). Toribio (1990) misunderstood this feature and described *T. beltrani* as a species with “ausencia total de ojos”. Of course this was a mistake because this species has eyes (Figures 7d, 8d), although these are obviously in a regressive stage. *T.
*martinezi* and *T. torressalai* n. sp., both cave-dwelling species, have slightly bigger eyes (moderate microphthalm) (Figures 7a, b, 8a, b).

The best feature to differentiate these species is the shape of the median lobe of the aedeagus (Figures 3, 9–11) (not the inner sac, similar in the four species).

If we use quantitative features, such as the size (length and width) of adults (Table II; Figure 6), we observe that *T. alicantinus* is the smallest species and *T. martinezi* is the biggest one. However, there is an overlap in range (=5.4–6.0 mm) between both species, where we find also the ranges of *T. beltrani* and *T. torressalai* n. sp. (Figure 6). So these biometric data are not conclusive for distinguishing the species.

One possible hypothesis is that the four species could represent only one widely polytypic species. However, it seems that this hypothesis of reductionism is not correct because each species represents a totally isolated population with stable morphological features (aedeagus and the size of the eyes). Therefore, we think they are valid species, in which divergence is rather recent (quantum model of geographical speciation). As a result of this, we have a group of sibling species isolated in different hypogean localities. Among the genus *Trechus* there are many other examples of sibling species whose differences are

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Figure 9. *Trechus martinezi*, aedeagus. (a) Median lobe in left lateral view; (b) median lobe in right lateral view; (c) median lobe in dorsal view; (d) median lobe in ventral view; (e) left paramere; (f) right paramere. Scale bar: 0.3 mm.
smaller than in the studied group. These consist of very light differences in the male genitalia and frequently it is necessary to know, previous to their determination, the locality from where they were collected. In the Iberian Peninsula we have several examples of binomial species, such as the woodland species *Trechus distigma* Kiesenwetter and *Trechus ceballosi* Mateu (see Mateu 1953), the epigeous-lucifugous species *Trechus fulvus* and *Trechus lallemantii* Fairmaire (see Jeannel 1927), or the cavernicolous species *Trechus beusti* (Schaufuss) and *Trechus pieltaini* Jeannel (see Ortuño and Marcos 2003).

Key to the species of the *T. martinezi*-lineage

1. Tempora with a slight sinuation (Figure 7c, d); eyes clearly reduced (not convex).
   Tempora longer than eyes (Figures 7c, d, 8c, d) . . . . . . . . . . . . . . . . . . . . . . 2
Tempora with a distinct angle (Figure 7a, b); eyes slightly reduced, slightly convex and as long as tempora or slightly longer (Figures 7a, b, 8a, b) .... 3

2. Aedeagus with a short apical lamina with its tip truncated and slightly hook-shaped (Figure 11a–d). Very reduced eyes (more visible in their posterior margin) (Figures 7d, 8d) ....... Trechus beltrani Toribio [Antennae in T. beltrani are not longer than in T. alicantinus against the opinion of Toribio 1990]

– Aedeagus with twisted apical lamina, slightly longer and narrower (Figure 3a–d). Elytral striae clearly pitted (Figure 12a) ....... Trechus torressalai new species

3. Aedeagus with its short and wide apical lamina barely twisted (Figure 9a–d). Elytral striae barely pitted (Figure 12b) ....... Trechus martinezi Jeannel

– Aedeagus with a distinct angle (Figure 7a, b); eyes slightly reduced, slightly convex and as long as tempora or slightly longer (Figures 7a, b, 8a, b) .... 3

2. Aedeagus with a short apical lamina with its tip truncated and slightly hook-shaped (Figure 11a–d). Very reduced eyes (more visible in their posterior margin) (Figures 7d, 8d) ....... Trechus beltrani Toribio [Antennae in T. beltrani are not longer than in T. alicantinus against the opinion of Toribio 1990]

– Aedeagus with twisted apical lamina, slightly longer and narrower (Figure 3a–d). Elytral striae clearly pitted (Figure 12a) ....... Trechus torressalai new species
Biogeographical comments

The *T. fulvus*-group has an Ibero-Mauretanian distribution with the exception of *T. fulvus* Dejean, a species with a wider northern distribution reaching Norway (Jeannel 1927). In the Iberian Peninsula the *T. fulvus*-group has 10 species: *T. martinezi* Jeannel, *T. alicantinus* Español, *T. beltrani* Toribio, *T. torressalai* n. sp., *T. machadoi* Jeannel, *T. breuili* Jeannel, *T. lallemantii* Fairmaire, *T. fulvus* Dejean, *T. arribasi* Jeanne, and *T. gloriensis* Jeanne. All these species (except *T. fulvus*) have a very reduced distribution and are always linked to subterranean environments. *T. martinezi*, *T. alicantinus*, *T. beltrani*, and *T. torressalai* n. sp. are endemic species from the north-eastern Betic Mountains and they form the *T. martinezi*-lineage (Figure 13): *T. martinezi* lives in a cave in the Mariola orographical sector; *T. alicantinus* is known from two caves in the Serrella orographical sector; *T. beltrani* lives in the mesocavernous shallow substratum in the Serrella orographical sector (more exactly in

Figure 12. Detail of elytral striae. (a) *Trechus torressalai* n. sp.; (b) *Trechus martinezi*. Scale bar: 0.1 mm.
Sierra de Bernia); finally, *T. torressalai* n. sp. is only known from a cave in the La Marina orographical sector, in the vicinities of Dénia city.

During the Pleistocene glacial periods (mainly during Würm glaciation), the south and south-eastern Iberian Peninsula were covered by a a very moist and Mediterranean vegetation (Llobera and Valladares 1989) with a mesotherm and hygrophilous-associated fauna. Ancestors of the *T. martinezi*-lineage should be part of these woodland-refugium area communities (*sensu* Bellés 1987) from the north-eastern Betic Mountains. When climatic conditions changed, this lineage was affected by a dramatic loss of distribution areas (the vegetation communities also changed). Part of these populations could find a safe refuge in some subterranean environments where they survived. Genetic drift was increased by the founder effect arising from a cladogenetic process which led to the *T. martinezi*-lineage.

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