

# Phylogenetic evidence for multiple invasions and speciation in caves: the Australian planthopper genus *Solonaima* (Hemiptera: Fulgoromorpha: Cixiidae)

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**Abstract.** The Australian genus *Solonaima* comprises thirteen described plus two undescribed species. Six are cavernicolous, obligate or not, and are found in different caves. The phylogeny presented here confirms the monophyly of the genus. This phylogeny was compared with the estimate obtained using the method of Marques and Gnasparini, who recommend coding characters susceptible to parallelism differently from the others. Further comparison was made with a cladogram derived from the matrix from which characters susceptible to parallelism were withdrawn. Scenarios concerning historical invasions of caves were tested using phylogenetic inference. The most-parsimonious hypothesis proposed four invasions of the caves, within two of which a diversification of species took place.

## Introduction

The Australian planthopper genus *Solonaima* Kirkaldy, 1906 comprises nine epigeal species and six cavernicolous species, and could provide an excellent model to test hypotheses on the evolution of the choices of habitat made by the species of the group for the following reasons: the known *Solonaima* species have been postulated to form a monophyletic unit (Hoch & Howarth, 1989b), which will be tested by a cladistic analysis; it contains extant epigeal and cavernicolous species; there is information on geographical distribution and ecology; the cavernicolous species colonize a wide variety of cave habitat.

## Description of the cave areas

*Chillagoe Tower Karst.* The towers are the remnants of a Silurian reef that was inundated, eroded and transformed into a band of Karst towers more than 150 km in length (Ford, 1978), reaching from south of Chillagoe northwards to Mt. Mulgrave. Only a small fraction has been explored. In the Chillagoe area, the Karst towers are up to 100 m high

and each may contain several caves. The towers are separated by sediments that form the surrounding plain.

*Lava tube at Undara (Bayliss Cave).* Most of the passage is a deep cave zone, in permanent darkness, with high humidity and sometimes high carbon dioxide concentrations (Howarth, 1988; Howarth & Stone, 1990). Root curtains of epigeal plants hang from the ceiling and provide the food resources for *S. baylissa* (Hoch & Howarth, 1989a).

The evolution of obligate cavernicolous or troglitic terrestrial organisms has been controversial. Different hypotheses have been formulated and/or modified with time (Vandel, 1964; Culver, 1982; Howarth, 1987). The more traditional view, the so-called relict hypothesis (Vandel, 1964), assumes that changes in climatic conditions on the surface are prerequisite of cave adaptation and troglitic populations trapped inside caves. After extinction or extirpation of surface populations, such troglitic populations gradually acquire cave adaptations and develop trogliticisms, such as loss of eyes, wings and bodily pigment (Howarth, 1972; Hoch, 1994). The discovery of rich, diverse troglitic faunas on 'relatively' young oceanic islands in the tropics, like Hawaii, which may not have experienced climatic extremes, led Frank Howarth to propose an alternative theory (Howarth, 1972, 1980, 1981). He postulated that the driving force for the evolution of obligate cavernicolous organisms was the utilization of previous unexploited food resources, e.g. tree roots, which

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penetrate the ceiling of Hawai'ian lava tubes and abound in the caves. In this model, the so-called adaptive shift hypothesis, species formation occurs through parapatric or sympatric speciation, with closely related species continuing to exist on the surface in the same area. According to Howarth's hypothesis, the process of cave adaptation is a case of adaptive radiation, rather than the response to adverse ecological conditions. He also recognized that there is no evidence for a linear relationship between time and the degree of any structure loss. Acquisition of troglomorphy will be a function of several factors, which are not mutually exclusive (Howarth, 1987).

## Materials and methods

### Morphological phylogeny

The phylogeny presented here was based on thirty-three characters (Table 1, Appendix), thirty-one of which were informative. Three species formed the outgroup, *Cixius nervosus* (Linnaeus, 1758), *Tachycixius pilosus* (Olivier, 1791) and *Hemitropis seticulosus* (Lethierry, 1874). The ingroup contained fifteen species of *Solonaima*: *S. baylissa* Hoch & Howarth, 1989; *S. bifurca* Hoch, 1988; *S. cedrivula* Hoch, 1988; *S. halos* Hoch & Howarth, 1989; *S. irvini* Hoch & Howarth, 1989; *S. minuta* Hoch, 1988; *S. ornata* Hoch, 1988; *S. pallescens* (Distant, 1907); *S. pholetor* Hoch & Howarth, 1989; *S. riocampa* Hoch, 1988; *S. solonaima* Kirkaldy, 1906; *S. stonei* Hoch & Howarth, 1989, *S. sullivani* Hoch & Howarth, 1989; undescribed species 1 and 2. The characters used for this phylogeny were selected from the head capsule, legs, wing venation, dorsal part of the thorax and male and female genitalia. The characters were directly observed or collected from the literature for some species (Hoch, 1988). Except for the undescribed species 1 and 2, all the *Solonaima* spp. observed for this study are kept in alcohol in the Museum für Naturkunde in Berlin.

### Cladistic methods

The analysis was performed with PAUP version 4.0b.10 (Swofford, 1996) and MACCLADE version 4.05 (Maddison & Maddison, 2002). Calculation of the index of Bremer (1994) was performed for the resolved nodes of the retained cladogram. Rooting the cladogram was made by outgroup comparison with a basal polytomy. All uninformative characters were excluded when the consistency index (CI) was calculated. All the characters had the same weight. 'Nonsensical' character states were coded with a dash and the nonobserved character states with a question mark. PAUP treats both as uncertain characters. The characters were not ordered or orientated. The three options of optimization available in PAUP were used (Acctran, Deltran and Minf). We performed a branch-and-bound search. A series of cladistic analyses was performed with the same matrix, except that each species included in the outgroup (three in

**Table 1.** Data matrix for *Solonaima* spp. and three outgroup taxa: *Cixius nervosus* (Linnaeus, 1758), *Tachycixius pilosus* (Olivier, 1791) and *Hemitropis seticulosus* (Lethierry, 1874).

	-	-	-	-	-	-	-	-	1	1	1	1	1	1	1	1	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
<i>S. solonaima</i>	1	0	0	0	0	?	0	0	?	0	1	1	0	1	0	1	1
<i>S. pallescens</i>	1	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	1
<i>S. ornata</i>	1	0	0	0	0	0	1	1	?	0	1	1	0	1	0	0	2
<i>S. minuta</i>	1	0	0	0	?	?	0	0	?	0	1	1	0	1	0	0	1
<i>S. cedrivula</i>	1	0	0	0	?	?	0	1	?	0	1	1	1	1	0	0	2
<i>S. riocampa</i>	1	0	0	0	0	0	0	0	?	1	1	1	1	1	0	1	1
<i>S. bifurca</i>	1	0	0	0	?	?	0	1	?	0	1	1	1	1	0	0	1
<i>S. sullivani</i>	1	0	0	0	0	?	0	0	1	0	1	0	1	0	1	0	1
<i>S. pholetor</i>	1	0	0	1	0	0	0	1	1	0	1	1	0	1	0	1	1
<i>S. stonei</i>	1	0	0	1	0	0	0	1	1	0	1	1	0	1	0	0	1
<i>S. halos</i>	1	0	1	2	1	0	0	1	1	1	1	1	0	1	0	1	1
<i>S. irvini</i>	1	0	1	2	1	0	0	1	1	1	1	1	0	1	0	1	0
<i>S. baylissa</i>	1	0	2	3	2	1	1	1	1	1	0	-	-	0	0	0	0
n. sp. 1	1	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1	1
n. sp. 2	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1
<i>C. nervosus</i>	0	0	0	0	0	0	0	0	0	1	0	1	2	0	1	1	1
<i>T. pilosus</i>	0	0	1	0	0	0	0	0	0	1	0	1	2	0	1	0	1
<i>H. seticulosus</i>	1	1	2	0	0	0	0	2	0	1	0	0	-	-	1	0	0

	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3
	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3

<i>S. solonaima</i>	0	?	?	?	?	0	0	0	1	1	1	1	1	0	0	0	0
<i>S. pallescens</i>	0	?	1	?	0	?	?	?	?	?	0	2	2	1	0	0	0
<i>S. ornata</i>	?	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?
<i>S. minuta</i>	?	?	1	?	0	0	1	1	1	0	0	1	1	0	0	1	1
<i>S. cedrivula</i>	?	?	?	?	?	?	0	0	0	1	0	0	?	1	0	1	0
<i>S. riocampa</i>	?	?	?	?	?	?	0	1	0	0	0	3	1	1	0	0	0
<i>S. bifurca</i>	?	?	1	?	0	1	0	0	0	0	0	0	0	1	0	1	0
<i>S. sullivani</i>	1	0	?	1	?	0	0	1	0	1	1	1	1	0	0	0	0
<i>S. pholetor</i>	0	0	1	1	0	1	0	0	1	0	1	2	1	0	0	0	0
<i>S. stonei</i>	0	0	1	1	0	1	0	0	1	0	2	2	0	0	0	0	0
<i>S. halos</i>	0	?	1	?	1	0	0	0	0	0	1	1	1	0	0	1	1
<i>S. irvini</i>	1	0	1	1	1	0	0	0	0	0	2	1	1	0	0	1	1
<i>S. baylissa</i>	1	0	1	1	0	0	0	0	1	0	1	1	0	1	1	0	1
n. sp. 1	0	0	1	1	0	1	0	0	1	0	1	1	1	0	0	0	0
n. sp. 2	0	?	?	?	?	?	0	0	0	1	0	3	1	1	0	0	0
<i>C. nervosus</i>	1	1	0	0	0	2	0	0	0	0	0	0	0	1	1	0	0
<i>T. pilosus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>H. seticulosus</i>	0	1	1	1	0	2	0	0	0	0	0	0	0	1	0	0	0

total) was placed alternatively in the first position in the matrix, to detect any changes between relationships of outgroup taxa. Such a disruption within a cladogram has been observed previously (Soulier-Perkins, 2001).

A second analysis with PAUP was executed with a matrix in which two characters (4 and 5) were coded as suggested by Marques & Gnaspini (2001). The character 3 coding for the ocellus was retained because within the Cixiidae, the absence of the median ocellus or its reduction in size is observed not only within the cavernicolous species but also in epigeal species. Even if we agree with criticisms of

this methodology (Desutter-Grandcolas *et al.*, 2003), we were curious to see how this coding could affect the resolution, and if any information was useful. In the Marques and Gnaspini method, each character suspected of having undergone a parallel evolution is included in the matrix but coded differently from the other characters. The procedure should allow us to escape the two errors that we may have committed: in proposing them as true synapomorphies if they are not or disregarding them as true synapomorphies if they are (Marques & Gnaspini, 2001). A third analysis was performed with these two characters removed from the matrix.

#### Optimization of attributes

Characters for which the primary homology is not attested cannot be introduced in a phylogenetic analysis. Such characters are called attributes. However, in reference to an already built phylogeny, they can be optimized and analysed. Thus, habitat can be treated as an attribute (Desutter-Grandcolas, 1997).

Mapping of the habitats, cavernicolous or epigeal, on the obtained phylogenetic reconstructions of the group *Solonaima*, allows us to present the most-parsimonious hypothesis on the evolution of habitat choice in this genus. Such a scenario could be presented as such, as no further information is available. However, this hypothesis can be collated to regional geological events where the cavernicolous species were found and checked for any possible incongruence between geographical/geological events and the postulated habitat evolution of the *Solonaima* spp. The methodology followed appears similar to that proposed by Zeppelini Filho (1997), except that here the optimization of the attribute was considered as a valid methodology that produces a testable hypothesis subject to refinement if and when further information becomes available.

### Characters, troglomorphism and character descriptions

#### Varying degrees of troglomorphism

Within the cavernicolous species, some characters have undergone alterations during the evolutionary process of cave adaptation, namely reduction of tegmina and wing and loss of eyes and pigmentation. The degree of troglomorphism does not correspond with the ages of the caves in which the species occur. When we observe these characters, we cannot know if they result from parallel evolution due to independent adaptation to the same environment or if they are inherited from a single common ancestor. These phenomena make the use of these characters for phylogenetic analysis difficult.

*Solonaima sullivanii* from Mt. Mulgrave shows virtually no modification from its surface relatives. It occurs in two vertical caves that are subject to desiccation by cool air flow

from the outside within a single tower and is therefore considered as presumably troglophile by Hoch & Asche (1988). However, this species was never found outside the cave, so it could very well be a troglobite.

*Solonaima pholetor* and *S. stonei* from the Chillagoe Karst show some eye and wing reduction, but are still capable of flight. They are considered trogliphilic, facultative cave species (Hoch & Asche, 1988), but as with *S. sullivanii* no epigeal representatives have been found and, as such, they could very well be considered as troglobites. Such a course is tempting to the author, as these two species do show some troglomorphisms.

*Solonaima irvini* and *S. halos* are nearly blind, have non-functional wings and are largely pigmentless. They are restricted to deeper passages with stagnant air and are regarded as an obligate cavernicolous (troglitic) species (Hoch & Asche, 1988).

*Solonaima baylissa* is totally blind, flightless and pigmentless, collected only from the deep cave zone and recognized as an obligate cave species by Hoch & Asche (1988). Specimens of this troglobite were found in caves some 30 km distant from each other. The possibility of subterranean communication cannot be ruled out.

#### Character descriptions

**Head capsule.** The lateral ocelli are generally present in most *Solonaima* spp., but are reduced or absent in some cavernicolous species. Some reductions are also observable for the compound eyes, which are missing in *S. baylissa*. The median ocellus is reduced or absent in some species of the ingroup and on *Tachycixius pilosus* and *Hemitropis seticulosus*, which belong to the outgroup. The frons is generally longer than wide and bears a median carina that stretches longitudinally. This carina can be absent, as in *S. ornata* and *S. baylissa*. Within the ingroup, except for *S. baylissa* for which the vertex is extremely reduced, a carina divides the vertex into two fields. The posterior field forming an almost perpendicular angle with the anterior field. The antennae of *Solonaima* spp. have an enlarged pedicel, the length of which is at least three times greater than its diameter.

**Wings.** Undergoing the evolutionary process of cave adaptation, the wings present reductions in some species. These reductions are the result of a series of modifications of characters found on the wings. Only one character could be coded for the mesothoracic wings. Some species show only one point of insertion on the basal cell for Sc + R and M, whereas among others M arises distinctly from Sc + R.

**Legs.** The metathoracic tibiae possess no lateral spines, except for two species used as the outgroup, *Cixius nervosus* and *Tachycixius pilosus*. The only studied species that has less than six apical spines on the metathoracic tibiae is *Hemitropis seticulosus*.

**Female characters.** In all the *Solonaima* spp., anal tubes were observed to be short but with a clearly defined apex. Observed posteriorly, the female genitalia shows a zone of wax secretion, but only for the outgroups *Tachycixius pilosus* and *Cixius nervosus* the secreting area is not separated medially in two zones. For these two taxa as well, the length of their anal tube from its base to urite X is two times longer than its diameter. By contrast, *Hemitropis seticulosus* and the six *Solonaima* spp., for which the female genitalia were observed, have this part of the anal tube short and its length is less than two times its diameter.

**Male characters.** The anal tube may present some specific features. For the species *S. minuta*, *S. halos* and *S. irvini*, the base of the anal tube shows two lateral extensions. The phallic complex presents four types of spines: the terminology used to designate them is the same as in Hoch & Howarth (1989b).

## Results

### Phylogeny hypothesis (Fig. 1)

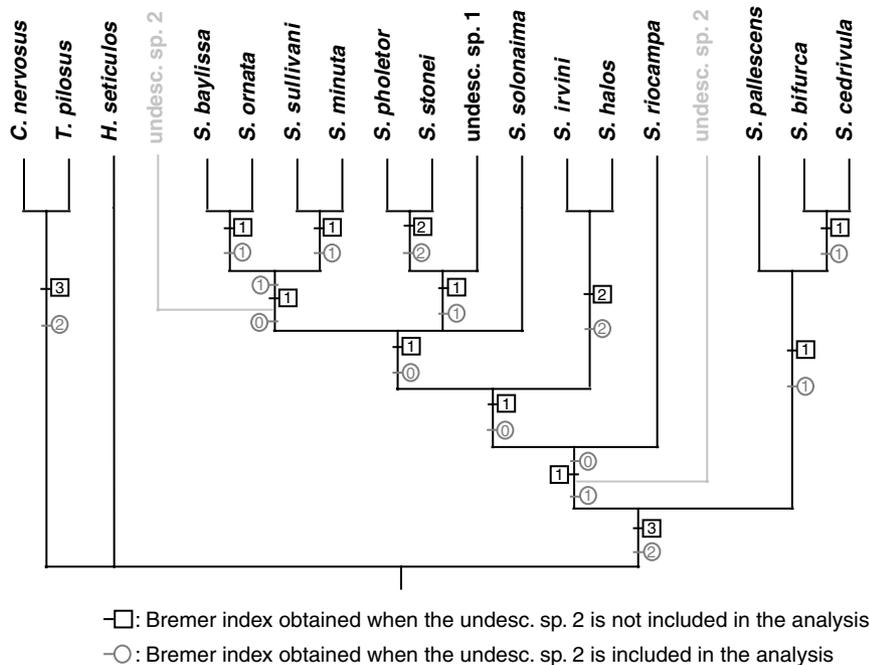
Two cladograms were obtained (length = 76 steps, CI = 0.58, retention index (RI) = 0.64). In both cladograms the ingroup, the genus *Solonaima*, appears as monophyletic, but even if the species chosen for the outgroup are suspected to be close relatives, we cannot conclude definitively that the genus *Solonaima* is a monophyletic lineage.

The only difference between the two cladograms obtained is the place occupied by undescribed species 2 that remains uncertain, as indicated in Fig. 1. The Bremer index for each

resolved node is presented (Fig. 1). The switch of position of this species in the two cladograms is probably linked to the fact that we only possess a single headless specimen. For this reason, many characters were coded as unknown for that species. We proceeded to a new search without this specimen and found only one tree (Fig. 1) (length = 75 steps, CI = 0.59, RI = 0.64).

The ingroup is characterized by three synapomorphies: character 11, the pedicel of the antennae is at least three times longer than its diameter; character 14, the two fields composing the vertex are positioned at almost 90° to each other; and character 15, the junction between the frons and clypeus is almost straight. Together the sister species *S. cedrivula* and *S. bifurca* plus the species *S. pallescens* form a monophyletic lineage, which is the sister group of all other *Solonaima* spp.

The result of the second analysis, according to Marques & Gnaspi (2001) methodology, gave two equally parsimonious cladograms (tree length = 81, CI = 0.55, RI = 0.62). These two trees have the same configuration as those obtained previously. A similar result was obtained if characters 4 and 5 were excluded from the matrix. Two trees were found with length = 71, CI = 0.55, RI = 0.62. The organization of the taxa within the cladograms for these two trees was identical to that found with the Marques & Gnaspi methodology and, equally, to that found including characters 4 and 5. Thus, the use of their method did not give a different result from the two others. The cladograms presented no better resolution, and the CI and RI were lower. For these reasons, the only phylogenetic hypotheses that were retained are presented in Fig. 1 and were obtained using the matrix in Table 1. The scenario test, presented here, was based on these reconstructions.



**Fig. 1.** Cladogram obtained with thirty-three characters, three taxa in the outgroup, with fourteen or fifteen *Solonaima* spp., depending on whether the undescribed species 2 (in grey) is included in the analyses. The Bremer index (or decay index) is indicated for each node

Scenario test (Figs 2, 3)

Which habitat did the ancestor of the *Solonaima* group occupy? A cave or an epigeal habitat? After mapping on the phylogeny the occurrence of the actual cavernicolous and epigeal taxa, we optimized it and retained the most-parsimonious hypothesis (Figs 2, 3) according to which the ancestor of the genus *Solonaima* was living in an epigeal habitat (four steps) rather than in a cave, for which six steps are needed. Four invasions of the subterranean environment are observed. After colonization of this new habitat, two species seem to have undergone speciation and these two ancestral species gave the actual species *S. stonei* and *S. pholetor* from the first ancestor and *S. halos* and *S. irvini* from the second. The caves in which *S. sullivani*, *S. stonei* and *S. pholetor* are found are open, wide and in some zones appear as if to overlap with the surface habitat. This may explain why these species are not so troglomorphic, even if restricted to these caves. In the karst towers where *S. halos* and *S. irvini* are found, the caves seem to be deeper and more isolated from the exterior. Finally, the last type of cave we could identify are those in which *S. baylissa* is found. These are very deep, humid, and in total darkness. The concentration of carbon dioxide in the air is high, perhaps up to 200 times ambient (Howarth, 1987). If we map these three different habitats onto the phylogenetic trees, the most-parsimonious scenario suggests that the ancestor was an epigeal species, then four times the ancestors of the actual species colonized the three different types of habitat (four steps) and in two of them they diversified. All scenarios in which the *Solonaima* spp. would have colonized the open cave habitat from which they could move to a deeper environment or return to the epigeal life, are longer (seven to eight steps).

Discussion

What was, or is, the driving force for the evolution of cave adaptation in *Solonaima* populations? Different scenarios are conceivable.

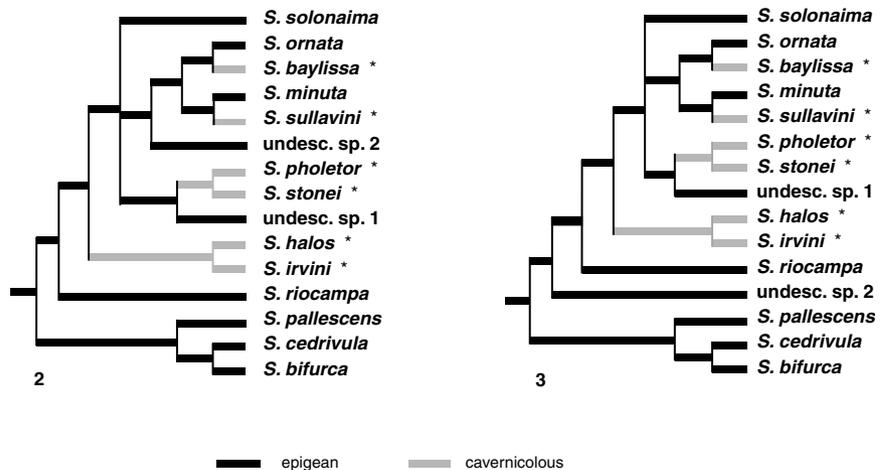
Some facts appear to point to the scenario supporting the relict hypothesis for the evolution of cave-adapted *Solonaima* species, like the allopatric distribution of cavernicolous and epigeal species (Fig. 4). Deterioration of ecological conditions on the surface: it is conceivable that in the course of the gradual aridification of the Australian continent during the Miocene, when rainforests retreated to less than their current refuge along and east of the Great Dividing Range, some *Solonaima* populations sought shelter in the more humid cave habitats and developed cave adaptations, whereas others retreated with the rain forests where they survive today. This is supported by the observation of adult Cixiidae other than *Solonaima* spp., which are often found in caves where, in dry summers, they apparently hide during the day.

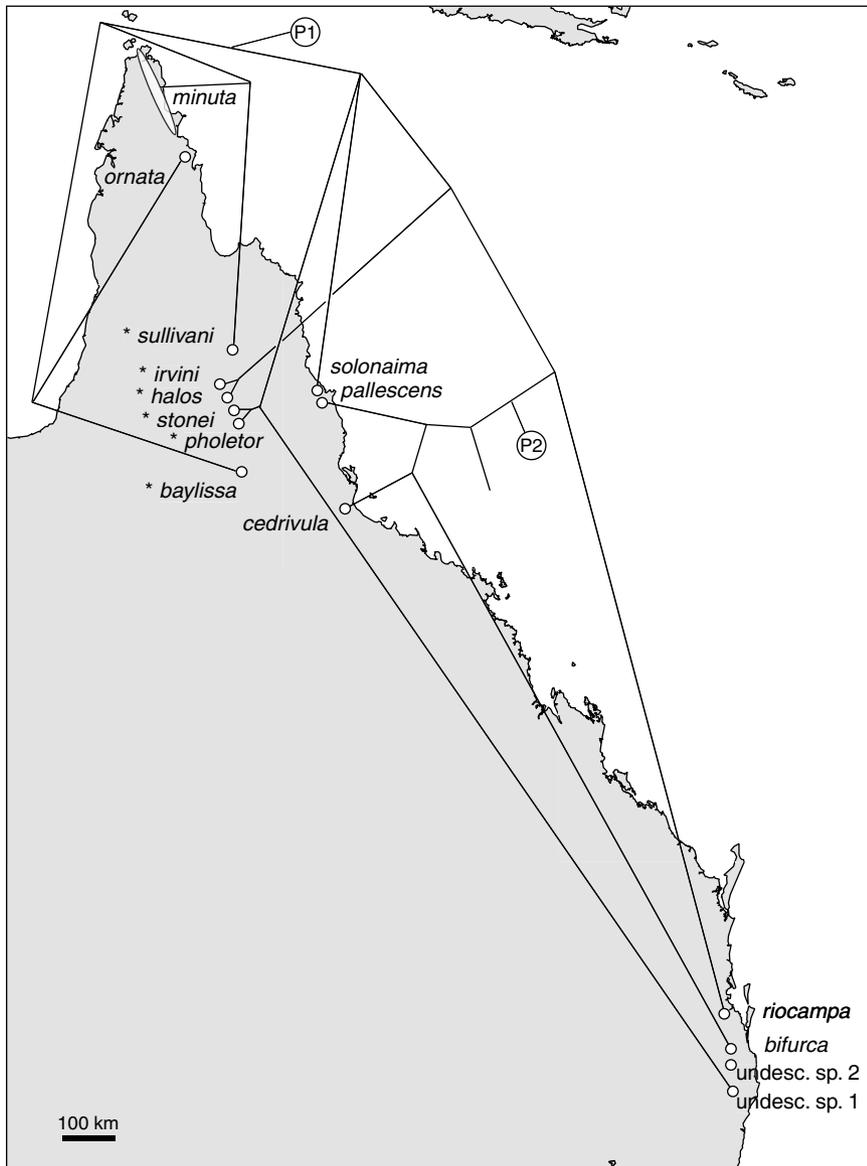
Other facts support an adaptive shift. When the caves started to present an abundant number of tree roots, some *Solonaima* populations invaded the caves to utilize unexploited food resources. Such a shift would be facilitated if these populations presented some features of preadaptation to such a cave environment. Within the family of Cixiidae, the absence of compound eyes in the early larval stages and larvae feeding on roots have been observed (Sforza *et al.*, 1999). Can such characteristics be considered as preadapted features?

No return to the epigeal life is observed in the optimization retained. In the case of the first hypothesis, because the *Solonaima* spp. took refuge in caves as the rainforest disappeared around them, the cavernicolous species became trapped and isolated, as if upon an island. In the case that the *Solonaima* spp. did enter caves to exploit newly abundant food resources, they would have had no special reason to return to the surface. These species can even diversify within the caves, which is as observed on the cladograms. A third, hybrid hypothesis, could equally be considered.

Even if the *Solonaima* spp. went into the caves at a different period in time to use new food resources, when the aridification of Australia started, even if some species were already in the caves, others joined them to take shelter. The disappearing forest around these caves could be a

**Figs 2, 3.** Scenario hypotheses on the evolution of life habitat for the genus *Solonaima*, depending on the ancestral optimization. The shortest hypothesis is found with an epigeal ancestor (four steps). \* identifies the cave species in the cladogram





**Fig. 4.** Superimposition of the phylogenetic hypothesis on the geographical distribution of the genus *Solonaima*. P1 and P2, possible positions of the undescribed species 2 in Fig. 1. \* indicates the name of the cave species

reason for the absence of a return to an epigean life within the actual species observed.

**Conclusion**

Withdrawing the two characters susceptible to parallel evolution or using the Marques & Gnaspini method led us to obtain two cladograms. These cladograms were similar to the two previously reconstructed, except for the CI and RI, which were lower. For this group of insects and with regard to the characters used to build the phylogeny, our method seems to be the most appropriate. The ancestor of the group *Solonaima* lived in an epigean habitat. Four cave invasions were observed throughout the evolution of this genus. In

two of these, a diversification of species took place in the cave environment. Currently, six species of cave-dwelling *Solonaima* are known. No return to epigean life was observed. Many caves are unexplored, which makes it likely that some undescribed species of *Solonaima* remain to be discovered. Adding the characters of these species to our matrix and running a new cladistic analysis should be a good test to see if our scenario remains valid on the obtained tree.

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## Appendix

### Character list for the matrix in Table 1

1. *Metathoracic tibia laterally armed with spines*: (0) yes; (1) no.
2. *Number of spines on the apex of the metathoracic tibia*: (0) six; (1) less than six.
3. *Median ocellus*: (0) fully developed; (1) strongly reduced; (2) absent.
4. *Composed eyes*: (0) dark brown and fully developed; (1) ommatidia-bearing area slightly reduced; (2) present, ommatidia-bearing area reddish and small; (3) absent.
5. *Lateral ocelli*: (0) clearly identifiable; (1) present but reduced to half its size; (2) absent.
6. *Frons shape*: (0) width narrower along vertex; (1) width narrower along clypeus margin.
7. *Median carina of the frons*: (0) present; (1) obsolete or absent.
8. *Proportions (length): frons (f)/clypeus (cly)*: (0)  $f < cly$ ; (1)  $f = cly$ ; (2)  $f > cly$ .
9. *Length of labium*: (0) short: maximum length does not extend beyond metatrochanters; (1) long: maximum length extends beyond metatrochanters.
10. *Length of frons*: (0) more than two times its width; (1) less than two times its width.
11. *Length of the pedicel of the antennae compared with its diameter*: (0) not longer than two times its diameter; (1) at least longer than three times its diameter.
12. *Transverse carina cutting the vertex in two fields*: (0) absent; (1) present.
13. *Anterior field of the vertex when vertex separated transversally by a carina*: (0) rectangular; (1) pentagonal; (2) rounded anteriorly.

14. *Vertex with two fields positioned almost 90° to each other:* (0) no; (1) yes.
15. *Junction between frons and clypeus:* (0) almost straight; (1) strongly curved.
16. *Arising of Sc + R and M on the tegmina:* (0) from two different points on the basal cell; (1) from the same point.
17. *Tegmina: transversal vein between M and Cu veins:* (0) absent; (1) present between veins after each has undergone one independent division; (2) present and prior to M splits.
18. *Median carina of the prothorax:* (0) present; (1) absent.
19. *Apex of anal tube of the females:* (0) short but clearly defined; (1) apex missing.
20. *Female wax-secreting area medially separated by a membranous area:* (0) no; (1) yes.
21. *On lateral view, length of female anal tube between its base and urite X:* (0) two times longer than its diameter; (1) much shorter than two times its diameter.
22. *Female pregenital sternite:* (0) not abruptly bent; (1) abruptly bent.
23. *Upper margin of gonostyli:* (0) developed into a sharp edge orientated anteriorly; (1) developed into a sharp edged orientated dorsomedially; (2) rounded.
24. *On lateral view, upper posterior margin of the gonostyli:* (0) rounded; (1) flattened.
25. *On lateral view, junction between dorsal and posterior margin of the pygophore:* (0) continuous and rounded; (1) sharp and shaped like a small process.
26. *Angle at the junction between upper and anterior margin of the pygophore, on lateral view:* (0) >45°; (1) ≤45°.
27. *Median dorsal lump on the periandrium:* (0) absent; (1) present.
28. *Spine a of the periandrium:* (0) absent; (1) present and orientated posteriorly; (2) present and orientated dorsally; (3) present and orientated ventrally.
29. *Spine b of the periandrium:* (0) absent; (1) present and simple; (2) present and ornamented apically; (3) present and ornamented basally.
30. *Spine c of the periandrium:* (0) absent; (1) present.
31. *Spine d on the male genitalia:* (0) present; (1) absent.
32. *Male anal tube:* (0) not hood-shaped; (1) hood-shaped.
33. *Lateral basal extensions on the male anal tube:* (0) absent; (1) present.