



The first fossil spider cricket (Orthoptera: Gryllidae: Phalangopsinae): 20 million years of troglobiomorphosis or exaptation in the dark?

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A new spider cricket (Orthoptera: Gryllidae: Phalangopsinae) is described from an adult female preserved in Early Miocene (Burdigalian) amber from the Dominican Republic. *Araneagrillus dylani* gen. et sp. nov. represents the first fossil record of Phalangopsinae, and is assigned to the tribe Luzarini, subtribe *Amphiacustina* stat. nov. A cladistic analysis of *Amphiacustina* places *Araneagrillus* gen. nov. within a clade comprising *Arachnopsita*, *Leptopedetes*, *Longuripes*, *Mayagrillus*, *Nemoricantor*, and *Prolonguripes*. This clade is the sister group to a clade comprising *Amphiacusta*, *Cantrallia*, and *Noctivox*. The results of this analysis suggest that: (1) the common ancestor of all *Amphiacustina* was epigean, and was likely to have been cavicolous and/or straminicolous; (2) strict troglotism evolved twice within *Amphiacustina*, once in the lineage leading to *Noctivox* and again in the clade comprising *Mayagrillus*, *Arachnopsita*, *Longuripes*, and *Prolonguripes*; and (3) *Prolonguripes* is secondarily epigean, having reverted to life above ground. The occurrence of *Araneagrillus* gen. nov. in amber indicates that it was not troglotic, but was instead more likely to have been straminicolous, living on the ground and foraging amongst leaf litter. *Araneagrillus* gen. nov. possesses a number of characters that are usually considered to be adaptive to a troglotic life history, suggesting that many so-called troglobiomorphies are not adaptations to life in caves, but are instead likely to have been exaptive.

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ADDITIONAL KEYWORDS: *Amphiacustae* – Dominican amber – *Ensifera* – Neotropics.

Crickets of the subfamily Phalangopsinae (spider crickets) are agile, long-legged gryllids common in tropical and subtropical regions around the world. Readily identified by their spider-like habitus and prominent dark banding on the legs, phalangopsine crickets are primarily nocturnal, and are regularly encountered in the understory of tropical forests near ground level, in leaf litter, or amongst rocks or dead wood (Desutter-Grandcolas, 1995). Many species are cavernicolous, and frequent caves and dark rocky gullies, as well as man-made environs such as wells, drift-shafts, and the underside of wooden bridges (Otte & Alexander, 1983). Several species are gregarious: particularly the troglotic forms, which often

congregate in large numbers in caves, and have evolved complex population structures and courtship behaviours (Boake, 1984a, b; Desutter-Grandcolas, 1995). Other phalangopsine crickets have almost aposematic coloration, and are thought to mimic ants, although their relationships with other spider crickets are uncertain at present (Mesa & Zefa, 2004).

The classification of spider crickets is controversial. Several authors (e.g. Hebard, 1928; Zeuner, 1939; Otte & Alexander, 1983; Otte, 1994; Nischk & Otte, 2000) have regarded Phalangopsinae as a subfamily within Gryllidae, whereas others have elevated it to family status (e.g. Chopard, 1968; Desutter-Grandcolas, 1995; Mesa & Zefa, 2004; Prado, 2006). Desutter (1988) divided the spider crickets into three families, Paragrillidae, Neoacridae, and Phalangopsidae, although these families and their various

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subfamilies are regularly reorganized as subfamilies or tribes within Gryllidae, or synonymized with other gryllid subgroups (e.g. Otte & Alexander, 1983; Nischk & Otte, 2000; OSF, 2008). This ongoing systematic instability highlights the need for a rigorous and comprehensive phylogenetic analysis of the group. Nevertheless, it is clear that in terms of taxonomic diversity (see Desutter-Grandcolas, 1995), the spider crickets constitute one of the most speciose groups of Grylloidea, and it is perhaps surprising that they have been unknown as fossils until now. However, the cavernicolous and troglobitic habits of many Phalangopsinae probably reduces their preservation potential quite significantly, and might explain their prior absence from the fossil record. Herein, I describe the first fossil spider cricket: a new genus and species of the tribe Luzarini, subtribe Amphiacustina stat. nov., from Early Miocene Dominican amber.

The Luzarini comprise some 191 species in 53 genera distributed in South and Central America, the West Indies, and Central Africa. This disjunct distribution suggests a Mesozoic origin for the group, indicating that they radiated prior to the break-up of Gondwana during the Cretaceous period. The tribe is distinguished from other Phalangopsinae on the basis of the male genitalia (discussed below), and although the relationships of a few subgroups have been examined in much detail (Desutter, 1987, 1988; Desutter-Grandcolas, 1992, 1993, 1999), a comprehensive phylogeny for the entire tribe is still wanting. Nevertheless, several subgroups have been recognized within Luzarini, supported by numerous synapomorphies concerning the structure of the male epiphallus (e.g. Desutter-Grandcolas, 1992). Of these subgroups, Amphiacustae Hubbell, 1938 is perhaps the best known, with their taxonomy and phylogeny having been studied intensively by Desutter-Grandcolas (1992, 1993, 1995, 1999), Desutter-Grandcolas & Otte (1997), and Desutter-Grandcolas, D'Haese & Robillard (2003). Because of their cavernicolous and troglobitic habits, along with the availability of phylogenetic data, the Amphiacustae have proved valuable in testing hypotheses of troglobiomorphosis, and the evolution of troglobitic life histories (Desutter-Grandcolas, 1993, 1995, 1999). The concept of troglobiomorphosis – that cave-dwelling organisms are subject to a number of distinct morphological transformations (so-called troglobiomorphies) resulting from their subterranean habits (e.g. loss or reduction of eyes and wings, cuticular depigmentation, increased length of sensorial appendages, etc.) – has dominated discussions of the evolution of cavernicolous and troglobitic organisms for the last four decades (Barr, 1968; Ginet & Decu, 1977; Howarth, 1983; Barr & Holsinger, 1985; Camacho, 1992; Juber-

thie & Decu, 1994; Desutter-Grandcolas, 1999). This idea, however, has proved controversial, and the question of how to interpret troglobiomorphies in terms of primary homology, homoplasy, and adaptive significance is still the subject of ongoing debate (e.g. Marquès & Gnaspini, 2001; Desutter-Grandcolas *et al.*, 2003). Therefore, the discovery of a fossil member of the Amphiacustae is of great significance, providing an opportunity not only to shed light on the evolution of these fascinating crickets, but also to impart historical perspective on the nature of character evolution with respect to troglobiomorphosis.

MATERIAL AND METHODS

The holotype of *Araneagryllus dylani* gen. et sp. nov. is an adult female preserved in a comparatively large, rounded piece of Dominican amber, along with numerous syninclusions (listed below), deposited in the Division of Invertebrate Zoology (Entomology), American Museum of Natural History, New York (AMNH). The specimen was studied using a Zeiss stereomicroscope, and drawings made with the aid of a camera lucida. Photomicrographs were produced using a digital SLR camera attached to an Olympus stereomicroscope, with the specimen immersed in oil. The terminology generally follows that of Otte & Alexander (1983). The age and origin of Dominican amber has been reviewed by Itturalde-Vinent & MacPhee (1996), Grimaldi & Engel (2005), and Penney (2008).

SYSTEMATICS

FAMILY GRYLLIDAE LAICARTING, 1781

SUBFAMILY PHALANGOPSINAE BLANCHARD, 1845

NEC SAUSSURE, 1878

Phalangopsites Blanchard, 1845: 245.

Phalangopsites Saussure, 1878: 403.

Phalangopsitidae Bruner, 1916: 344.

Phalangopsinae Hebard, 1928: 1.

Phalangopsidae Chopard, 1949: 670.

Type genus: Phalangopsis Audinet-Serville, 1831.

Remarks: Priority for family-group names based on the type genus *Phalangopsis* dates from Phalangopsites Blanchard, 1845, and not from Phalangopsites Saussure, 1878, as has been widely purported in the literature.

TRIBE LUZARINI HEBARD, 1928

Luzarae Hebard, 1928: 1.

Luzarini Hebard, 1928: 1.

Luzarinae Desutter-Grandcolas, 1993: 1.

Type genus: Luzara Walker, 1869.

Remarks: Desutter-Grandcolas (1992: 95) defined the Luzarini based on the morphology of the male genitalia, stating that ‘chez les Luzarinae [*sic*], toute la partie médiane de l'épiphalle est régressée, notamment les lophi médians; d'autre part, les “bras épiphalliques” ainsi formés acquièrent une structure complexe, avec généralement une ou deux zones de rupture ou d'articulation et des épines latérales’. The retrograde median region of the epiphallus is unique amongst Luzarini, and is likely to be apomorphic. The complex ‘bras épiphalliques’, or ‘epiphallic arms’, and their lateral lobes are highly variable: their morphology and spatial associations with the epiphallic parameres have proved very useful at lower taxonomic levels (e.g. Desutter-Grandcolas, 1992, 1993; Desutter-Grandcolas & Otte, 1997).

**SUBTRIBE AMPHIACUSTINA HUBBELL, 1938
STAT. NOV.**

Amphiacustae Hubbell, 1938: 206.

Type genus: *Amphiacusta* Saussure, 1874.

Remarks: The priority of family-group names based on the type genus *Amphiacusta* dates from Amphiacustae Hubbell, 1938. This name has subsequently been used to refer to a group of genera comprising *Amphiacusta*, *Arachnopsita*, *Cantrallia*, *Leptopedetes*, *Longuripes*, *Mayagryllus*, *Nemoricantor*, *Noctivox*, and *Prolonguripes* (Desutter-Grandcolas, 1993, 1999). The monophyly of this group is well supported by the apical migration of sclerites in the epiphallic arms (termed the ‘C-sclerites’ by Desutter-Grandcolas, 1993) and the endophallic apodeme without a mediodorsal crest. The group includes some 84 species in the aforementioned genera, distributed throughout Central America and the West Indies.

Hubbell (1938) formed the name Amphiacustae using his standard suffix for family-group names beneath the rank of subfamily and although the group has been intensively studied since then (Desutter-Grandcolas, 1993, 1997, 1999; Desutter-Grandcolas & Otte, 1997), it has never been assigned a rank. Thus, Hubbell's (1938) original spelling of the name (using the suffix -ae) has never been questioned. The suffixes of family-group names are regulated by the International Code of Zoological Nomenclature (ICZN) at the ranks of superfamily, family, subfamily, tribe, and subtribe (ICZN, 1999: article 29.2). The suffixes of names at other ranks within the family group are not formally regulated, but do have widely accepted standard suffixes (e.g. -oidae for an epifamily, -iti for a supertribe, -ita for an infratribe, etc.). The suffixes of rankless taxa are likewise unregulated by the ICZN, and their use has become increasingly desirable in recent years because of the widespread use of cladistic methodology and the need to name

important nodes within phylogenies; particularly in cases where the assignment of a specific rank would be superfluous. Nevertheless, the use of the name Amphiacustae as a rankless taxon retaining its original suffix is somewhat problematic because of the similarity of the name with that of the type genus. This has the potential to cause confusion, and so the group is here assigned the rank of subtribe and the suffix is emended to ‘-ina’, in accordance with ICZN regulations.

GENUS ARANEAGRYLLUS GEN. NOV.

Etymology: The new genus-group name is formed from a combination of the Latin words *aranea*, meaning ‘spider’, and *gryllus*, meaning ‘cricket’: literally ‘spider cricket’, in reference to the vernacular name of phalangopsines. The gender is masculine.

Type species: *Araneagryllus dylani* sp. nov.

Diagnosis: Female: head with comparatively small fastigium, protruding only slightly beyond the antennal fossae and in line with the vertex; subocular furrow prominent, distally curved, meeting weak frontal costa near frontoclypeal suture/anterior tentorial pit; compound eyes suboval; ocelli absent; pronotum wider than long, saddle-shaped, with prominent dark band near pleural margins and rows of long marginal setae; procoxa markedly more robust than mesocoxa; mesotibia with two apical spurs; metatibia with two parallel rows of between ten and 12 small dorsal spines, four long and robust subapical spurs, and three apical spurs (median one markedly longer than the others); subgenital plate broadly triangular, with a small but distinct median notch in the posterior margin. Male: unknown.

ARANEAGRYLLUS DYLANI SP. NOV. (FIGS 1–3)

Etymology: The specific epithet is a noun in the genitive case, and is named in honour of my son, Dylan L. Heads. The gender is masculine.

Type: Holotype female: Dominican Republic, Early Miocene (Burdigalian, 18–20 Mya) Dominican amber; AMNH specimen number DR-12-32. Syninclusions: this piece of amber is particularly rich in biotic inclusions, including an isopod, a thysanuran, a collembolan, an auchenorrhynchan, two chalcidoid wasps, and numerous Diptera. The specimen is notable for the development of a white emulsion, particularly around the abdomen and mouthparts.

Diagnosis: As for the genus (*vide supra*).

Description: Female: body form robust (Figs 1, 2A); 12.11-mm long, measured from head to abdominal apex (excluding ovipositor). Head hypognathous (Fig. 2B); vertex broad, with numerous dark spots extending towards the fastigium, which protrudes



Figure 1. *Araneagrillus dylani* gen. et sp. nov., photomicrograph of holotype AMNH DR-12-32. Scale bar: 3 mm.

between the antennal fossae and is covered with a patch of short setae; frons gently sloping; frontal costa shallow, indistinct; subocular furrow distinct, curved medially towards the frontoclypeal suture; genae almost triangular in shape, covered in minute pits, with two dark spots beneath the compound eyes and a much smaller dark spot towards its ventral margin; compound eyes well developed, globose, situated high on the head, and protruding laterally; ocelli absent; antennal fossae situated directly anterior of the compound eyes; scape large, longer than wide and pedicel markedly smaller, only slightly longer than wide; first, second, and third flagellomeres small, as long as wide; subsequent flagellomeres markedly longer than wide; clypeus, labrum, and other mouthparts largely obscured by white emulsion; mandible apparently strong; maxillary palp long, terminal palpomere markedly inflated apically; labial palp smaller, largely obscured by emulsion. Pronotum shield-like, wider than long, with prominent median and marginal carinae and irregularly spaced short setae; pleural margin with prominent dark band and pale 'lip' on anterior pleural lobe; median carina with dark stripe, bordered laterally by several dark spots; anterior and

posterior margins of pronotum with prominent rows of long setae. Meso- and metanotae and abdominal tergites broad, decreasing in size posteriorly and of largely uniform dark coloration; posterior margins of abdominal tergites with rows of setae. Abdomen largely obscured by emulsion; cerci incomplete (truncated by surface of amber), broad basally, narrowing apically, with a dense covering of setae; epiproct triangular, covered with emulsion; ovipositor incomplete (truncated by surface of amber), strong basally, narrowing apically; subgenital plate broad basally, narrowing slightly posteriorly, with a small median posterior notch. Pro- and mesothoracic legs long, robust (Fig. 3A, B). Procoxa large, broadly articulated with prosternum; protrochanter much smaller, largely obscured by a large bubble; profemur broad basally, narrowing very slightly towards apex, covered in fine setae and numerous irregular dark patches; numerous longer setae on the dorsal surface, particularly distally; genicular lobes prominent, inflected; protibia a little over half the length of profemur, with three dark bands and two apical spurs of equal length; tympana absent; probasitarsus three-quarters as long as protibia, with prominent apical spine; second tarsomere small; third tarsomere long, gracile. Mesocoxa approximately half the size of procoxa; mesotrochanter small, triangular; mesofemur similar to profemur, with irregular dark patches, prominent genicular lobes, but with more numerous long setae; mesotibia a little over half the length of mesofemur, with three dark bands and two apical spurs of equal length; tarsus as in the prothoracic leg. Metathoracic leg long, robust, saltatorial (Fig. 3C); metafemur strongly inflated basally, with numerous dark patches along the outer facets and dark bands distally; metatibia equal in length to metafemur, with four dark bands; denticulate with two parallel rows of between ten and 12 short spines and four long sub-apical spurs; three apical spurs, with the median spur markedly longer; metabasitarsus long, with a single dark band, and one long apical spur; second tarsomere much reduced; third tarsomere long, gracile, slightly curved.

CLADISTICS

A cladistic analysis was undertaken in order to establish the phylogenetic position of *Araneagrillus* gen. nov. within Amphiacustina. The phylogeny of the group was investigated by Desutter-Grandcolas (1993), based largely on comparative studies of male genitalia. *Araneagrillus* gen. nov. was added to her original matrix of 22 morphological characters (Table 1; for characters, see Desutter-Grandcolas, 1993: 63–66) and analysed in PAUP 4.0 beta 10 (Swofford, 2002). An exhaustive search resulted in 28

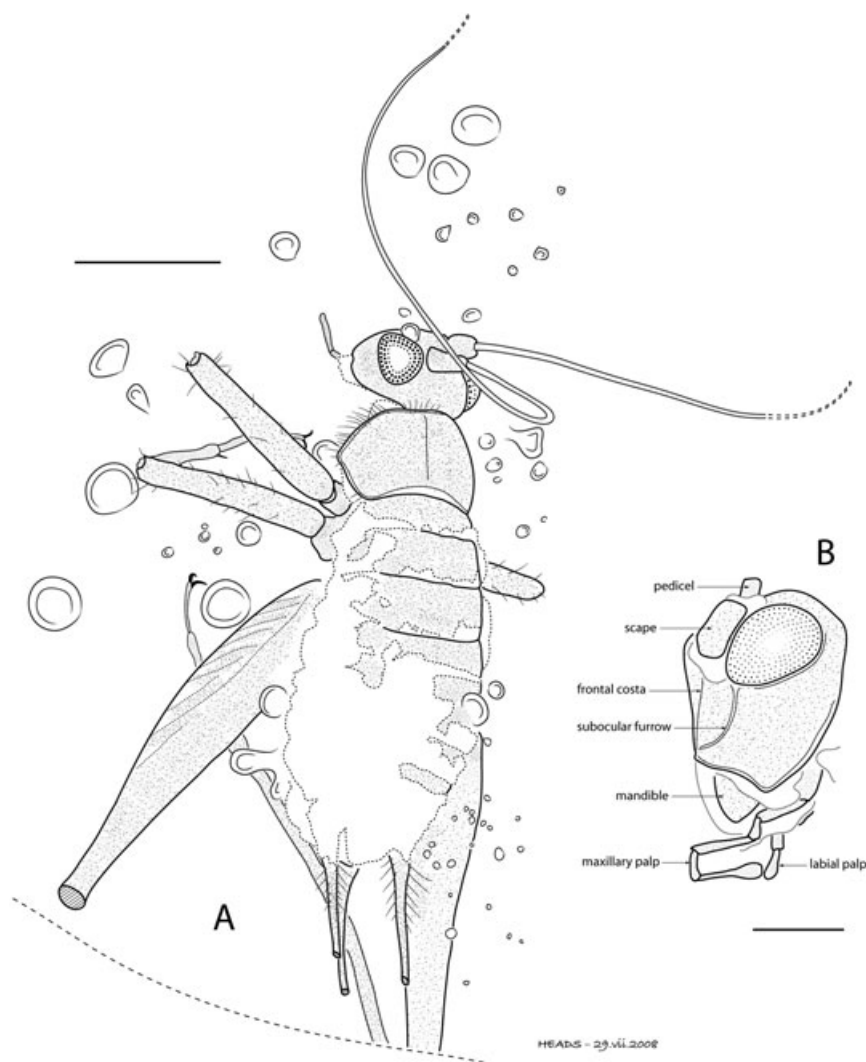


Figure 2. *Araneagrillus dylani* gen. et sp. nov., camera lucida drawings of holotype AMNH DR-12-32. A, general habitus of specimen. Scale bar: 3 mm. B, left lateral view of head. Scale bar: 1 mm.

equally parsimonious topologies. Only three of the 22 characters could be scored for *Araneagrillus* gen. nov. and the strict consensus tree was largely unresolved as a result of the missing data. However, the 50% majority rule consensus tree (Fig. 4) showed considerable resolution and was exported to MacClade 4.06 (Maddison & Maddison, 2003) for character distribution assessment.

The topology of the majority rule consensus cladogram shown in Figure 4 is in broad agreement with that of Desutter-Grandcolas (1993: fig. 109). *Araneagrillus* gen. nov. is placed within a clade comprising *Nemoricantor*, *Leptopedetes*, *Mayagrillus*, *Arachnopsita*, *Longuripes*, and *Prolonguripes*, which are united by the mesotibia with two apical spurs and the median apical spur of the metatibia being markedly longer than the others. This clade has a sister-group

relationship with a clade comprising *Amphiacusta*, *Noctivox*, and *Cantrallia* (hereafter referred to as the 'Amphiacusta clade'), united by the ectophallic arc extending above and beyond the ectophallic fold. Within the former clade, *Nemoricantor* and *Leptopedetes* are sister taxa (the 'Nemoricantor clade') and are distinct from a clade comprising *Mayagrillus*, *Arachnopsita*, *Prolonguripes*, and *Longuripes* (the 'Mayagrillus clade'). In the trees presented by Desutter-Grandcolas (1993), these two clades are sister taxa, although in the present analysis they form an unresolved trichotomy with *Araneagrillus* gen. nov. Clearly, more data is needed in order to resolve the relationships of these taxa, and a more exhaustive search for characters should include aspects of the external morphology and internal anatomy of both males and females.

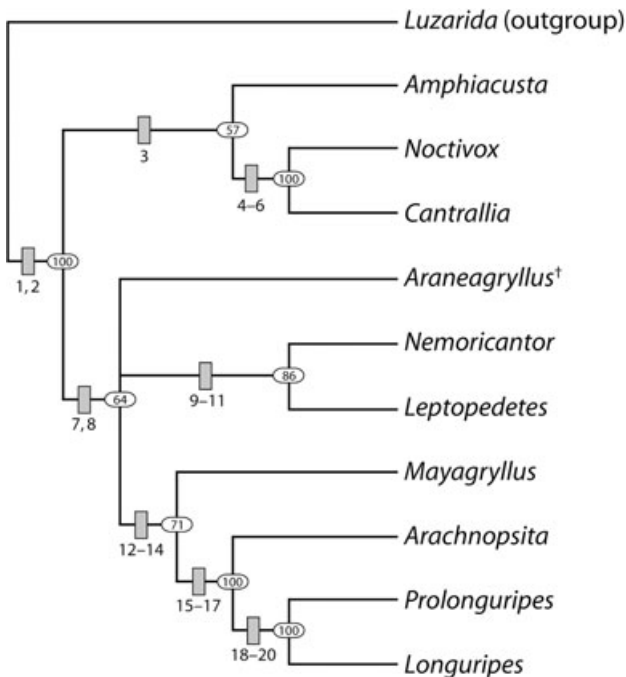


Figure 4. Cladogram of amphiacustine relationships (50% majority rule consensus tree of 28 equally parsimonious topologies: tree length, $L = 29$; consistency index, $CI = 0.90$; retention index, $RI = 0.91$). The percentage support for each node is given within an oval. Synapomorphies are indicated by numbers 1–20, and are explained in Table 2.

The present cladistic analysis, together with those of Desutter-Grandcolas (1993, 1997, 1999), enable a detailed assessment of the distribution of supposedly troglobiomorphic characters onto the phylogeny of Amphiacustina. When the life histories of the various genera are mapped onto the phylogeny (Fig. 5), three important conclusions regarding the evolution of Amphiacustina can be drawn: (1) the ancestral amphiacustine was epigeal and was most likely cavi-colous and/or straminicolous, like most other non-amphiacustine Luzarini; (2) strict troglobitic life histories evolved twice within Amphiacustina, once in the lineage leading to *Noctivox* (polymorphic) and again in the *Mayagrillus* clade; and (3) *Prolonguripes* reverted to an existence outside of caves and is therefore secondarily epigeal. These conclusions are corroborated by the results of Desutter-Grandcolas (1993). The life history of *Araneagrillus* gen. nov. cannot be known with certainty, although its occurrence in amber indicates that it was not troglobitic. Indeed, *Araneagrillus* gen. nov. was probably straminicolous, living at ground level and foraging amongst leaf litter. The occurrence of other ground-dwelling taxa (Isopoda, Thysanura and Collembola) in the same piece of amber as the holotype also

Table 2. Explanation of the synapomorphies in Fig. 4

1. C-sclerites located at the apex of the epiphallallic arm (B-sclerite without any particular development), from which they are distinctly separate.
2. Endophallallic apodeme without mediodorsal crest between endophallallic sclerite and apex of ectophallallic fold.
3. Ectophallallic arc extended above ectophallallic fold, and protruding beyond it.
4. Male metanotal gland globose.
5. Epiphallallic sclerite with visor-like median projection.
6. Epiphallallic parameres 1 and 2, large, spine-like.
7. Mesotibia with two apical spurs.
8. Median inner apical spur of metatibia longer than dorsal apical spur.
9. C-sclerite reduced, forming a soft, quadrangular lobe.
10. Ectophallallic apodemes large and robust, with an abutment that supports the epiphallallic sclerite.
11. Lateral lamina of endophallallic apodeme markedly elongate.
12. Epiphallallic–ectophallallic membrane with pair of non-glandular invaginations.
13. Epiphallallic paramere 2 elongate, bordering the entire dorsal surface of the epiphallallic arm.
14. Membrane separating the A-sclerite from the epiphallallic parameres inflated, displacing the A-sclerite posteriad of the basal plate of the C-sclerite.
15. Metafemora very thin, even basally.
16. C-sclerite differentiated and complex, comprising a long, thin plate, a lateral spine or notch, and a more or less developed ventral pouch.
17. C-sclerite vertically articulated with epiphallallic arm.
18. Invaginations of epiphallallic–ectophallallic membrane developed into two large glands.
19. Membrane between A-sclerite and epiphallallic parameres greatly developed, altering the entire shape of the epiphallallic arm.
20. C-sclerite with a large glandular system formed by the ventral pouch and the lateral spine, located on the outer face of the epiphallallic arm.

supports this assertion. Nevertheless, *Araneagrillus* gen. nov. does possess several morphological characters thought to be troglobiomorphic – notably the loss of ocelli, the absence of auditory tympana (suggesting the possible absence or non-functionality of the stridulatory apparatus in the male as a result of aptery or brachyptery), and elongate legs and palpi – suggesting that these features may not in fact be adaptations to the cave environment, and thus, not troglobiomorphic at all. This hypothesis can be tested by mapping the distribution of supposedly troglobiomorphic characters onto the phylogeny (Desutter-Grandcolas, 1999).

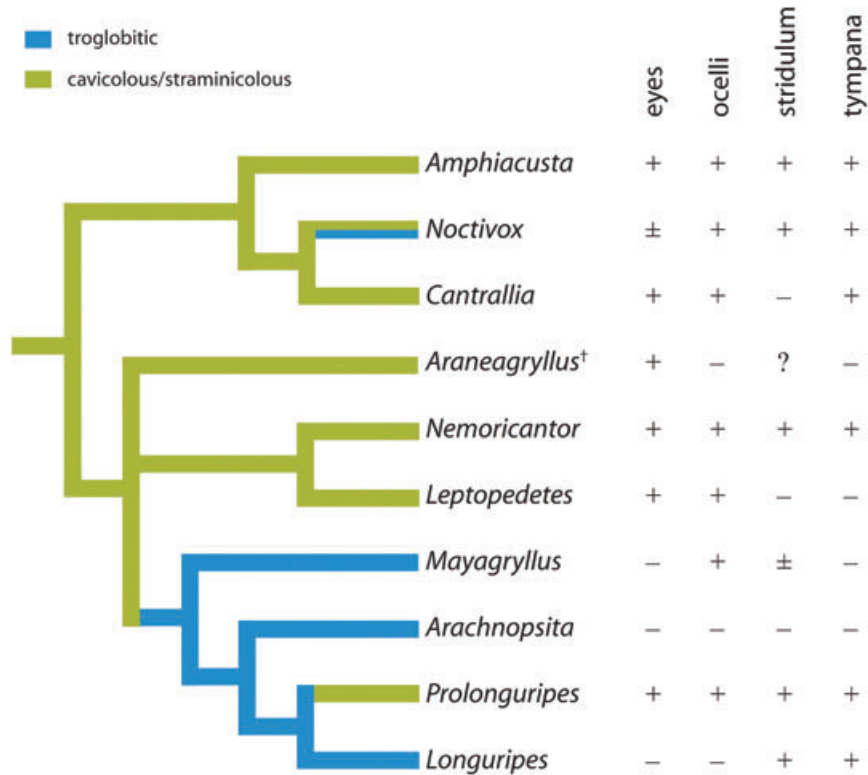


Figure 5. Phylogenetic inference assessment of Amphiacustina. Life histories are mapped onto the phylogeny in blue (strict troglobitic) and green (cavicolous/straminicolous epigean), and the distributions of the supposedly troglobiomorphic characters are shown on the right. Key: eyes large (+) or reduced (-); ocelli present (+) or absent/reduced (-); stridulatory apparatus (stridulum) present and functional (+) or absent/non-functional (-); auditory tympana present (+) or absent (-); in all cases, the ± symbol indicates polymorphism.

Figure 5 illustrates the distribution of four supposed troglobiomorphies in Amphiacustina: eye size, presence or absence of ocelli, functionality or absence/non-functionality of the stridulum in males, and presence or absence of auditory tympana. Eye size appears to be strongly correlated with life history, with troglobites having much smaller eyes than their epigean relatives (see also Desutter-Grandcolas, 1999). Note that this character is polymorphic in *Noctivox*, which contains both troglobitic and epigean species. However, all other characters show no particular pattern with regard to phylogeny or life history. Ocelli are absent in *Arachnopsita* and *Longuripes*, but are present in *Mayagrillus* and troglobitic species of *Noctivox*. Moreover, ocelli are absent in *Araneagrillus* gen. nov., which was almost certainly epigean. Data for the stridulum and the auditory tympana also show no apparent correlation with life history type. It is clear from this analysis that, with the exception of eye size, many characters thought to be troglobiomorphic are also present in epigean taxa, and cannot, therefore, be considered as troglobitic adaptations. Indeed, despite the selective advantages

that such characters may impart on troglobites, it is impossible that they evolved as a result of the selective pressures of life in the cave environment.

The idea that troglobiomorphies are adaptations to life in caves is largely based on a strict adherence to the so-called 'adaptationist programme' (*sensu* Gould & Lewontin, 1979). Indeed, the possibility that such structures may be the result of exaptation (Gould & Vrba, 1982) has often been granted little more than lip service (Jones, Culver & Kane, 1992; Culver, Kane & Fong, 1995). The logic of such an adaptationist explanation is sound enough; troglobiomorphies are found to be widely distributed amongst groups of phylogenetically unrelated organisms (e.g. Culver & Fong, 1986), and would naturally lead one to assume that such structures were the product of convergent evolution resulting from similar selective pressures. Such an approach is nonetheless flawed, in that it fails to separate current utility from historical origin: a common error that has long hindered the evolutionary analysis of form (Gould & Lewontin, 1979; Gould & Vrba, 1982; Gould, 1997, 2002). It is clear from the results of the present

analysis that the a priori assumption that all troglobiologies are adaptations to life in caves must be dropped in favour of a more objective phylogenetic test of their historical origins, free from the influence of their current utility in troglobites. Such an approach has been pioneered by Desutter-Grandcolas (1993, 1995, 1997, 1999), who has used phylogenetic inference to test the troglobiogenesis hypothesis. Her conclusions – which are corroborated by the results presented herein – clearly show that many troglobiologies are also present in the epigean relatives of troglobitic taxa, and therefore cannot be considered adaptations to the cave environment. The discovery of *Araneagrillus* gen. nov., with its unique combination of characters, provides an historical perspective on this problem and confirms the presence of supposed troglobiologies in an extinct epigean relative. It is clear, then, that although some features (such as eye reduction and cuticular depigmentation) may be the result of natural selection or perhaps genetic drift, others are exaptive in nature: i.e. they evolved in epigean ancestors and were co-opted by their troglobitic descendants. Thus, evolution in caves is considerably more complex than was previously realized and a more pluralistic approach to its study is needed, lest we remain in the dark.

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