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The cricket fauna of Chiapanecan caves (Mexico): systematics, phylogeny and the evolution of troglobitic life (Orthoptera, Grylloidea, Phalangopsidae, Luzarinae)

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SUMMARY

The present study deals with the cavernicolous Grylloidea of Chiapas. It details the composition of this fauna, which belongs exclusively to the Phalangopsid group Amphiacustae, and considers its troglobitic evolution in the methodological framework of Comparative Biology. This method consists in analysing the evolution of biological features in reference to phylogeny, using character state optimization.

The material studied comes mostly from Italian biospeological expeditions, but also from the author's work in Mexico, from North American biospeological expeditions achieved in Central America and the West Indies, and from the collections of the Academy of Natural Sciences of Philadelphia, the Museum National d'Histoire naturelle de Paris and the University of Michigan Museum of Zoology.

I first present a systematic and phylogenetic analysis of Amphiacustae. Six new genera are defined and the genus Amphiacusta Saussure, 1874 is crearly delimited; twenty-three of the twenty six species considered in the paper are new and described. A key for genera and species groups is given. Phylogenetic relationships among genera are established using cladistics (implicit enumeration of Hennig 86 program).

The evolution of troglobitic Amphiacustae is then analyzed. Available data on the biology of Amphiacust genera are presented and compared with what is known on other Phalangopsidae. Three biological attributes are moreover defined (troglobitic *versus* non troglobitic; cavicolous *versus* non cavicolous; leaf litter foraging *versus* leaf litter not foraging). The mapping of the attributes upon our cladogram shown that Amphiacustae evolved twice toward cave life and that their ancestral habitat could be characterized by cavicolous habits and leaf litter foraging.

The results are discussed in reference to theories on troglobitic taxa evolution, and to the exaptation concept of Gould & Vrba (1982). This leads to three main conclusions: 1/ Amphiacust adaptation to caves could be the result of a tentative to exploit karstic resources in Central America; 2/ An epigean dispersion by cave living species can be hypothesized; 3/ For Grylloidea, having cavicolous habits at ground level appears to be exaptative to troglobitic life.

INTRODUCTION

Dealing with troglobitic animals, it is hardly avoidable to question how they have evolved to live in caves. Extensive debates have

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addressed the origin of cave live in temperate regions, leading to the traditional view that troglobites are relicts which refuged in caves under climatic stress (Barr, 1968; Vandel, 1964). Since a few years, new insights have been provided in this research area, mainly due to field data in tropical caves (Juberthie, 1984). Among the main works published on the subject, those of Howarth (1991 and references therein) on Hawaii seem to be the most informative and fruitful. They lead this author to consider troglobitic life as an adaptation to exploit a new set of resources; this adaptation would be the result of a shift in the ecology of epigean species. In this theory, caves are thus not a refuge, but a conquest. Both theories consider cave environment as accessible only to pre-adapted taxa. It is clear that they may not be exclusive, but apply to different situations (Holsinger, 1988).

I propose to test these theories with the Grylloid troglobites from Chiapas (Mexico).

Recent developments in Comparative Biology provide a methodological frame to analyze the evolution of biological traits, in reference to phylogenetic relationships (e.g. Brooks & McLennan, 1991). Applied to troglobitic adaptation, they would allow to test how cave colonization has appeared in Amphiacustae, and to make hypotheses on the factors responsible for this evolution. This approach necessitates however a basic knowledge on the relationships and ecology of troglobites and of their epigean sister taxa, which are rarely taken into account (Deeleman-Reinhold, 1981; Peck, 1981).

Up to now, cavernicolous Grylloidea from Chiapas, and from Central America in general, had never been studied except for the genus *Paracophus* Chopard, 1947 (Phalangopsidae) distributed in Northeastern Mexico (Hubbel, 1972), and for the monotypic genus *Tohila* Hubbell, 1938 (described in the Pentacentridae, and moved to the Phalangopsidae by Desutter (1990)) from Yucatan. Only a few species were known; their relationships were not established and they had been tentatively placed in the Phalangopsid genus *Amphiacusta* Saussure, 1874 (Hubbell, 1938; Chopard, 1947, 1968). The material now at hand shows that Chiapanecan troglobites belong to a diversified group of Phalangopsid genera, the Amphiacustae s. str. (nov. def.), endemic to Central America and the West Indies (Desutter-Grandcolas, in prep.). *Amphiacusta* s.str. is distributed almost exclusively in the Greater Antilles. As in other parts of the world (Leroy, 1967), all the Central American troglobitic Grylloidea belong to the family Phalangopsidae.

I will successively establish the taxonomic composition of the Chiapanecan troglobitic fauna of Grylloidea and analyze the phylogeny of Amphiacustae and the available data on their biology. A possible scenario for troglobitic evolution of Amphiacustae is proposed. These results are discussed in reference to theoretical framework on troglobitic evolution (pre-adaptation, determinant factors), together with the dispersal mode of troglobitic Chiapanecan taxa.

Nine genera are recognized in the Amphiacustae; six of them are present in Chiapas, all being new to science and defined here. *Amphiacusta* is also redefined. Twenty-three species are described.

This paper is a part of a more extensive analysis of the Phalangopsidae from Central America and the West Indies (Desutter-Grandcolas, in prep.).

MATERIAL AND METHODS

Material

The numerous Italian (Sbordoni & al., 1987 and references therein) and American (Reddell, 1971 and references therein) expeditions that have been conducted for many years in Central America brought an important Phalangopsid material, mostly from caves. Dr. Hubbell (1972) studied the *Paracophus* material from Northeastern Mexico. He began the study of the Amphiacust material, but unfortunately never finished it. In 1991, I had the opportynity to resume his work with UMMZ financial support. The present paper on the Luzarin group Amphiacustae is the first part of a study on Central American and West Indian Phalangopsidae, that I base on the material mentioned above, but also on the results of my own field work in Central America and on ANSP, UMMZ and MNHP collections.

In the systematic treatment, Dr. Hubbell is associated to the descriptions of the species he had sorted out and labelled in collection. The character analysis (both for taxonomic and phylogenetic purpose) and the phylogenetic treatment presented here are entirely of my own, as are the evolutionary interpretations.

Methods

Systematic context. The group Amphiacustae is created by Hubbell in 1938, in agreement with Hebard (Hubbell, op. cit., p. 206), as one of three subdivisions of Phalangopsinae (our Phalangopsidae): Luzarae, Heterogrylli and Amphiacustae. In Chopard's 1956 key of Phalangopsidae, these 3 groups are mentioned, but their generic composition is different from that proposed by Hubbell; in particular, several genera placed by Hubbel in Amphiacustae are moved to Heterogrylli. Later, in his 1968 Catalogue, Chopard considers only two groups, Luzarini and Heterogryllini (that he certainly conceives as subfamilies, according to his Catalogue foreword and other papers), all the genera once placed in Amphiacustae being listed in Heterogryllini; Amphiacustae themselves are no more mentioned.

These successive modifications of Phalangopsid subdivisions express the vagueness of group definitions, based on homoplasic or unsufficiently stated characters (size, length of legs, tegminal and tympanum development, fastigium width, pronotum shape, ..., with many exceptions and «variability» in each group). Hubbel himself (1938) insists on the necessity to revise and redefine the hypothesized groups and discusses the delicate problem of character choice. In this context, the study of male genitalia brings most valuable new information on phylogenetic systematics of Phalangopsidae (Desutter, 1990): if a thorough and definite phylogenetic hypothesis is not yet achieved for the whole family, due to known material gaps, two subfamilies have been defined in the Neotropical Region (Phalangopsinae and Luzarinae), and generic and tribal groupings are based on synapomorphies (Desutter-Grandcolas, 1991, 1992a, c). This leads also to a reappraisal of morphological features.

Our redefinition of Amphiacustae will thus differ from those given by preceding authors. Except for *Amphiacusta* Saussure, 1874, all the genera considered here are new to science. The other genera placed in Amphiacustae by Hubbell belong either to Phalangopsinae: *Uvaroviella* Chopard, 1923, *Phalangopsis* Serville, 1831, either to other groups of Luzarinae: *Endecous* Saussure, 1878 and *Dyscophogryllus* Rehn, 1901 belonging to Desutter's 1990 group B, including *Luzarida* Hebard, 1928 and *Luzara* Hebard, 1928; *Cophus* Saussure, 1874, is an endemic genus from Cuba, whose relationships are yet unresolved; *Hemicophus* Saussure, 1878 could not be examined.

A general study of neotropical Phalangopsidae (Desutter, 1990) leads to the preliminary hypothesis that Amphiacustae could be the sister group of the other South American Luzarinae, whose presence outside South America is limited to the southern Lesser Antilles and to a few genera / species in Central America and in some of the Greater Antilles. An extensive study of Central American and West Indian Phalangopsidae will be presented elsewhere (Desutter-Grandcolas, in prep.).

Systematic and phylogenetic analysis. Systematic and phylogenetic analysis are based on the cladistic method. For each genus, I will give a diagnosis, indicate known data on its distribution and biology and discuss its monophyly and relationships. Phylogeny is worked using implicit enumeration option of Henning 86 program, version 1.5 (Farris, 1988).

Characters. Most of the characters used in our phylogenetic analysis concern male genitalia. I will first briefly present their structure and constituent elements.

Male genitalia in Grylloidea are composed of three concentric layers, called epiphalle, ectophalle and endophalle, separated by invaginations. They are dorso-ventrally asymmetrical their ventral part being extremely reduced, and their dorsal part developed, sclerotized and protruding (Desutter, 1990). No intromission organ exists in Grylloidea.

The largest invagination is located between ephiphalle and ectophalle: it includes a dorsal membrane (= **epi-ectophallous membrane**) and a pair of long and large sclerotized apodemes (= **ectophallic apodemes**), connected by a median bridge (= **ectophallic arc**). This invagination is bordered dorsally by the epiphallic sclerite, and ventrally by an elongate membranous ectophallic structure (= **ectophallic fold**).

The second important invagination is endophallic: it forms an apodeme (= **endophallic apodeme**), connected to the **endophallic sclerite**. Basically, Phalangopsidae show an endophallic apodeme composed of 2 lateral lamina and a medio-dorsal crest, this last element particularly developed in many Luzarinae.

In some families of Grylloidea, a dorsal pouch forms on the endophalle (= **dorsal cavity**). In Phalangopsidae, dorsal cavities are rare; they correspond to abnormal, hypertelic structure disturbing the genitalic organization (for example in *Cophus*, *Smicrotes*

Desutter-Grandcolas, 1992c, ...). These structures are autapomorphic for the genera they belong to.

Epiphallic structures are complex and numerous. Basically, they include a basal sclerite (= **epiphallic sclerite**), extended laterally by a pair of rods (= **rami**), a pair of lobes variably individualized from the base (= **median lophi**) and two pairs of sclerites located on the inferior side of the epiphalle, and connected to ectophallic apodemes (= **epiphallic parameres 1 & 2**). These structures may be completed by various elements characteristic of a definite taxon or group of taxa.

In Luzarinae, the median part of epiphalle regressed, thus forming two «epiphallic arms». Moreover, several sclerites are formed from the apex of epiphallic arm. These are: **C-sclerite**, located on dorsal side of epiphallic arm; **A-sclerite**, more or less clearly disconnected from epiphallic arm by sclerotization discontinuity, and separating it from epiphallic parameres; and **B-sclerite**, that is the base of epiphallic arm, to which the other two sclerites are directly or indirectly linked.

The formation of epiphallic arms, and of separate A-, B- and C-sclerites are apomorphic traits of Luzarine, but the position and structure of these sclerites are peculiar to each group of genera (Desutter-Grandcolas, 1992c).

Biological data. Biological data have been taken in the literature or are the results of field observations from the author in Peru (Desutter, 1990), French Guiana (Desutter-Grandcolas, 1992c) and Mexico. They allow to define three biological attributes that I propose to test in reference to phylogeny in order to study the evolution of Amphiacustae toward caves. Their states in each genus are listed in figure 112. These attributes are: 1 - Troglobitic (1) *versus* non troglobitic (0). 2 - Cavicolous (1) *versus* non cavicolous (0). 3 - Foraging in leaf litter (1) *versus* not foraging in leaf litter (0).

In the course of the discussion, I will use the expression «cave adaptation» because the taxa considered here as troglobitic possess the characters that are assumed to indicate a real fitness to cave environment (Howarth, 1980). I do not intend to test the selective value of these modifications, but only the evolution of the biological attributes defined above.

Biological analysis. Comparative Biology as referred to in this paper considers the evolution of biological features of organisms in reference to a phylogenetic frame independently established (Brooks & McLennan, 1991). The distribution of the features state on the cladogramm is analyzed by the process of character state optimization, leading to one or several parsimonious hypotheses on features changes or appearance (Carpenter, 1989; Ross & Carpenter, 1991). This method is particularly adapted to the analysis of features for which homologies cannot be easily established (such as most ecological and behavioural traits), or which can be suspected of homoplasy (Grandcolas, 1991). It finally should lead to the elaboration of testable evolutionary scenarios, and allow a reappraisal of the nature of adaptation (Coddington, 1988; Gould & Vrba, 1982).

Adaptation and exaptation. «A feature is an adaptation only if it was built by natural selection for the function it now performs» (Gould & Vrba, 1982: 5). The definition of a feature as an adaptation implies: first a phylogeny is available to delimit the feature in an evolutionary context (Coddington, 1988); second, that one has demonstrated for the taxon studied an increase in fitness in a definite environment or situation due to the feature considered.

A pre-adaptation is «the existence of a prospective function prior to its realization» (Simpson, 1944 in Barr, 1968: 81). The orthogenetic connotation of this term is highly misleading and can lead to short-cuts or false interpretations of the evolutionary history of a phylum, especially when disconnected from a phylogenetic frame. Gould & Vrba (op. cit.) propose to use the term exaptation to qualify a feature that assumes a function for which it has not been selected (such as feathers for flight in Birds). In this context, a «pre-adaptation» should be considered as a «potential, unrealized exaptation».

LIST OF GENERA AND SPECIES INCLUDED

1. Genus *Amphiacusta* Saussure, 1874

   Distribution: Greater Antilles (West Indies)

2. Genus *Longuripes* Desutter-Grandcolas & Hubbell, n. gen.

   Distribution: Mexico (Chiapas, Oaxaca)

sbordonii group:

1. *Longuripes sbordonii* Desutter-Grandcolas & Hubbell n. sp. CHIS
2. *Longuripes pseudogigas* Desutter-Grandcolas, n. sp. OAX
3. *Longuripes evanesca* Desutter-Grandcolas, n. sp. CHIS
4. *Longuripes stenopsita* Desutter-Grandcolas, n. sp. OAX
5. *Longuripes minor* Desutter-Grandcolas, n. sp. CHIS
6. *Longuripes altaminor* Desutter-Grandcolas, n. sp. CHIS

arganoi group:

7. *Longuripes arganoi* Desutter-Grandcolas & Hubbell, n. sp. CHIS
8. *Longuripes surchiapaneca* Desutter-Grandcolas, n. sp. CHIS
9. *Longuripes intermedia* Desutter-Grandcolas, n. sp. CHIS

stenops group:

10. *Longuripes stenops* Desutter-Grandcolas & Hubbell, n. sp. OAX

3. Genus *Prolonguripes* Desutter-Grandcolas, n. gen.

Distribution: Guatemala, Honduras

4. Genus *Arachnopsita* Desutter-Grandcolas & Hubbell, n. gen.

Distribution: Guatemala

1. *Arachnopsita usumacinta* Desutter-Grandcolas, n. sp.
2. *Arachnopsita pequegna* Desutter-Grandcolas, n. sp.
3. *Arachnopsita cavicola* (Saussure, 1897) (*Arachnomimus*)

5. Genus *Mayagryllus* Desutter-Grandcolas & Hubbell, n. gen.

Distribution: Mexico (Chiapas, Yucatan), Belize, Guatemala

1. *Mayagryllus apterus* Desutter-Grandcolas & Hubbell, n. sp.
2. *Mayagryllus tilaensis* Desutter-Grandcolas, n. sp.
3. *Mayagryllus tumbalaensis* Desutter-Grandcolas, n. sp.

Other species included: *Mayagryllus yucatanus* (Hubbell, 1938)

6. Genus *Noctivox* Desutter-Grandcolas & Hubbell, n. gen.

Distribution: Mexico (except most Northwestern regions).

1. *Noctivox sanchezi* Desutter-Grandcolas, n. sp.
2. *Noctivox ocote* Desutter-Grandcolas, n. sp.
3. *Noctivox minor* Desutter-Grandcolas, n. sp.
4. *Noctivox tzotzila* Desutter-Grandcolas & Hubbell, n. sp.
5. *Noctivox clava* Desutter-Grandcolas, n. sp.
6. *Noctivox longixipha* Desutter-Grandcolas, n. sp.
7. *Noctivox dissimilis* Desutter-Grandcolas, n. sp.
8. *Noctivox hubbelli* Desutter-Grandcolas, n. sp.

Other species included: *Noctivox bolivari* (Chopard, 1947) (*Amphiacusta*)

7. Genus *Nemoricantor* Desutter-Grandcolas & Hubbell, n. gen.

Distribution: From Chiapas (Mexico) in the North to Costa Rica in the South.

1. *Nemoricantor maya* (Hubbell, 1938) (*Amphiacusta*)
2. *Nemoricantor aztecus* (Saussure, 1897) (*Endacustes*)

Two additional new Amphiacust genera exist in Central America but are not known from Chiapas. They will be described in another paper (Desutter-Grandcolas, in prep.). When mentioned (in particular in the phylogenetic analysis), they will be called respectively group A and group B:

Group A is close to *Nemoricantor* and is known from southern Central America (from Nicaragua to Panama), from tropical and premontane forest, at altitudes ranging from 78 to more than 3000 m. No direct biological observations has been found on that genus; however, by its arachnoid morphology and by the locations of its captures (at night on trail in forest), it resembles *Phalangopsis* Serville, 1831 (Phalangopsinae). As *Phalangopsis*, the group A could be cavicolous, hiding during the day in hollow trees (dead or alive), burrows, or when possible, in caves (near the entrance), and wandering at night in leaf litter to feed (Desutter-Grandcolas, 1992c).

Group B is close to *Noctivox* and is known from Eastern Mexico north of the Isthmus of Tehuantepec (Tamaulipas, Hidalgo, San Luis Potosi, Queretaro, Puebla) in deciduous tropical forest and in various temperate forests, from 400 to 1200 m. This genus is active in leaf litter at night and hides during the day in crevices or in burrows (pers. obs.).

Abbreviations

Institutions. ANSP: Academy of Natural Sciences, Philadelphia, USA. MHNG: Muséum d'Histoire naturelle, Genève, Switzerland. MNHP: Muséum National d'Histoire naturelle, Paris, France. UMMZ: University of Michigan Museum of Zoology, USA. UTVR: University «Tor Vergata», Rome, Italy.

Male genitalia. A: epiphallic A-sclerite; arc: ectophallic arc; b. C: basal plate of C-sclerite; C: epiphallic C-sclerite; e.: epiphallic sclerite; ect. ap.: ectophallic apodeme; ect. gl.: gland on the epi-ectophallic membrane; ect.s.: sclerotized extension of ectophallic arc above the ectophallic fold; E.E.I.: epi-ectophallic invagination; end.ap.: endophallic apodeme; e.p.: epiphallic parameres (1 or 2); fd.: ectophallic fold; gl. C: glandular ventral pouch of C-sclerite; mb.: membrane separating A-sclerite from epiphallic parameres; r.: rami; s.C: lateroventral spine of C-sclerite; x: location of epi-ectophallic glands.

Female genitalia. A: ventral view, B: dorsal view, C: lateral view.

Measures. Lpron: pronotal median length; wpron: pronotal posterior width; LFIII: hindfemora length; LTIII: hindtibiae length Lel: median length of right elytra in males; we: width of right elytra in males (at the level of the anterior angle of the mirror); Lovip: length of female ovipositor.

SYSTEMATIC ANALYSIS OF AMPHIACUSTAE

1. Genus *Amphiacusta* Saussure, 1874

Amphiacusta Saussure, 1874, Miss. Mexique: 444.
Amphiacustes Saussure, 1878, Mém. Soc. Genève, 25: 569.

Type species: *Amphiacusta annulipes* (Serville, 1831) (Fig. 1-3).

Distribution: Greater Antilles (mainly Hispaniola, but also Jamaica and the Bahamas Islands). Some species have been mentioned from Cuba, but this material has not been examined (De Zayas, 1973; Bonfils, 1981).

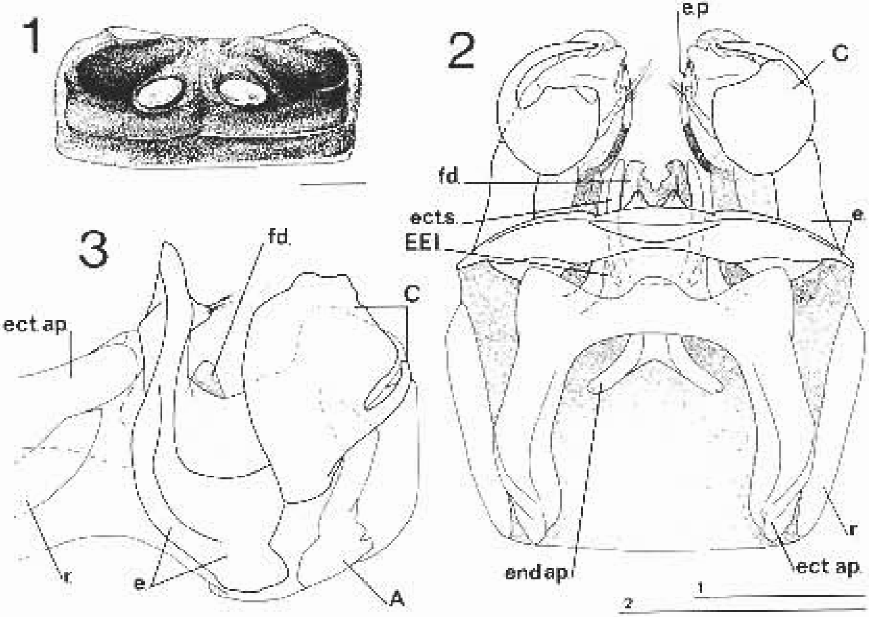

Fig. 1-3 — *Amphiacusta annulipes* (Serville, 1831). Fig. 1: Male metanotal gland; Fig. 2-3: male genitalia, dorsal (scale 1) and lateral view (scale 2). Abbreviations: p.10. Scales: 1 mm

Diagnosis

Species of medium to large size, brown spotted with yellow; pronotum margin bordered with yellow, except for the anterior angles of lateral lobes. Legs not particularly slender; femora I, II and tibiae ringed. Hindtibiae serrulated and with 4 pairs of subapical spurs. Tibiae II with 3 apical spurs (dorso-inner one missing). Tibiae I with 2 tympana. First hindtarsomeres with 2 rows of spines (inner one with only a few spines). Eyes and ocelli not reduced, the eyes protruding. Fastigium at the level of vertex; no distinct basal furrow, but a half-circle trace between the lateral ocelli.

Males. Elytra well developed, not enlarged; stridulatory apparatus complete, but apical field reduced; lateral field large. Metanotum with a pair of flat, ellipsoid formations; their margins more or less raised above the metanotal surface (Fig. 1). Susanal plate with elongate apical angles.

Male genitalia (Fig. 2-3). Epiphallic sclerite without a median visor, but with 2 more or less membranous lobulae bearing long setae (median lophi?). C-sclerites well developed, comprising a large plate and a large lateroventral spine; no globular pouch near the base of the spine. A-sclerites distinct, more or less of a reverse-T shape. Membrane separating A-sclerite and epiphallic parameres not inflated. Epiphallic parameres 1 and 2 lobeshaped and more or less sclerotized, without protruding highly sclerotized parts (compare to *Noctivox* for example). Ectophallic arc extended above ectophallic fold by a pair of protruding, long and thin sclerites. Ectophallic fold generally short. Ectophallic apodemes not particularly enlarged at their bases. Endophallic apodemes generally short, more or less divergent.

Female. Apterous.

Female genitalia. Copulatory papilla surrounding membrane not particularly thickened or hardened.

Monophyly and relationships

The monophyly of *Amphiacusta* is ascertained by the peculiar shape of its C-sclerites, and by the pair of ectophallic extensions above ectophallic fold. An extension of the ectophallic arc is recognized also in *Noctivox* and group B, in which it is however single and median. It has never been observed in any other Phalangopsid genus, and can thus be considered as a synapomorphy of these three genera.

Another characteristic of these taxa is the number of apical spurs on median tibiae (three, instead of four in most of the other Phalangopsidae, and two in the other Amphiacust genera). The status of this character is however more difficult to ascertain (possible homoplasy).

The 'median lophi' could indicate a similar relationship: their important development in some *Amphiacusta* species, and the structure of *Noctivox* epiphallic visor (in particular its setiferous areas) could suggest a structural cline between *Amphiacusta* and *Noctivox* group. The homology between these structures cannot however be established with certainty.

Ecology

Amphiacusta has been intensively collected in West Indian caves. Several authors mention however that it leaves the caves at night to wander and feed outside (Peck, 1974; Wolcott, 1948). This genus has also been cited as living in hollow trees and other humid and obscure places (De Zayas, 1973).

2. Genus *LONGURIPES* Desutter-Grandcolas & Hubbel, n. gen.

Type species: *Longuripes sbordonii* Desutter-Grandcolas & Hubbell, n. sp.

Distribution: Mexico (Oaxaca and Chiapas states).

Longuripes is recorded from tropical rainforest, deciduous tropical forest, temperate forest and «area of cloud forest and temperate - tropical transition». It ranges from 60 to 2520 m in altitude.

Diagnosis

Species (Fig. 4) light brown coloured, the legs not ringed (except in *arganoi* group). Legs long and thin, with a distinctly filiform apical part. First hindtarsomeres without serrulation. Serrulation on hindtibiae reduced. Hindtibiae with most often 5 outer and 4 inner subapical spurs. Tibiae II with only 2 apical spurs (inner and outer dorsal spurs lost). Tibiae I with 2 well developed tympana. Ocelli reduced or lost, eyes reduced. Fastigium large, below the level of the vertex and with a basal furrow (Fig. 5), this furrow straight or slightly incurved (not half-circled as in *Amphiacusta* and *Noctivox*).

Male. Elytra well developed, covering at least two thirds of the abdomen. Stridulatory apparatus complete; apical field reduced. Lateral field large. Susanal plate with more or less elongated apical angles, generally small (except in *L. stenops*, n. sp.). Metanotum and almost always first tergites with pairs of transversally elongated bumps, probably glandular (Fig. 6).

Male genitalia. C-sclerites with a long and slender basal plate, vertically articulated on epiphallic arm, a long lateroventral spine and a distinctive ventral pouch; pouch and spine hollow, with a distinct subapical aperture on the spine (draining duct of glandular pouch?). Membrane separating A-sclerite and epiphallic parameres inflated and slightly sclerotized (with several longitudinal ventral furrows), pushing aside A-sclerite behind C-sclerite basal plate. Epiphallic parameres small compared to this membrane; parameres 2 forming a gutter where C-sclerites basal plate inserts itself. Ectophallic fold long, its apex coming largely up between epiphallic

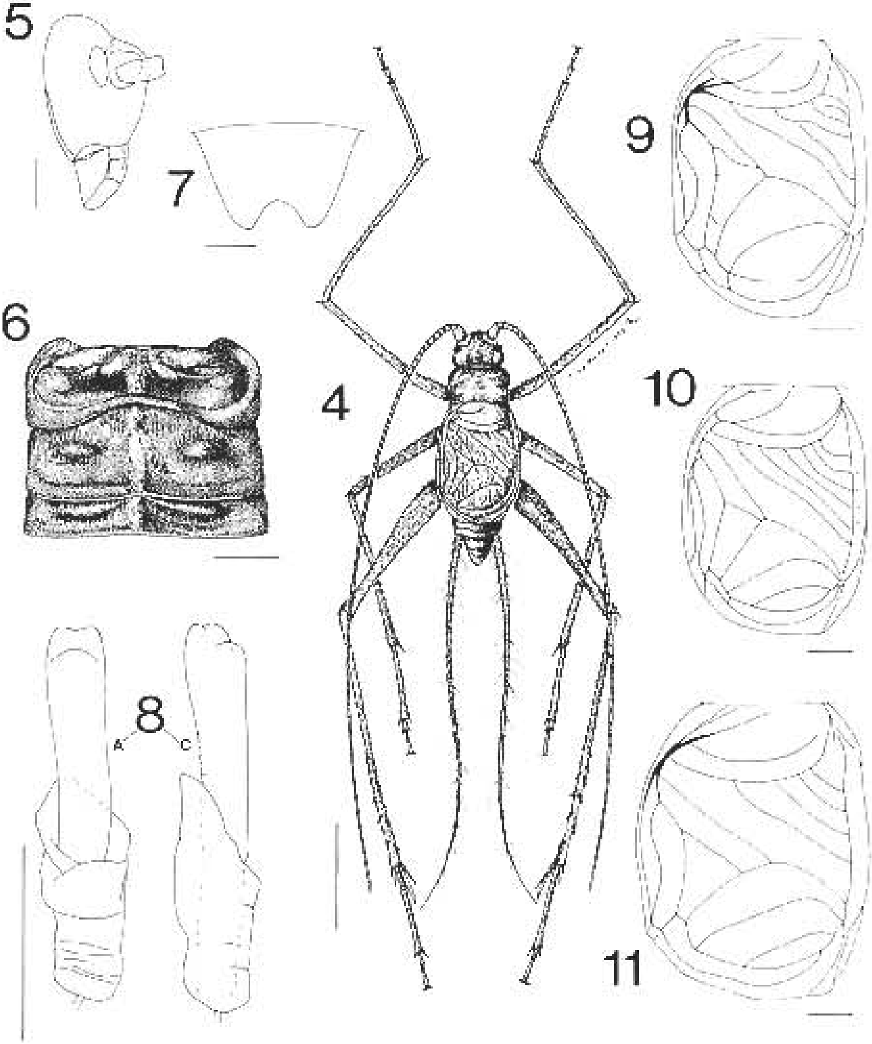

Fig. 4-11 — Genus *Longuripes*, n. gen. Fig. 4: *L. sbordonii*, n. sp., habitus of male: Fig. 5: id., lateral view of the head; Fig. 6: id., male metanotal and tergal gland; Fig. 7: id., female subgenital plate; Fig. 8: id., female copulatory papilla; Fig. 9: id., male elytra; Fig. 10: Male elytra of *L. pseudogigas*, n. sp.; Fig. 11: Male elytra of *L. evanesca*, n. sp. (scales: 1 mm, except for figure 4: scale 5 mm).

arms (character much more pronounced than in *Amphiacusta*). Epi-ectophallic membrane, above the arc, slightly sclerotized and with a pair of very membranous pouches (certainly glandular). Median lophi generally lacking (except in *arganoi* group, where they are represented by 2 small sclerotized lobes).

Female. Apterous.

Female genitalia. Copulatory papilla long and slender, its base surrounded by hardened membrane, mostly developed dorsally, where it is thickened and sclerotized. Spermathecal duct short and thin. Spermatheca small.

Monophyly and relationships

Longuripes belongs to a group of genera including *Prolonguripes*, *Arachnopsita* and *Mayagryllus*, characterized by a) the development and modification of the membrane separating A-sclerite and epiphallic parameres (membrane inflated, pushing aside A-sclerite and more or less absorbing epiphallic parameres), b) the formation of a pair of invaginations of epi-ectophallic membrane, and c) development of epiphallic parameres 2.

With *Prolonguripes* and *Arachnopsita*, *Longuripes* shares the same apomorphic structure of C-sclerites (vertically articulated on epiphallic arm, and comprising a slender basal plate, a lateral spine and a ventral swelling). These 3 genera have also very thin hind femora.

With *Prolonguripes*, *Longuripes* shares the following synapomorphies a) form and b) glandular system of C-sclerites, and c) formation of epi-ectophallic glands.

Longuripes apomorphies are the subapical position of the aperture of C-sclerites spine and the extreme swelling of C-sclerites ventral pouch.

Longuripes species belong to 3 species groups according to morphological and male genitalia characters:

1. *sbordonii* group: Species with limbs not ringed. Male genitalia: C-sclerite ventral pouch largely inflated, more ellipsoidal than spherical. Epi-ectophallic glandes with a distinct median axis. C-sclerite basal plate and lateral spine very long and thin. Male stridulatory file with less than 270 teeth.

Two subgroups can be distinguished according to make stridulatory file: - less than 190 teeth, and more often close to 100 (species included: *L. stenopsita,* n. sp., *L. minor,* n. sp., *L. altaminor,* n. sp.); - more than 190 teeth, and more often greater than 200 (species included: *L. sbordonii,* n. sp., *L. pseudogigas,* n. sp. and *L. evanesca,* n. sp.).

Both subgroups are known in Chiapas and in Oaxaca.

2. *arganoi* group: Species with ringed limbs. Male genitalia: C-sclerite ventral pouch not much inflated, more or less rounded; epi-ectophallic glands pouch like, without a median axis; C-sclerite basal plate typically enlarged at its apex; C-sclerite lateral spine larger and shorter than in other *Longuripes* species groups. Male stridulatory file with less than 230 teeth.. Other characters of this group are posterior margin of female subgenital plate not or slightly bisinuated, almost straight (it is more clearly bisinuated in the other two species group), and copulatory papilla long and slender, its apex flat and concave dorsally.

Species included: *L. arganoi,* n. sp., *L. intermedia,* n. sp. and *L. surchiapaneca,* n. sp.

3. *stenops* group: Species with limbs not ringed. Male genitalia: C-sclerite ventral pouch and epi-ectophallic glands similar to those of *arganoi* group. Male stridulatory file with more than 350 teeth.

Species included: *L. stenops,* n. sp. Ground known from Oaxaca only.

These species groups seem at least partly distributed according to altitudes. *Stenops* and *arganoi* groups are known above 1500 m, and up to 2300 m for the second. *sbordonii* group is massively present under 600 m, *minor* subgroup ranging from 600 to 1500 m. In Chiapas, all the species known from localities at altitudes less than 600 m belong to *sbordonii* subgroup. Altitudes are however not available for *L. arganoi* and *L. pseudogigas*, and not completely known for *L. altaminor.*

Biology

By its morphology and the location at which it has been captured in caves (up to half a mile from entrance), *Longuripes* can be considered as troglobitic.

sbordonii group:

Longuripes sbordonii Desutter-Grandcolas & Hubbell, n. sp. (Fig. 4-9, 12, 13).

Type locality: Mexico, Chiapas, Berriozabal.

Type material: Male holotype: Mexico, Chiapas, Berriozabal, cueva de Paso Burro, 900 m, 3-X-1973 (V. Sbordoni), in alcohol, UTVR. Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UTVR. Paratypes: Same locality, same date, same collector as the holotype: 1 male, in alcohol, MNHP. Chiapas, Cintalapa, Benito Juarez I, II sumidero de Pecho Blanco, 720 m, 1 male, 24-IV-1984 (V. Sbordoni), in alcohol, UTVR; id., 1 male and 1 female, 19-20-IV-1984 (V. Sbordoni, C. De Monte, A. Gobetti), in alcohol, UTVR. Chiapas, Ocozocoautla, Lago Malpaso, sistema de la Lucha (= cueva de la Lucha), 360 m, 1 male and 2 females, 7-III-1982 (A. Gobetti, J.F. Pittet), in alcohol, UTVR; id., 1 male, 10-IV-1986 (M. Lucarelli, G. Carchini), in alcohol, UTVR. Chiapas, Ocozocoautla, Lago Malpaso, rio Negro, m 115, cueva del Perro de Agua, 1 male, 16-IX-1973 (V. Vomero), in alcohol, MNHP; id., cueva de l'Agua Purificada, 1 male, 15-IX-1973 (R. Argano), in alcohol, UTVR. Chiapas, Ocozocoautla, Lago Malpaso, m 125, rio Encajonado, cueva del Burro, 1 male and 2 females, 15-IX-1973 (R. Argano), in alcohol, UTVR; id., 2 females, in alcohol, MNHP. Chiapas, Ocozocoautla, La Lucha, sistema de los Ojos del Tigre, 560 m, 1 male and 6 females, 28-IV-1986 (A. Gobetti, V. Sbordoni), in alcohol, UTVR; id., 1 female, in alcohol, MNHP.

Diagnosis

Species of great size, easily recognizable by their male genitalia.

Male. Elytra (Fig. 9): mirror slightly larger than long and crossed by a unique transversal vein. File: 191 - 257 teeth (mean number 218, n = 8). Dorsal bumps present on metanotum and tergite 1 (and generally 2). Susanal plate with small posterior angles.

Male genitalia. Huge size. Ectophallic apodemes divergent at their apex; C-sclerites with a basal plate slightly enlarged at the apex (outer apical angle not protruding) and with a long and slender lateral spine, whose apex is located well below the apex of epiphallic parameres (Fig. 12-13).

Female. Ovipositor long compared to those of other species. Posterior margin of subgenital plate largely indented (Fig. 7).

Female genitalia. Copulatory papilla long, slightly and regularly enlarged toward the apex and plicated dorsally and at its base; apex bilobated. Membrane casing as on figure 8.

Variation: Specimens captured at El Ocote present several differences: the male genitalia are bigger, the male size larger, the stridulatory file has fewer teeth (174-196, mean number 184, n = 3) and the apex of female copulatory papilla is more bilobated. The status of these specimens is still uncertain.

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Males	1.7-1.9	12.2-13.9	14.8-16.1	6.1-6.3	3.7-4.1	—
(n=3)	1.8	13	15.6	6.2	3.9	
Females	2.1-2.8	15.5-18	18.1-20.1	—	—	12.1-16.1
(n=4)	2.6	16.8	19.5			14.5

Other material examined: Mexico, Chiapas, Ocozocoautla, Lago Malpaso, m 125, rio Encajonado, cueva del Burro, 1 male, 15-IX-1973 (R. Argano), in alcohol, UTVR. Chiapas, Ocozocoaulta, La Lucha, sistema de los Ojos del Tigre, 560 m, 1 male, 28-IV-1986 (A. Gobetti, V. Sbordoni), in alcohol, UTVR. Chiapas, Ocozocoautla, La Lucha, cueva de la Sal, 1 female, 5-IV-1986 (M. Lucarelli, V. Sbordoni), in alcohol, UTVR; id., 1 female, in alcohol, MNHP. Chiapas, Cintalapa, cueva de los Camarones, 1 female, 6-IV-1984 (V. Sbordoni), in alcohol, UTVR; id., 1 female, 17-IV-1986 (V. Sbordoni), in alcohol, UTVR; id., 1 female, in alcohol, MNHP. Chiapas, Tuxtla Gutierrez, Ocozocoautla, Piedra Parada, El Ocote, grotte, jour, 5 males and 6 females, 2-XI-1990 (L. Desutter), MNHP.

Longuripes pseudogigas Desutter-Grandcolas, n. sp. (Fig. 10, 14, 15, 18).

Type locality: Mexico, Oaxaca, 12 km N Valle Nacional.

Type material: Male holotype: Mexico, Oaxaca, 12 km N Valle Nacional, cueva del Guayabo, 29-XII-1972 (J. Reddel, D. McKenzie, M. McKenzie, S. Murphy), in alcohol, UMMZ. Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UMMZ. Paratype: Same locality, same date, same collector as the holotype, in alcohol, 1 male and 2 females, UMMZ; id., 1 male, MNHP.

Diagnosis

Male. Elytra (Fig. 10): mirror larger than long, and crossed by 2 transversal veins. Cell bordered by the mirror and the chords no more than twice as large at its base than at its apex, its margines straight. File: 230-240 teeth (n = 2). Dorsal bumps present on metanotum and tergites 1-3 not very large.

Male genitalia (Fig. 1-5). Epiphallic sclerite protruding (Fig. 14); dorsal edge of epiphallic parameres high; basal plate of C-sclerites with a long outer apical angle; ectophallic apodemes almost straight (compare fig. 12 and 14).

Female. Subgenital plate posterior margin less indented than in *L. sbordonii*.

Female genitalia. Copulatory papilla very slightly enlarged toward the apex and plicated dorsally; apex flat and almost not bisinuated (Fig. 18).

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Males (n = 3)	1.8-2	13.5-13.6	16.2-17.5	5.8-5.9	3.8-3.9	—
	1.9	13.5	16.7	5.8	3.9	
Females (n = 2)	2.4-2.5	15-15.6	17.3-17.8	—	—	10.2-10.9

Other material examined: Mexico, Oaxaca, 12 km N Valle Nacional, cueva del Guayabo, 29-XII-1972 (J. Reddell, D. McKenzie, M. McKenzie, S. Murphy), in alcohol, 1 female, MNHP. This female is smaller than *L. pseudogigas* females; its copulatory papilla is shorter and larger, and the thickened membrane surrounding it almost round.

Longuripes evanesca Desutter-Grandcolas, n. sp. (Fig. 11, 16, 17).

Type locality: Mexico, Chiapas, Ocozocoautla, Lago de Malpaso.

Type material: Male holotype: Mexico, Chiapas, Ocozocoautla, Lago de Malpaso, m 115, cueva del Perro de Agua, 16-IX-1973 (R. Argano), in alcohol, UTVR. Female allotype: Same locality, same date, same collector as the holotype, UTVR. Paratypes: Same locality,

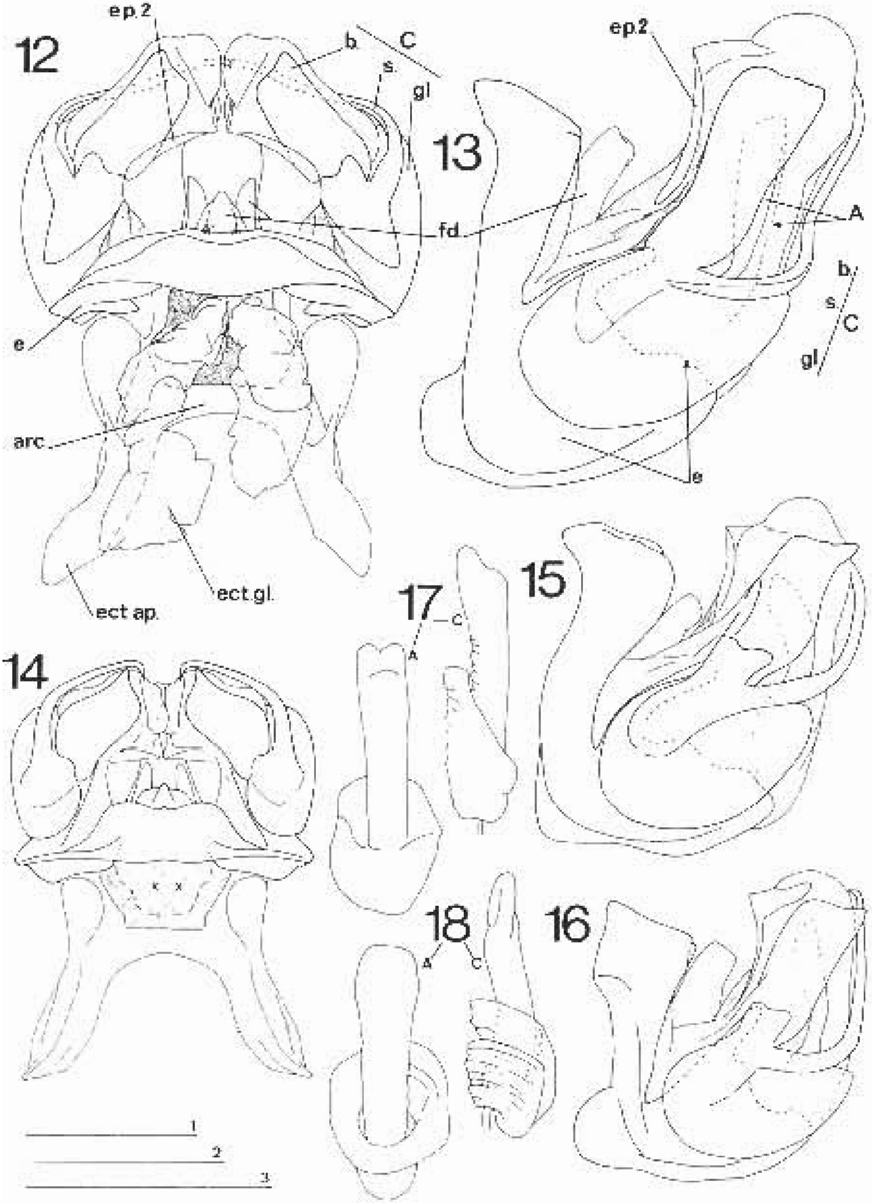

Fig. 12-18 — Genus *Longuripes*, n. gen. Male genitalia (dorsal view: scale 1, lateral view: scale 3) Fig. 12-13; *L. sbordonii*, n. sp. (dorsal and lateral view); Fig. 14-15: *L. pseudogigas*, n. sp. (ventral and lateral view); Fig. 16: *L. evanesca*, n. sp. (lateral view). Female genitalia (scale 2): Fig. 17: *L. evanesca;* Fig. 18: *L. pseudogigas*. Scales: 1 mm. Abbreviations: p. 10.

same date as the holotype, 1 male (V. Sbordoni), in alcohol, UTVR. Chiapas, Ocozocoautla, Lago de Malpaso, rio Negro, m 115, cueva de l'Agua Purificada, 1 male, 15-IX-1973 (V. Vomero), in alcohol, MNHP. Chiapas, Ocozocoautla, Lago de Malpaso, m 125, rio Encajonado, cueva del Burro, 1 male and 1 female, 15-IX-1973 (V. Vomero), in alcohol, UTVR. Chiapas, Ocozocoautla, Lago del Malpaso, rio Venta riva sinistra, m 114, piccola grotta, 1 female, 15-IX-1973 (V. Sbordoni), in alcohol, MNHP.

Diagnosis

Species very similar to *L. pseudogigas*, but recognizable by the following characters:

Male. Elytra longer and larger. Venation (Fig. 11): mirror much more large than long, and crossed by two transversal veins; cell delimited by the mirror and the anal vein more than twice as large at its base than at its apex. Stridulatory file with 264-267 teeth (mean number 266, n = 3).

Male genitalia (Fig. 16). Genitalia somewhat smaller, the epiphallic sclerite not so protruding; dorsal edge of epiphallic parameres not as high as in *L. pseudogigas,* and outer apical angle of C-sclerite basal plate larger.

Female. Posterior margin of subgenital plate similar to that of *L. sbordonii.*

Female genitalia. Copulatory papilla small, plicated dorsally, very slightly enlarged toward the apex. Apex bilobated and not flat (Fig. 17).

Longuripes evanesca is very similar to *Longuripes sbordonii*, from which it can be distinguished by its smaller size, by the elytra and the genitalia of the males, and the lenght of the ovipositor and of the copulatory papilla in the females. The two species are sympatric.

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Males	1.6-1.8	11-13.3	12.9-14.9	6.8-7.1	4.4-4.9	—
(n=4)	1.7	12.4	13.9	7	4.6	
Females	2.3-2.5	14.4-14.8	17-17.4	—	—	9.8-10.5
(n=3)	2.4	14.6	17.2			10.2

Longuripes stenopsita Desutter-Grandcolas, n. sp.
(Fig. 19,20,23,27,30)

Type locality: Mexico, Oaxaca, Tuxtepec.

Type material: Male holotype: Mexico, Oaxaca, Tuxtepec, Acatepec, cueva del Zopilote, 6-VIII-1973 (V. Sbordoni), in alcohol, UTVR. Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UTVR.

Diagnosis

Male. Elytra (Fig. 23): mirror larger than long, and crossed by a unique transversal vein; vein normally joining the inner chord and the mirror shifted, and joining the inner chord and the diagonal vein, the cells thus defined of specific shape (compare for example with *L. surchiapaneca*, Fig. 37). File with 171 teeth (another male, from near Valle Nacional has a file of 136 teeth). Susanal plate with very small posterior angles. Dorsal bumps present on metanotum and tergite 1, but extremely small; metanotal posterior margin rounded and raised dorsally.

Male genitalia as on the figures 19-20. Note the form of C-sclerite basal plate.

Female. Posterior margin of subgenital plate bisinuated (Fig. 27).

Female genitalia (Fig. 30). Copulatory papilla greatly enlarged just before the apex.

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Male (n = 1)	1.6	12.8	16.3	5.4	3.8	—
Female (n = 1)	2.3	15	18.6	—	—	11.4

Other material examined: Mexico, Oaxaca, Grutas de Monteflor, 6 km. N of Valle Nacional, 5 females, 28-XII-1972 (J. Reddel, D. McKenzie, M. McKenzie, S. Murphy), in alcohol, UMMZ; 1 male and 2 females, in alcohol, MNHP.

Longuripes minor Desutter-Grandcolas, n. sp. (Fig. 21,24,25,31)

Type locality: Mexico, Chiapas, Chiapa de Corzo.

Type material: Male holotype: Mexico, Chiapas, Chiapa de Corzo, m. 810, grotta Roberto, 9-IX-1973 (V. Sbordoni), in alcohol, UTVR.

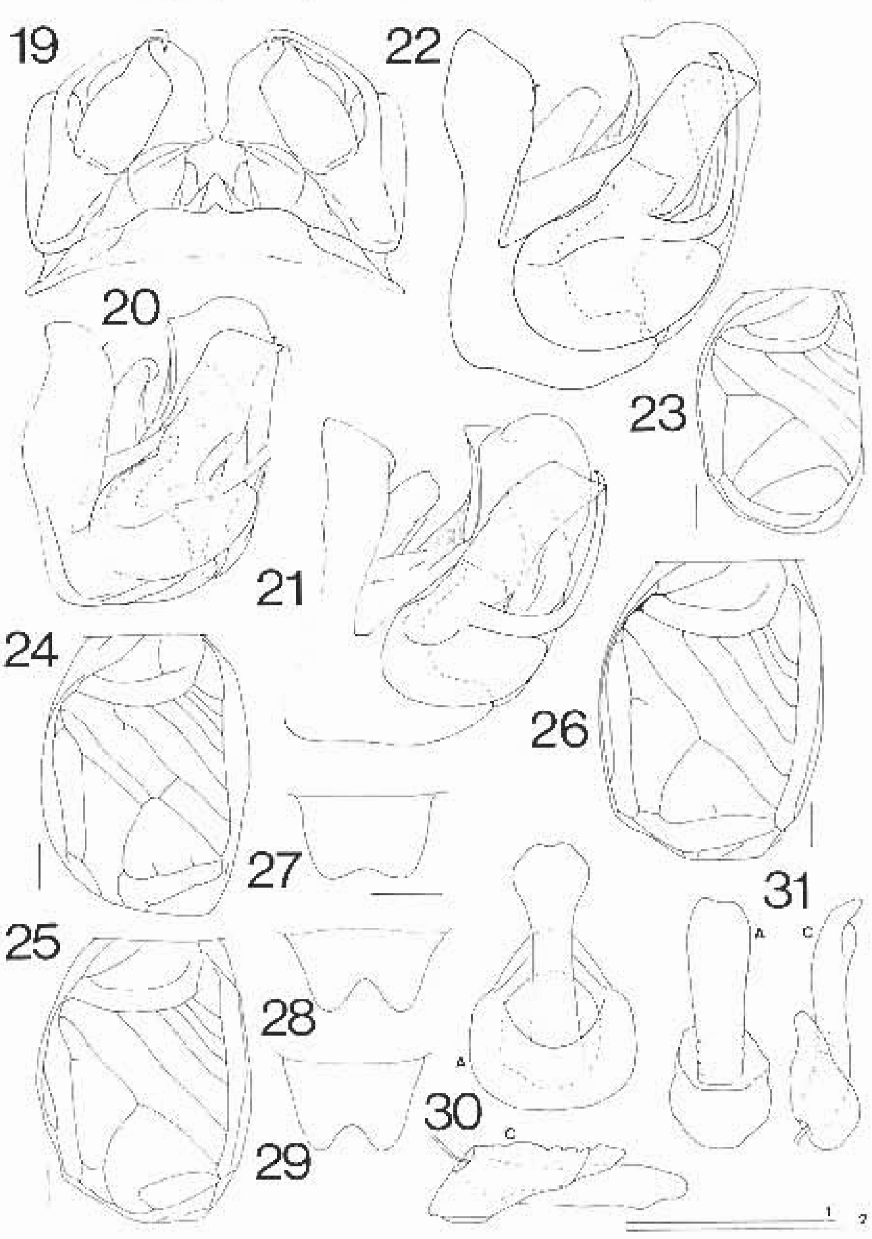

Fig. 19-31 — Genus *Longuripes*, n. gen. Male genitalia (scale 2): Fig. 19-20: *L. stenopsita*, n. sp. (dorsal and lateral view); Fig. 21: *L. minor*, n. sp. (lateral view); Fig. 22: *L. altaminor*, n. sp. (lateral view). Male elytra: Fig. 23: *L. stenopsita*; Fig. 24-25: *L. minor*; Fig. 26: *L. altaminor*. Female subgenital plate: Fig. 27: *L. stenopsita*; Fig. 28: *L. minor*; Fig. 29: *L. altaminor*. Female copulatory papilla (scale 1): Fig. 30: *L. stenopsita*; Fig. 31: *L. minor*. Scales: 1 mm.

Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UTVR. Paratypes: Same locality, same date, same collector as the holotype: 2 males and 1 female, in alcohol, UTVR; same locality, same date as the holotype, 1 male and 1 female (V. Vomero), in alcohol, MNHP; Chiapa de Corzo, m 650, Cueva del Chorreadero, 1 male and 2 females, 25-II-1971 (V. Sbordoni), in alcohol, UTVR. Chiapas, roadside cave, 1.5 mi past Balneario, 10 mi NE Tuxtla Gutierrez, 2690 ft., 1 male and 1 female, 18-V-1972 (D. Mc.Kenzie), in alcohol, UMMZ. Chiapas, Ocozocoautla, cueva del Muju, m 680, 1 male and 1 female 5-X-1973 (V. Sbordoni), in alcohol, UTVR.

Diagnosis

Species very close to the preceding, but recognizable by the following characters:

Male. Elytra (Fig. 24 - 25): venation variable, always incomplete or «disturbed», the vein joining the inner chord and the mirror generally lacking or shifted. When complete, mirror crossed by a unique transverse vein. File with 107-123 teeth (mean number 115, n = 8). Elytra longer than in *L. stenopsita* (compare the measures). Dorsal glands present on metanotum, and sometimes on tergite 1, and bigger than in *L. stenopsita*.

Male genitalia somewhat bigger than those of *L. stenopsita*, and as on the figure 21.

Female. Ovipositor smaller than 10 mm. Subgenital plate posterior margin indented (Fig. 28).

Female genitalia. Copulatory papilla slightly and regularly enlarged before the apex. Apex more or less bilobated, and asymmetrical. Membrane casing surrounding the base of the papilla distinctively inflated (Fig. 31).

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Males	1.6	12.1-12.7	14.1-14.7	6.5-6.6	4.3-4.4	—
(n=3)		12.4	14.3	6.5	4.3	
Females	2.1-2.3	13.3-16.1	15.4-18.2	—	—	8.7-9.6
(n=3)	2.2	15.1	17.1			9.3

One female from Chiapas, Ocozocoautla, Lago de Malpaso, rio Negro, m 115, cueva de l'Agua Purificada 15-IX-1973, (V. Vomero) presents a copulatory papilla similar to that of the females studied, but with an apex somewhat flatter and larger, and a base also larger and shorter. Its size is bigger (measures: 2.4, 14.6, 15.8, 10.4 mm, respectively). It may represent a local variation or an altitudinal differentiation of *L. minor.*

Longuripes altaminor Desutter-Grandcolas, n. sp. Fig. 22,26,29)

This species is very close to *Longuripes minor,* from which it can be distinguished mostly by its greater size, male genitalia and ovipositor length. It lives at a higher altitude than *L. minor* (1320-1350 m *versus* 650-810 m).

Type locality: Mexico, Chiapas, Tuxtla Gutierrez, cueva de las Pinas Ramas.

Type material: Male holotype: Mexico, Chiapas, Mexico - Tuxtla Guitierrez Hwy km 1112, cueva de las Pinas Ramas, 19-VIII-1967 (J. Reddell, J. Fish, T. Evans), in alcohol, UMMZ. Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UMMZ. Paratypes: Same locality, same date, same collector as the holotype, 2 males, in alcohol, UMMZ; id., 1 male (genitalia number 945) in alcohol, UMMZ; id., 1 male, in alcohol, MNHP; Chiapas, 27 km E Tuxtla Gutierrez on Pan Am, cueva de Pinas Ramas, 1 male, 12-VIII-1969 (S. & J. Peck), in alcohol, UMMZ. Chiapas, Ocozocoaulta, Rancho del Cielito, cueva de Cerro Brujo, m 1320, 1 male, 22-III-1971 (R. Argano), in alcohol, UMMZ (genitalia number: 952). Chiapas, Ocozocoautla, cueva de las Canicas, m 1350, 1 male, 22-III-1971 (V. Sbordoni), in alcohol, UTVR; id., 1 male (22-III-1971), MNHP.

Diagnosis

Species more closely related to *L. minor* that to any other species. In particular, male elytra similar (Fig. 26; file: 108-123 teeth, mean number: 116, n=4).

L. altaminor is recognizable by the following characters:

Male genitalia of bigger size, with longer epi-ectophallic glands. C-sclerites ventral pouches much more developed; basal plates larger at their apex (Fig. 22).

Female. Ovipositor length greater than 10 mm. Subgenital plate posterior margin more deeply indented (Fig. 29).

Female copulatory papilla quite similar to that of *L. minor,* but the apex more bilobated and not asymmetrical. In a female paratype of Ocozocoautla, Rancho del Cielito, the papilla is mostly enlarged just before the apex, and as regularly as in the allotype.

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Males	1.6-1.8	12.8-14.7	15-16.5	6.5-7.1	4.3-4.5	—
(n = 3)	1.7	13.5	15.4	6.7	4.4	
Female (n = 1)	2.2	17.1	19.7	—	—	10.4

Variation: One male paratype from Rancho del Cielito (cueva de las Canicas) possesses a normal venation in the mirror (a unique transverse vein).

Other material observed: Mexico, Chiapas, Ocozocoautla, Rancho del Cielito, cueva de Cerro Brujo, m 1320, 1 female, 22-III-1971 (R. Argano), in alcohol, UTVR; id. 1 female (V. Sbordoni), in alcohol, MNHP. Measures of these two females: 2.5 - 3; 15 - 15.5; 17.1 - 17.8; 11.3 - 12.7, in mm, respectively.

arganoi group:

Longuripes arganoi Desutter-Grandcolas & Hubbell, n. sp. (Fig. 32, 33, 36,39)

Type locality: Mexico, Chiapas, Tumbala.

Type material: Male holotype: Mexico, Chiapas, Tumbala, cueva de Cuncumpa, 16-17-IV-1991 (V. Sbordoni), in alcohol, UTVR. Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UTVR. Paratypes: Same locality, same date, same collector as the holotype, in alcohol, 2 females UTVR, and 1 female MNHP; Chiapas, Yaialon, Emiliano Zapata, cueva de la Ventana de Ajabalhna, 1 male and 2 females, IV-1991 (V. Sbordoni), in alcohol, UTVR; id., 1 male, MNHP.

Diagnosis

Male. Elytra (Fig. 36): vein joning the inner chord and the mirror lacking. File with 171-188 teeth (mean number: 179, n = 3). Dorsal bumps present on metanotum and tergite I (these reduced); metanotal posterior margin rounded and prominent. Susanal plate posterior angles small.

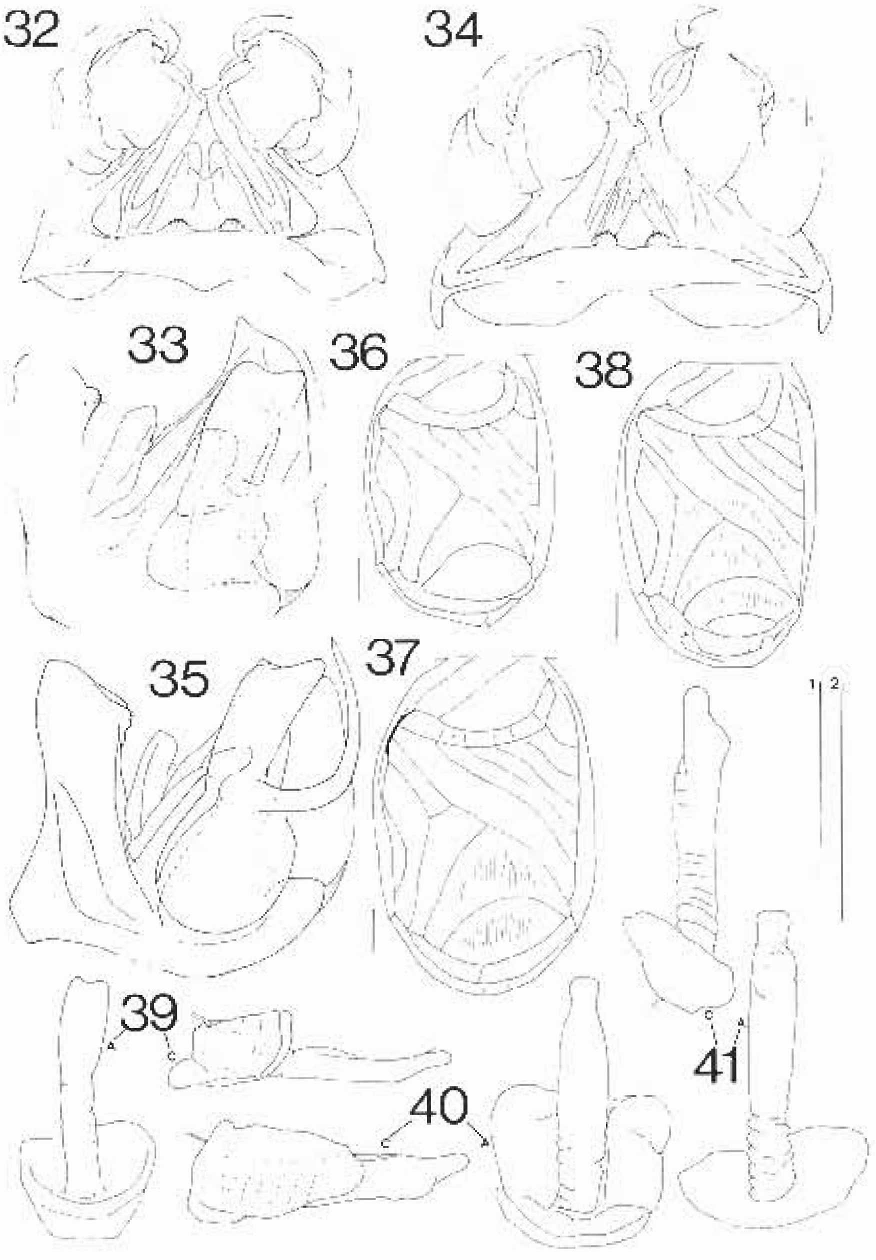

Fig. 32-41 — Genus *Longuripes*, n. gen. Male genitalia (dorsal and lateral view, scale 2): Fig. 32-33: *L. arganoi*, n. sp.; Fig. 34-35: *L. intermedia*, n. sp. Male elytra: Fig. 36: *L. arganoi*; Fig. 37: *L. surchiapaneca*, n. sp.; Fig. 38; *L. intermedia*. Female copulatory papilla (scale 1): Fig. 39: *L. arganoi*; Fig 40-41: *L. intermedia*. Scales: 1 mm.

Male genitalia as on the figures 32 - 33.

Female genitalia. Copulatory papilla enlarged before the apex; apex clearly bisinuated (Fig. 39).

Measures (in mm.):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Males (n=3)	1.7-2 1.8	13.6-14.2 (n=2)	15-15.4 (n=2)	6.6-2 6.1	4-4.4 4.2	—
Females (n=4)	2.2-2.5 2.4	13.6-15.9 15.1	14.3-17.3 16.5	—	—	9-10.3 9.8

Other material observed: Mexico, Chiapas, Tumbala, cueva de Cuncumpa, 1 female (identification uncertain), 16-17-IV-1991 (V. Sbordoni), in alcohol, UTVR.

Longuripes surchiapaneca Desutter-Grandcolas, n. sp. (Fig. 37)

Type locality: Mexico, Chiapas, Huixtla.

Type material: Male holotype: Mexico, Chiapas, Huixtla, m 2140, La Grandeza, Llano Grande, cueva de Llano Grande, 26-IX-1973 (A. Zullini), in alcohol, UTVR. Paratypes: Same locality, same date, same collector as the holotype, 1 male, in alcohol, UTVR; same locality, same date as the holotype, 1 male (V. Sbordoni), in alcohol, MNHP.

Diagnosis

Species very similar to the preceding, but bigger (compare the measures).

Male. Elytra (Fig. 37): vein normally located between the inner chord and the mirror shifted, joining the inner chord and the diagonal vein; the 2 cells thus delimited of a specific shape. File with 130-163 teeth (mean number: 150, n = 3). Dorsal bumps present on metanotum only, and small; posterior margin of metanotum very prominent. Susanal plate posterior angles small.

Male genitalia similar to those of *L. arganoi*, The basal plates of C.-sclerites somewhat larger and shorter.

Female unknown.

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel
Males	2-2.4	17.9-18.1	15.4-20.7	6.7-8.5	4.2-4.7
(n=3)	2.3	(n=2)	18.5	7.4	4.5

Other material observed: Mexico, Chiapas, Huixtla, m 2140, La Grandeza, Llano Grande, grutas de Llano Grande, 26-IX-1973, 6 larvae (V. Sbordoni), 2 larvae (A. Zullini), in alcohol, UTVR.

Longuripes intermedia Desutter-Grandcolas, n. sp.
(Fig. 34, 35,38, 40, 41)

Type locality: Mexico, Chiapas, San Cristobal de las Casas, La Quinta.

Type material: Male holotype: Mexico, Chiapas, San Cristobal de las Casas, La Quinta, cueva II de la Cañada, m 2270, 10-IX-1975 (V. Vomero), in alcohol, UTVR. Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UTVR. Paratypes: Same locality, same date, same collector as the holotype, 4 females, in alcohol, UTVR. id., 1 female, in alcohol, MNHP; Chiapas, grutas de Tenejapa n° 15, 1 male 15-II-1985 (A. Gobetti, J.F. Pittet), in alcohol, MNHP; Chiapas, Solistahuacan, Pueblo Nuevo, Arroyo Grande, cueva del Abuelito, 1 male, 1-IV-1988 (V. Sbordoni), in alcohol, UTVR; Chiapas, San Cristobal de las Casas, grutas de Rancho Nuevo, 1 male, 1-IV-1971 (V. Sbordoni), MNHP; Chiapas, Jitotol, m. 1600, cueva del Puente Redondo, 1 female, 29-VIII-1973 (V. Vomero), in alcohol, MNHP; Chiapas, Cueva de Colonia, Rincon, 60 mi. N of Chiapa de Corzo, 5900ft, 2 females, 30-V-1972 (D. McKenzie), in alcohol, UMMZ; id., 1 female, MNHP.

Diagnosis

Male. Elytra (Fig. 38): mirror crossed by two transverse veins, one sometimes broken (more rarely only one transverse vein). File with 212-223 teeth (mean number: 217, n=3). Dorsal bumps present on metanotum and tergite 1, another pair present on tergite 2 but smaller.

Male genitalia bigger than those of *L. arganoi* and *L. surchiapaneca*, and with slight differences on median lophi, C-sclerites basal plate and spine (Fig 34, 35).

Female genitalia (Fig. 40, 41). Copulatory papilla sligthly narrowed before the apex; apex clearly narrower than the base, slightly or not bisinuated (not bilobated as in *L. arganoi*).

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Males	1.8-2	12.6-15.7	13.9-17	5.9-6.8	3.8-4.1	—
(n = 3)	1.9	14.2	15.5	6.2	4	
Females (n=2)	2.4-2.6	16.4-17.2	17.9-19	—	—	9.8-10.3

Other material examined: Mexico, Chiapas, Comitan, cueva chica de San Agostin, m 2380, 1 male, 4-III-1971 (V. Sbordoni), UMMZ (genitalia missing). File with 209 teeth.

stenops group:

Longuripes stenops Desutter-Grandcolas & Hubbell, n. sp.
(Fig. 42 to 45)

Type locality: Mexico, Oaxaca, Huautla.

Type material: Male holotype: Mexico, Oaxaca, Huautla, Cueva Bonita del Presidente, 1 mi. N. of Huautla, 12-VIII-1967 (J. Reddel, J. Fish, T. Evans), in alcohol, UMMZ. Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UMMZ. Paratypes: Same locality, same date, same collector as the holotype, 1 male and 1 female, in alcohol, UMMZ; 1 male in alcohol, MNHP; 1 male and 1 female MNHP. Mexico, Oaxaca, Milliped caves, 1 male and 1 female 1965 (R. Russell), in alcohol, UMMZ. Mexico, Oaxaca, Milliped cave, 5 km NE of Huautla, 200 feet from entrance, in darkness, 1 male and 2 females, 1965 (W. Russell), in alcohol, UMMZ. Mexico, Oaxaca, Huautla, cueva San Augustin, 1 male, 30-XII-1966 (Russell, Raines), in alcohol, UMMZ. Mexico, Oaxaca, cueva arriba de Rio Iglesia, 4 mi. E of Huautla, 1 male and 1 female, 6-V-66 (B. Russell, J. Fish), 1700 m, in alcohol, MNHP.

Diagnosis

Size large.

Male. Elytral venation as on figure 42; minor larger than long, and crossed by 2 transverse veins. File: 371-396 teeth (mean number:

382, n = 5). Susanal plate posterior angles elongated, less than half the length of the plate; these and the apical half of susanal plate covered with long setae. Dorsal bumps present on metanotum and tergites 1-5; posterior margin of metanotum and tergites 1-2 rounded and dorsally prominent.

Male genitalia (Fig. 43, 44). C-sclerites ventral pouches more or less spherical, relatively small compared to the other species of the genus; basal plates not enlarged at the apex; lateroventral spines long and thin. Glands formed on epi-ectophallic membrane resembling a simple pouch, without an individalized median longitudinal axis.

Female. Posterior margin of subgenital plate bisinuated.

Female genitalia as on figure 45. Canal aperture surrounded by hardened membrane. Apex slightly bisinuated.

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Males	2-2.1	16.8-18.8	20.2-24	8.9-9	5.6-5.7	—
(n=3)	2.1	17.6	22.1	9	5.6	
Females	2.5-2.8	19-20	22.3-25.5	—	—	13.6-13.9
(n=3)	2.6	19.5	23.6			13.8

Other material observed: Mexico, Oaxaca, Huautla, cueva San Augustin, 1 female larva, 30-XII-1966 (Russell, Raines), in alcohol, UMMZ. Mexico, Oaxaca, Huautla, La Grieta, 1 fermale of uncertain identification, 23-V-1977 (T. Johnson), in alcohol, UMMZ.

3. Genus *PROLONGURIPES* Desutter-Grandcolas, n. gen.

Type species: *Prolonguripes phalangium* (Saussure, 1847), n. comb. (Fig. 46, 47)

Distribution: Guatemala, Honduras.

Prolonguripes is known from cloudforest (altitude 1800-1970 m).

Diagnosis

Species of darker colour than *Longuripes* and with contrasted facial markings (dark brown and yellow in dry specimens). Hind tibiae with 4 pairs of subapical spurs. Tympana and hind femora as

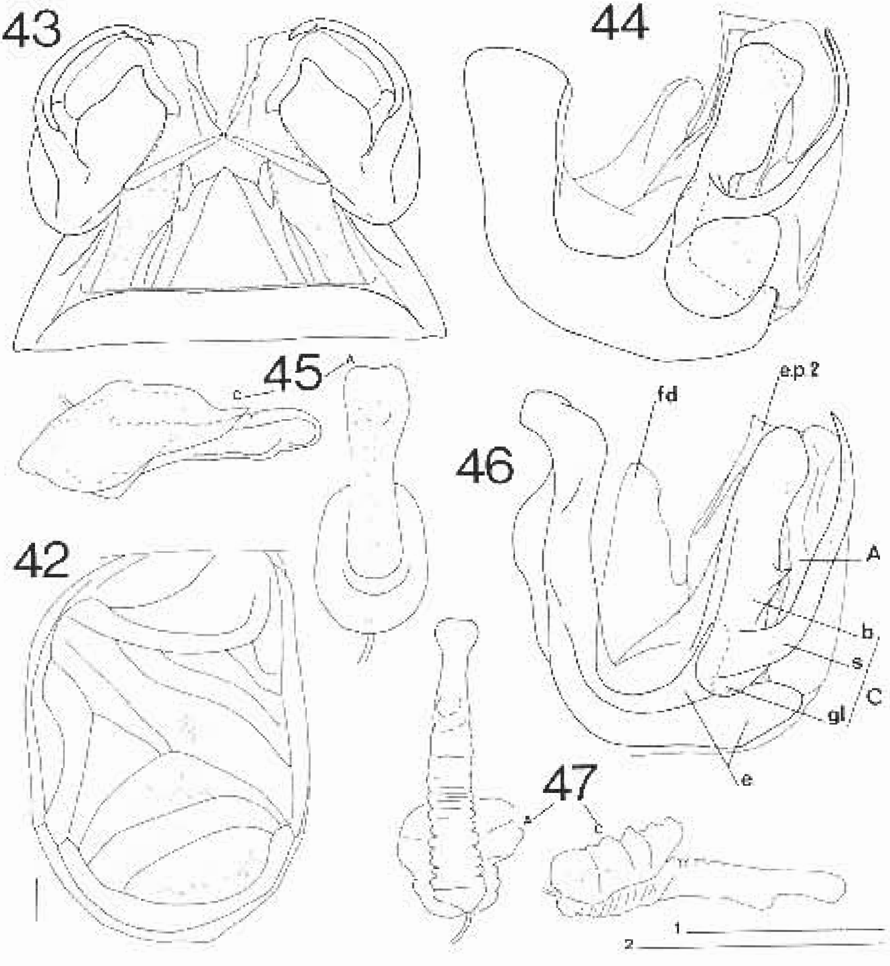

Fig. 42-47 — Genera *Longuripes*, n. gen. and *Prolonguripes*, n. gen. Fig. 42: *Longuripes stenops*, n. sp., male elytra; Fig. 43-44: id., male genitalia (dorsal and lateral view, scale 2); Fig. 45: id., female copulatory papilla (scale 1). Fig. 46: *Prolonguripes* n. sp. aff. *phalangium*, male genitalia (lateral view, scale 2); Fig. 47, id., female copulatory papilla (scale 1). Scales: 1 mm. Abbreviations: p. 10.

in *Longuripes*. First hindtarsomere serrulation reduced. Eyes bigger than in *Longuripes*; ocelli present. Fastigium similar to that of *Longuripes* but slightly narrower.

Male. Susanal and subgenital plates, dorsal glands and elytra as in *Longuripes*.

Male genitalia (Fig. 46). Genitalia differing from those of *Longuripes* by the very small size of C-sclerites ventral pouch, the apical position of draining duct aperture, the shape of C-sclerites basal plates (with one or two more or less elongated spines) and the sclerotization of epi-ectophallic membrane. Epiphallic parameres similar to those of *longuripes*.

Female genitalia. Copulatory papilla plicated, long and slender, with a distinctively constricted apex (Fig. 47).

Monophyly and relationships

Prolonguripes is close to *Longuripes* (see above). Its monophyly is attested by C-sclerites basal plate lateral spine(s), and epiectophallic membrane sclerotization.

Apart from *P. phalangium*, 3 species of *Prolonguripes* are known, one from Guatemala and two others from Honduras; they will be described in another paper.

Biology

The morphology of *Prolonguripes* is of a «normal» type, and it does not seem to be adapted to live in caves. One species has however been found in a cave in Guatemala (only one male and one female from one cave), while another species has been taken in Rosario Mines and in cloud forest (Honduras). Comparison with other Amphiacustae would suggest ecological characteristics close to those of *Noctivox* or *Nemoricantor* (see infra).

4. Genus *ARACHNOPSITA* Desutter-Grandcolas & Hubbell, n. gen.

Type species: *Arachnopsita usumacinta* Desutter-Grandcolas, n. sp.

Distribution: Guatemala (near Mexican border).

Arachnopsita is known only from tropical rainforest, altitude 100 to 240 m, and from the forests of Alta Verapaz mountains.

Diagnosis

Species apterous and of a uniform light brown colour, probably spotted with dark brown on body and face. Legs quite similar to those of *Longuripes* (hindfemora, apical spurs of tibiae II, hindtibiae serrulation, first hindtarsomeres), but tibiae I lacking tympanum and hindtibiae with 4 pairs of subapical spurs. Eyes reduced, extending slightly under the antennal pit. Ocelli absent or greatly reduced. Fastigium extending the vertex in an inclined plane (Fig. 48); basal furrow neatly marked (except in some dried specimen) and similar to that of *Longuripes* and *Prolonguripes* (but not concave as in these two genera).

Male without dorsal glands. Susanal plate posterior angles rounded and with long setae, but not elongated.

Male genitalia. Epiphallic sclerite with a median sharp point. C-sclerites with a basal plate vertically articulated on epiphallic arm, as in *Longuripes* and *Prolonguripes;* this plate slightly enlarged ventrally (but without an individualized pouch) and with a lateral notch more or less developed as a spine or hook. A-sclerites pushed aside behind C-sclerites basal plates. Epiphallic parameres similar to those of *Longuripes* and *Prolonguripes*, but parameres 2 larger and with a free tip. Epi-ectophallic membrane partly sclerotized, and with very small invaginations. Endophallic apodemes elongated, and close to each other.

Female genitalia. Copulatory papilla not particularly elongated, but large and very flat; apex rounded, more or less narrowed.

Monophyly and relationships

Arachnopsita is most closely related to *Longuripes* and *Prolonguripes* (see above: *Longuripes*). Its monophyly is ascertained by the formation of epiphallic median point. Another apomorphy could be the shape of female copulatory papilla.

Biology

As for *Longuripes*, *Arachnopsita* has always been collected in caves; it also shows a classically regressed morphology. This genus can thus be defined as troglobitic.

Apart from the species here described, 3 others are known from Guatemala; they will be described in another paper.

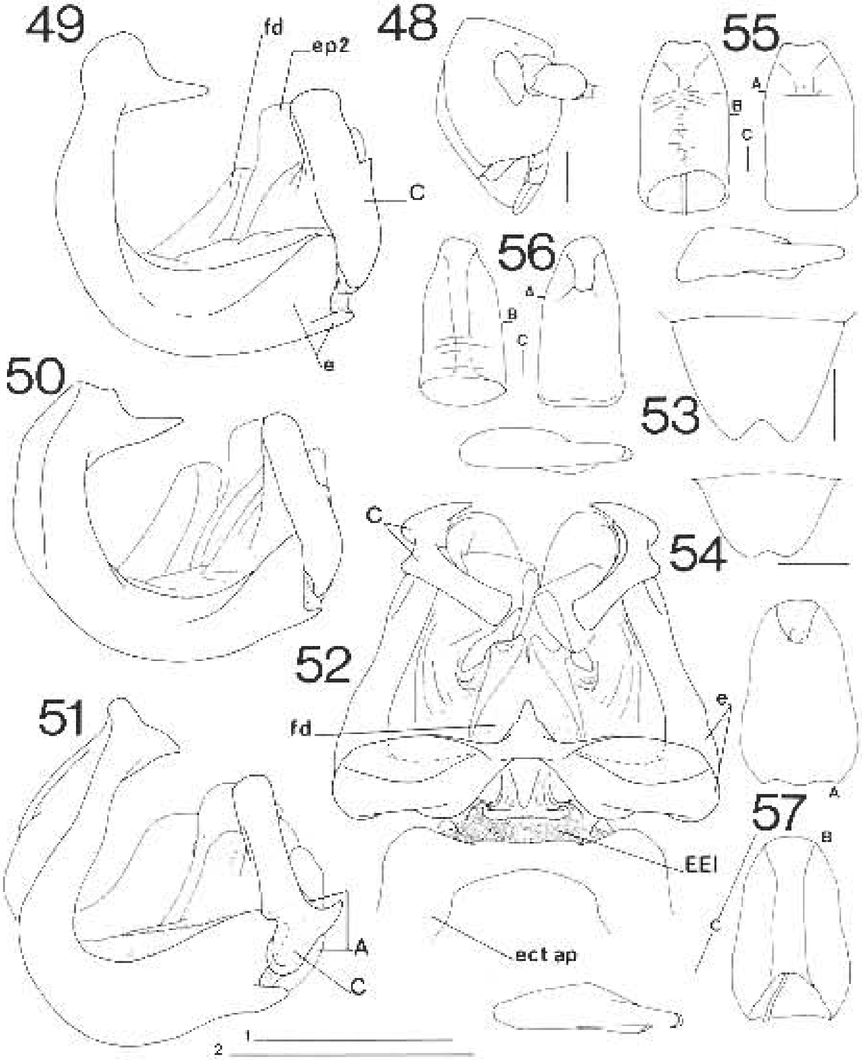

Fig. 48-57 — Genus *Arachnopsita*, n. gen. Fig. 48: Head of *A. usumacinta*, n. sp. Male genitalia (scale 2): Fig. 49: *A. usumacinta* (lateral view); Fig. 50: *A. pequegna*, n. sp. (lateral view); Fig. 51-52: *A. cavicola* (Saussure, 1897) (lateral and dorsal view). Female subgenital plate: Fig. 53: *A. usonacinta;* Fig. 54: *A. cavicola*, female copulatory papilla (scale 1): Fig. 55: *A. usonacinta; Fig. 56: A. pequegna;* Fig. 57: *A. cavicola*. Scales: 1 mm. Abbreviations: p. 10.

Arachnopsita usumacinta Desutter-Grandcolas, n. sp. (Fig.48,49,53,55)

Type locality: Guatemala, rio Usumacinta, near Yaxchilan.

Type material: Male holotype: Guatemala, rio Usumacinta, env. Yaxchilan, cueva del Tepescuintle, m 240, 13-III-1971 (R. Argano), in alcohol, UTVR. Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UTVR. Paratypes: Same locality, same date, same collector as the holotype, 1 female, in alcohol, UTVR; id., 1 male and 1 female, in alcohol, MNHP.

Diagnosis

Male genitalia (Fig. 49). C-sclerite lateral spine formed at midlenght of the sclerite (not at its base) and short; no ventral pouch clearly distinguishable. Epiphallic median hook long and relatively slender.

Female. Ovipositor quite small. Subgenital plate indented (Fig. 53).

Female genitalia (Fig. 55). Copulatory papilla relatively long, the apex slightly narrowed but not clearly individualised, and bisinuated.

Measures (in mm):

	Lpron	LFIII	LTIII	Lovip
Males (n=2)	2.1-2.3	12.4-13	13.9 (n=1)	—
Females (n=3)	2.9-3.3 3.1	16.1-19 17.4	19.5-21.8 20.5	10.7-11.4 11

Arachnopsita pequegna Desutter-Grandcolas, n.sp. (Fig. 50, 56)

Type locality: Guatemala, rio Usumacinta, near Yaxchilan.

Type material: Male holotype: Guatemala, rio Usumacinta, env. Yaxchilan, m 100, cueva di Yaxchilan, 9-III-1971 (A. Zullini), in alcohol, UTVR. Female allotype: Same locality, same date as the holotype (V. Sbordoni), in alcohol, UTVR. Paratypes: Same locality, same date, same collector as the allotype, 1 female, in alcohol, UTVR; same locality, same date as the holotype, 1 female (R. Argano), in alcohol, MNHP. Rio Usumacinta, env. Yaxchilan, cueva del Diablo, m 230, 1 male, 12-III-1971 (A. Zullini), in alcohol, MNHP.

Diagnosis

Species very close to the preceding, but of smaller size.

Male genitalia (Fig. 50). C-sclerites with a low and large lateral processus, not forming a real spine.

Female genitalia (Fig. 56). Copulatory papilla thinner than in *A. usumacinta*, its apex narrower and not clearly bisinuated.

Measures (in mm):

	Lpron	LFIII	LTIII	Lovip
Males	1.8-1.9	11.2-11.3	12.5	—
n(=2)				
Females	2.5-2.6	14.5-15.3	16.1-16.4	8.7-8.9
(n=3)	2.5	15	16.2	8.8

Arachnopsita cavicola (Saussure, 1897), n. comb. (Fig. 51, 52, 54, 57)

Arachnomimus cavicola Saussure, 1897, Biol. Centr.-Amer.: 251.
Endocous cavicola, Chopard, 1968, Orthop. Cat.: 280.

Type locality: Guatemala, cave of Lanquin in Vera Paz.

Type material: 1 female juvenile, MHNG (not examined).

An important material from the type locality has been examined, and allows a redefinition of that species.

Diagnosis

Male genitalia (Fig. 51, 52). Epiphallic median hook short and large. C-sclerite basal plate clearly enlarged ventrally (almost as in *Prolonguripes*, but no glandular structure distinguishable); lateral notch long and large, located near the base of the plate.

Female. Subgenital plate bisinuated at the apex, but not really indented (Fig. 54).

Female genitalia (Fig. 57). Copulatory papilla large and rounded, slighlty narrowed toward the apex (but not as in the other species); apex almost straight.

Measures (in mm):

	Lpron	LFIII	LTIII	Lovip
Males	2-2.1	10.4-11.2	10.5-12	—
(n=3)	2.1	10.9	11.5	
Females	2.2-2.7	12.7-15.1	13.3-16.3	9.3-11.4
(n=7)	2.5	13.7	14.4	10.2

Material examined: Guatemala, Alta Verapaz, cave 1 mi W of Lanquin, 20-IX-1961. (T.H. & S.P. Hubbell, I.J. Cantrall, T.J. Cohn): 4 males (genitalia n. 973, 1024) and 15 females, in alcohol, UMMZ; id., 2 males and 2 females, MNHP; id., 1 male and 1 female, dry, MNHP. Alta Verapaz, cueva de Lanquin, Lanquin, 1 female, 28-VIII-1969 (S. & J. Peck), in alcohol, UMMZ.

5. Genus *MAYAGRYLLUS* Desutter-Grandcolas & Hubbell, n. gen.

Type species: *Mayagryllus apterus* Desutter-Grandcolas & Hubbell, n. sp.

Distribution: Southern and South-Eastern Mexico (Yucatan, Chiapas, Tabasco), Guatemala, Belize.

Mayagryllus is known from tropical rainforest and deciduous tropical forest; in Northern Chiapas it has also been collected from a locality at 1600 m. It ranges from 120 to 1600 m in altitude.

This genus resembles *Longuripes* by its reduced eyes, its median tibiae, its hindfemora and its light brown uniform color. It can be distinguished from *Longuripes* by its fastigium and ocelli, its male and female genitalia, its hindtibiae (serrulation and subapical spurs), and the loss of tympana, male dorsal glands and elytra (except in *Mayagryllus yucatanus*).

It resembles *Arachnopsita* by the loss of tympana, male dorsal glands and elytra, its tibiae II and III and its general appearance (colour, eyes). It can be distinguished from that genus by its male and female genitalia and its ocelli.

Diagnosis

Species apterous (Fig. 68), except for the males of *M. yucatanus* (Hubbell, 1938), which have short elytra. Hindtibiae strongly serrulated and with 4 pairs of subapical spurs. Hindfemora shorter than in *Longuripes*, but with a filiform apical part. Tibiae II with 2 apical spurs. Tibiae I without tympanum. First hindtarsomeras with 2 rows of spines, the inner one reduced to 1 or a few spines. Eyes somewhat reduced (slightly longer than the antennal pit on the face). Ocelli present. Fastigium almost at the same level as the vertex, large (more or less as large as the scape) and with a basal furrow

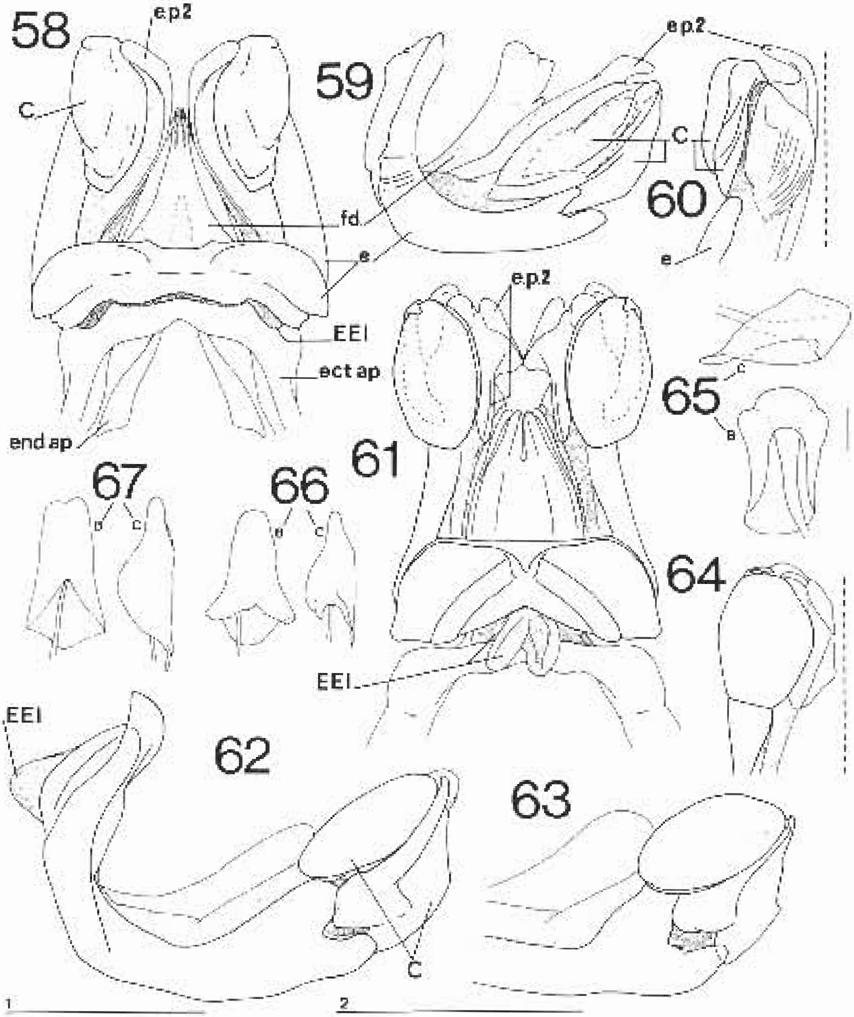

Fig. 58-67 — Genus *Mayagryllus*, n. gen. Male genitalia (scale 2): Fig. 58-60: *M. apterus*, n. sp. (dorsal and lateral view, and inner side of epiphallic arm); Fig. 61-62: *M. tilaensis*, n. sp. (dorsal and lateral view); Fig. 63-64: *M. tumbalaensis*, n. sp. (lateral and dorsal view of epiphallic arm). Female copulatory papilla (scale 1, except Fig. 65): Fig. 65: *M. apterus*; Fig. 66: *M. tilaensis*; Fig. 67: *M. tumbalaensis*. Scales: 1 mm (Fig. 65: Scale: 0.1 mm). Abbreviations: p. 10.

(Fig. 70); this furrow only slightly marked, but straight as in *Longuripes*, *Prolonguripes* and *Arachnopsita*.

Male without dorsal glands; posterior angles of susanal plate rounded, somewhat enlarged and with some long setae.

Male genitalia. C-sclerites more horizontal than vertical, not very mobile on epiphallic arm (if mobile, horizontally articulated), and comprising a large membranous dorsal part and a sclerotized hook-like ventral part. A-sclerites pushed aside behind C-sclerites basal plates. Membrane between A-sclerite and epiphallic parameres with distinct furrows. Epiphallic parameres 2 similar to those of *Arachnopsita*, but the free still more developed. Endophallic apodemes elongate.

Female genitalia. Copulatory papilla small, not slender and long as in *Longuripes*, its general shape triangular or quadrangulate.

Monophyly and relationships

Mayagryllus belongs to the *Longuripes* group of genera (see above). Its monophyly is attested by the shape and orientation of C-sclerites.

Mayagryllus species belong to 2 species groups according to male genitalia characters:

1. *apterus* group: Male genitalia short and large, the apex not particularly elongated. Endophallic apodemes largely separated and divergent.

This group includes *M. apterus*, n. sp. and *M. yucatanus*, from Belize and Yucatan (Mexico).

2. *tilaensis* group: Male genitalia long and narrow. Endophallic apodemes very close.

This group includes *M. tilaensis*, n. sp. and *M. tumbalaensis*, n. sp., from Chiapas (Mexico).

Biology

Mayagryllus has a cave adapted morphology, and I will consider it as troglobitic in the following discussions. Hubbel (1938) mentions that *M. yucatanus* has been encountered deep in caves, but also near cave entrances or even outside caves. This species shows elytra in males (very short, but functional), while other species are apterous.

Mayagryllus apterus Desutter-Grandcolas & Hubbell, n. sp. (Fig. 58-60, 65, 68, 70)

Type locality: Belize, St. Herman's cave, 10 mi S of Roaring creek.

Type material: Male holotype: Belize, St. Herman's cave, 10 mi S of Roaring creek, 16-I-1972 (D.Mc Kenzie), in alcohol, UMMZ. Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UMMZ. Paratypes: Same locality, same date, same collector as the holotype, 1 male and 1 female, in alcohol, UMMZ; id., 1 male and 1 female, in alcohol, MNHP; St Herman's cave, 2 female, VI-1974, chas (Goodnight), in alcohol, UMMZ; Caves branch, 400', Bucks Bypass cave, 1 male and 2 females, 14-VIII-1972 (S. Peck), in alcohol, UMMZ; id., 1 male and 1 female, in alcohol, MNHP; Caves branch, 500', Mountain Cow cave, animal leaf nest, 2 males and 2 females, 5-VIII-1972 (S. & J. Peck), in alcohol, UMMZ; Caves branch, 400', St. Herman's cave, upper dry passage, dung trap, 13 males, 2-20-VIII-1972 (S. & J. Peck), in alcohol, UMMZ; Caves Branch cave system, 5 km NNE Caves Branch, Cayo district, 1 male, 24-29-VII-1976 (L. Mc Natt, M. Shawcross), in alcohol, UMMZ; Waterfall cave, 5 km SSW Caves branch, Cayo district, 1 female, 10-VIII-1976 (L. Mc Natt & B. De Chatelets), in alcohol, UMMZ; Petroglyph cave, Cayo district, 1 male and 2 females, 27-V-1977 (L. Mc Natt), in alcohol, UMMZ; «Mayan» cave, nr Little Vaqueros creek, Blancaneaux Lodge, near Cayo, warm cave with thin roof penetrated by roots, 1/2 mi deep, 1 male and 1 female, 22-IV-1972 (T.E. Moore), in alcohol, UMMZ.

Diagnosis

Male genitalia relatively large and short (Fig. 58 - 60). Endophallic apodemes well separated and divergent. Ectophallic arc large. Epi-ectophallic membrane without clear invaginations. Sclerotized ventral part of C-sclerite shorter than the dorsal membranous part.

Female. Ovipositor well shorter than the hindfemora. Subgenital plate posterior margin slightly bisinuated.

Female genitalia (Fig. 65). Copulatory papilla very short, quadrangulate, enlarged before the apex. Ventral face sclerotized.

From the material at hand, there seems to exist an important dimorphism between males and females (see measures).

Measures (in mm):

	Lpron	LFIII	LTIII	Lovip
Males	2-2.3	12.5-13.8	14.7-15.8	—
(n=4)	2.2	13.1	15.2	
Females	2.7-2.9	15.3-17.9	18-21	10.2-12.4
(n=5)	2.8	16.5	19.7	11

Mayagryllus tilaensis Desutter-Grandcolas, n. sp. (Fig. 61,62,66)

Type locality: Mexico, Chiapas, Tila.

Type material: Male holotype: Mexico, Chiapas, Tila, Cueva de Nicolas Bravo, 1160 m, 1-X-1975 (R. Argano), in alcohol, UTVR. Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UTVR. Paratypes: Same locality, same date, same collector as the holotype, 1 female, in alcohol, UTVR; same locality, same date as the holotype: 2 males and 2 females (V. Vomero), in alcohol, MNHP; id., 2 males and 3 females (V. Sbordoni), in alcohol, UTVR; id., 1 male (A. Zullini), in alcohol, UTVR; same locality as the holotype, 3 males and 1 female, 2-X-1975 (V. Vomero), in alcohol, UTVR. Chiapas, Tila, cueva de Tchabo öet öet, 1050 m, 2 females, 1-X-1975 (V. Sbordoni), in alcohol, UTVR. Chiapas, Tila, cueva II Barrio F. Madero, 1160 m, 1 female, 2-X-1975 (R. Argano), in alcohol, UTVR.

Diagnosis

Male genitalia (Fig. 61, 62) long and narrow. Endophallic apodemes long, but not widely separated from each other; their apex slightly divergent. Ectophallic arc narrower than in *M. apterus* and *M. yucatanus*. Epi-ectophallic membrane with a pair of very short ear-like invaginations. Sclerotized ventral part of C-sclerite longer than the membranous dorsal part.

Female. Subgenital plate generally strongly bisinuated. Ovipositor shorter than the hindfemora.

Female genitalia (Fig. 66). Copulatory papilla longer than in *M. apterus* and *M. yucatanus*, its shape more triangular with a larger base.

Measures (in mm):

	Lpron	LFIII	LTIII	Lovip
Males	2.4-2.7	14.1-14.7	16.1-17.5	—
(n=3)	2.6	14.5	16.9	
Females	2.9-3	16.3-17.3	18-20.5	10.7-10.8
(n=3)	3	16.8	19.5	10.7

Other material examined: Mexico, Chiapas, Tila, Cueva de Nicolas Bravo, 1160 m, 1 male, 1-X-1975 (A. Zullini), in alcohol, UTVR. One male from Tabasco (Macuspana, grutas de Aguablanca, IV-1988, V. Sbordoni; in alcohol, MNHP) is of bigger size than the males from Tila (measures: 3 mm, 17.5 mm and 22 mm, respectively); its genitalia are also larger.

Mayagryllus tumbalaensis Desutter-Grandcolas, n. sp.
(Fig. 63, 64, 67).

Type locality: Mexico, Chiapas, Tumbala.

Type material: Male holotype: Mexico, Chiapas, Tumbala, cueva de Johiotshs, 1600 m, 18-I-1990 (V. Sbordoni), in alcohol, UTVR. Female allotype: Same locality, same date, same collector as the holotype, in alcohol, UTVR. Paratypes: Same locality same date, same collector as the holotype, 1 female, in alcohol, UTVR; id., 1 male and 1 female, in alcohol, MNHP. Chiapas, Tumbala, cueva de Cuncumpa, 1 female, 16-17-IV-1991 (V. Sbordoni), in alcohol, UTVR.

Diagnosis

Species very close to the preceding, and recognizable by the following characters:

Male genitalia (Fig. 63, 64). Membranous part of C-sclerite shorter and larger than in *M. tilaensis.*

Female. Subgenital plate generally slightly bisinuated at the apex.

Female genitalia (Fig. 67). Copulatory papilla not so enlarged at its base than in *M. tilaensis*, and very often bilobated at the apex.

Measures (in mm):

	Lpron	LFIII	LTIII	Lovip
Males (n = 2)	2.4	14.7-15.7	17.3-18.1	
Females (n = 2)	2.9	17.1-17.8	20.3-20.7	10.3-10.8

Other material examined: Mexico, Chiapas, Tumbala, cueva de Cuncumpa, 1 female, 16-17-IV-1991 (V. Sbordoni), in alcohol, UTVR (in bad condition). Chiapas, Yaialon, cueva III del Pulpitillo, 1 female, 11-I-1990 (V. Sbordoni, I. De Monte, A. Gobetti), in alcohol, MNHP.

6. Genus *NOCTIVOX* Desutter-Grandcolas & Hubbell, n. gen.

Type species: *Noctivox sanchezi* Desutter-Grandcolas, n. sp.

Distribution: Mexico. In the North West, only one species known, from Nayarit. No species known from the Yucatan Peninsula.

Noctivox has been collected in tropical rainforest, deciduous tropical forest, cloud forest and temperate forest, from 180 to 2450 m.

Diagnosis

Species of medium to large size, with complete elytra in the males (females apterous) and of generally dark brown coloration (except some species from Veracruz and Oaxaca). Legs relatively short, the hind femora stout (Fig. 69). Hindtibiae serrulated and with most often 5 pairs of subabical spurs. Tibiae II with 3 apical spurs, as in *Amphiacusta*. Tibiae I with 1 or 2 tympana. First hind tarsomeres with 1 or 2 inner spines (apart from apical spines) and a row of outer spines. Fastigium (Fig. 71) large and at the same level as the vertex. Basal furrow well marked, half-circled between lateral ocelli. Ocelli present and not reduced, eyes not reduced (except in some species from Oaxaca and Veracruz).

Male. Elytra covering from 2/3 to almost complete abdomen, enlarged or not. Lateral field large. Venation complete, but apical field reduced. Cell separating the mirror and the anal veins large, the vein delimiting its base joining the diagonal vein and not the mirror.

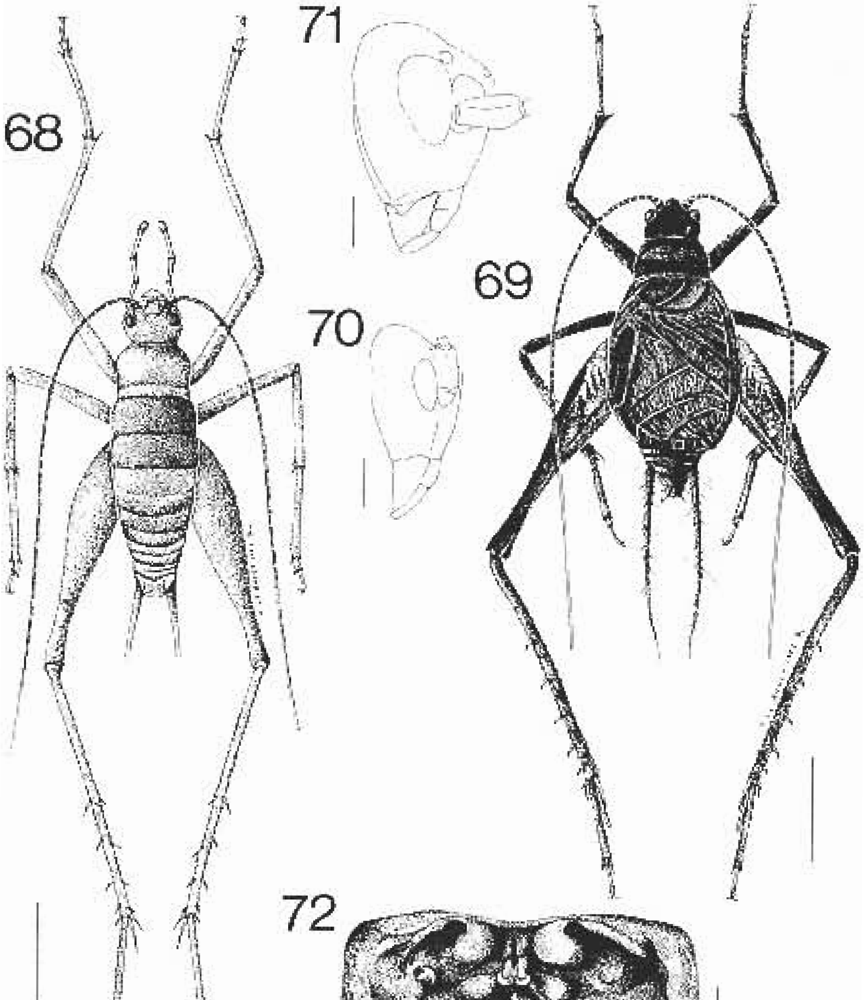

Fig. 68-72 — Genera *Mayagryllus*, n. gen. and *Noctivox*, n. gen. Male habitus (scale 5 mm): Fig. 68: *Mayagryllus apterus*, n. sp.; Fig. 69: *Noctivox sanchezi*, n. sp. Head (lateral view, scale 1 mm): Fig. 70: *M. apterus*; Fig. 71: *N. sanchezi*. Fig. 72: Male metanotal gland of *N. sanchezi* (scale: 1mm).

Metanotum glandular and complex (Fig. 72). Susanal plate with rounded and slightly elongate posterior angles.

Male genitalia. Epiphallic base extended dorsally, forming a kind of median visor. C-sclerites long and hooklike, or short and stout (see below). Epiphallic parameres 1 & 2 forming 2 pairs of elongate sclerites. Ectophallic arc extending over and beyond the ectophallic fold, forming an undivided median sclerite. Endophallic sclerite and apodemes short.

Female genitalia and subgenital plate. See later (species group definition).

Monophyly and relationship

Together with group B, *Noctivox* possesses the following apomorphies: formation of an epiphallic visor, development of a single extension of ectophallic arc above ectophallic fold, structure of male metanotal gland. Each genus is characterized by its global morphology, that of group B showing numerous derived characters (Desutter-Grandcolas, in prep.).

Available data suggest a closer relationship of these genera with *Amphiacusta* than with any other Amphiacustae (see above *Amphiacusta*).

The Chiapanecan species belong to 2 species groups recognizable by the following characters:

1. *sanchezi* group: Tibiae I with 2 tympana. Female subgenital plate longer than large, and with a deep V-shaped indentation. Male genitalia: C-sclerites long, hook-liked; epiphallic parameres all straight and narrow, the parameres 1 short, the parameres 2 long; epiphallic visor bisinuated. Female genitalia: copulatory papilla narrow at its base.

This group includes *N. sanchezi*, n. sp., *N. ocote*, n. sp., *N. minor*, n. sp., *N. tzotzila*, n. sp., *N. clava*, n. sp. and *N. longixipha*, n. sp.

2. *dissimilis* group: Tibiae I with 1 tympanum, on their inner side. Female subgenital plate larger than long, the apex stright or slightly bisinuated. Male genitalia: C-sclerites short and stout; epiphallic parameres 2 straight and narrow, but shorter than in *sanchezi* group; epiphallic parameres 1 having the shape of a large and short plate; epiphallic visor largely indented. Female genitalia: copulatory papilla base larger than its apex.

This group includes *N. dissimilis*, n. sp. and *N. hubbelli*, n. sp.

Noctivox females and larvae are densely covered with short setae, generally yellow, but black on localised areas. This patterns appears more clearly in *dissimilis* group.

Biology

In Chiapas and Tamaulipas, males were seen at night perched on tree trunks, at more or less 30 cm high, singing (calling song). During daytime, males and females hide most often under dead branches or in crevices; in this last refuge, males of Tamaulipas species were heard singing (courting song probably) in the morning (pers. obs.). This last observation could be similar to what has been observed in *Nemoricantor* (see below).

Some *Noctivox* species are adapted to cave life: their morphology resembles that of *Longuripes*, with functional elytra in males.

Noctivox sanchezi Desutter-Grandcolas, n. sp.
(Fig. 69, 71-73, 77, 81, 85, 88)

Type locality: Mexico, Chiapas, Tuxtla Gutierrez, Ocozocoautla, route d'Ocuilapa, Laguna Belgica.

Type material: Male holotype: Mexico, Chiapas, Tuxtla Gutierrez, Ocozocoautla, route d'Ocuilapa, Laguna Belgica, nuit, base tronc forêt, 19-X-1990 (L. Desutter). Female allotype: Same locality, same collector as the holotype, nuit base d'une chandelle, 18-X-1990. Paratypes: Same locality, same date, same collector as the holotype, 2 males. Same locality, same date, same collector as the allotype, nuit, près racines, cavités sous racines, 1 male and 1 female; id., nuit litière, 1 female. All specimens dry, MNHP.

Diagnosis

Species dark brown, with large elytra in males (Fig. 69). Face with a large longitudinal whitish band under the median ocellus, extending to the epistemal suture, and a narrow one under each antennal pit, this last one bifurcated under the antennal pit. Fastigium, vertex and posterior part of the cheeks dark brown; ocelli whitish. Anterior parts of cheeks whitish, this color extending along the posterior margin of the eyes. Mouthparts whitish, except on lateral margins of clypeus and labrum. Palpi whitish, their sides dark brown. Scapes whitish, with a dark brown spot on their anterior face. Pronotum dark brown, with a narrow yellow line along its posterior margin, and some diffuse yellow spots. Femora I and II dark brown, almost without yellow spots. Tibiae I and II diffusely ringed. Femora III dark brown, their bases whitish on both sides. Tibiae III dark brown, their ventral faces and the subapical spurs apex yellowish. Tarsi yellow brown.

Male. Metanotal gland as on figure 72. Elytra covering the whole abdomen, except for the susanal plate. Venation (Fig. 77): harp with 6 veins; mirror larger than long and crossed by 2 veins. Stridulatory file: 130-131 teeth (n=2).

Male genitalia (Fig. 73, 81). Epiphallic parameres 2 long, extending well beyond the epiphalle. Note the shapes of epiphallic visor and of C-sclerites.

Female. Subgenital plate indented on more than one third of its length (Fig. 85). Copulatory papilla as on figure 88.

Measures (in mm):

	Lpron	wpron	LFIII	LTIII	Lel	wel	Lovip
Males (n=3)	2.9-3.1 3	5.3-5.9 5.5	19.8-21 20.3	20.9-21.4 21.1	12.4-12.8 12.6	8.4-8.7 8,6	—
Females (n=3)	3.4-3.7 3.5	5.4 (n=2)	20.6-21.7 21.2	21.8-22.6 22.3	—	—	19.7-23.1 21.7

Noctivox ocote Desutter-Grandcolas, n. sp. (Fig. 74, 78, 82, 89)

Type locality: Mexico, Chiapas, Tuxtla Gutierrez, Ocozocoautla, Piedra Parada, El Ocote.

Type material: Male holotype: Mexico, Chiapas, Tuxtla Gutierrez, Ocozocoautla, Piedra Parada, El Ocote, 1068 m, nuit litère, 4-XI-1990 (L. Desutter). Female allotype: Same locality, same date, same collector as the holotype, 990 m, nuit sur tronc. Paratype: Same locality, same date, same collector as the holotype, 1068 m, nuit sur tronc (à 20 cm du sol), 1 male. All specimens dry, MNHP.

Diagnosis

Species very close to *N. sanchezi*, from which it differs by the following characters:

Size somewhat smaller.

Male. Elytra narrow (Fig. 78); stridulatory file with 102 teeth (n=1).

Male genitalia (Fig. 74, 82). Epiphallic parameres 2 shorter than in *N. sanchezi*; C-sclerites and epiphallic visor slightly different (compare the figures).

Female genitalia. Copulatory papilla longer, with a narrower base (Fig. 89).

Measures (in mm):

	Lpron	wpron	LFIII	LTIII	Lel	wel	Lovip
Males (n=2)	2.8-2.9	4.9-5.3	18.2-18.9	19.4-19.8	10.7-11.7	7.7-8.1	—
Female (n=1)	3.6	5.6	20.8	21.3	—	—	19.8

Noctivox minor Desutter-Grandcolas, n. sp. (Fig. 75, 79, 83, 86, 90)

Type locality: Mexico, Chiapas, Tuxtla Gutierrez, Angel Cortino Corzo, El Triunfo.

Type material: Male holotype: Mexico, Chiapas, Tuxtla Gutierrez, Angel Cortino Corzo, El Triunfo, 1517 m, 28-X-1990 (L. Desutter). Female allotype: Same locality, same date, same collector as the holotype, 1500-1600 m. Both specimens dry, MNHP.

Diagnosis

Species resembling *N. sanchezi* and *N. ocote*, but of smaller size, and recognizable by the following characters:

Face darker. Yellow line under the antennal pit very narrow. Lateral yellow line not extending along the posterior margin of the eye, the cheek thus entirely dark brown.

Male. Elytra (Fig. 79): mirror crossed by 3 veins. Stridulatory file with 153 teeth (n=1).

Male genitalia (Fig. 75, 83) recognizable by the form of C-sclerites and the width of A-sclerites.

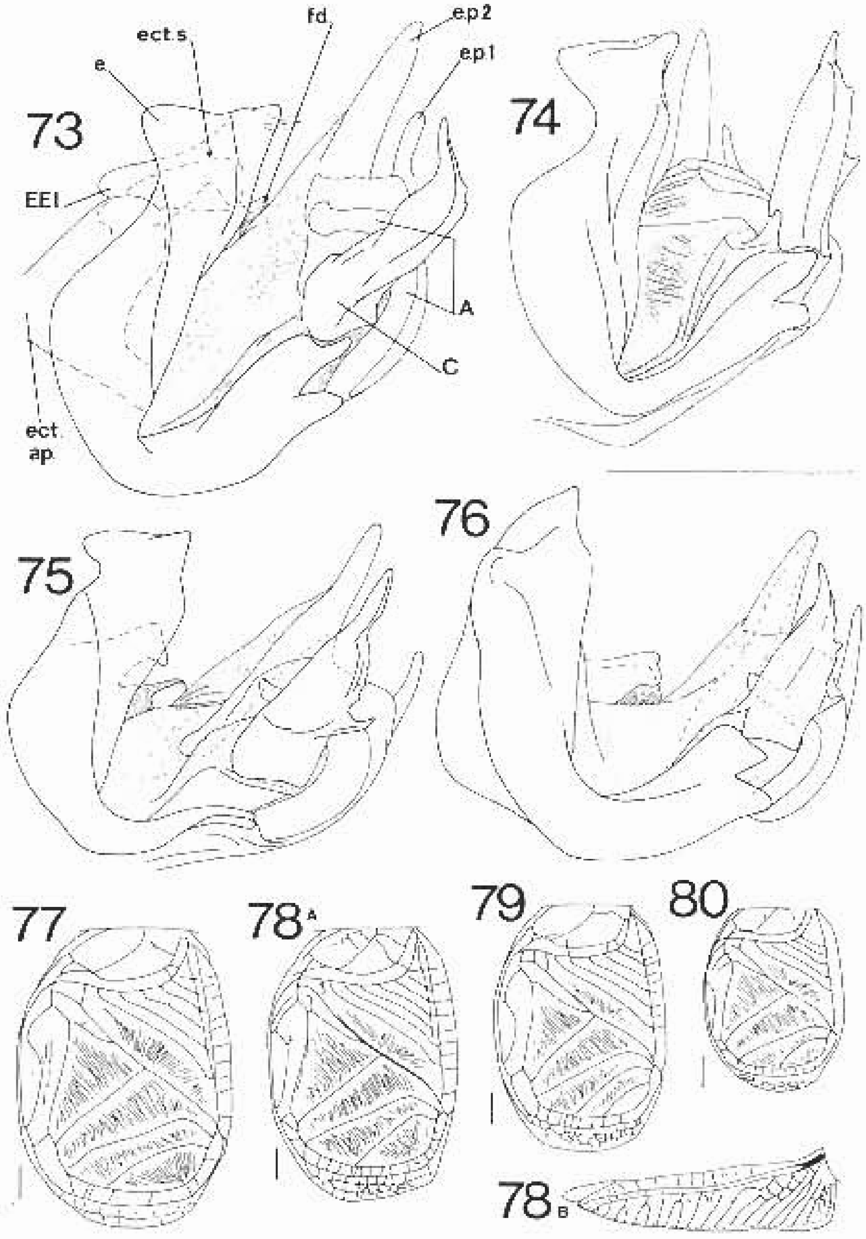

Fig. 73-80 — Genus *Noctivox*. Male genitalia (lateral view): Fig. 73: *N. sanchezi*, n. sp.; Fig. 74: *N. ocote*, n. sp.; Fig. 75: *N. minor*, n. sp.; Fig. 76: *N. tzotzila*, n. sp. Male elytra: Fig. 77: *N. sanchezi*; Fig. 78: *N. ocote* (dorsal and lateral fields); Fig 79: *N. minor*; Fig. 80: *N. tzotzila*. Scales: 1 mm. Abbreviations: p. 10

Female. Ovipositor comparatively longer than in *N. sanchezi* and *N. ocote*. Subgenital plate indented on less than one third its length (Fig. 86).

Female genitalia. Copulatory papilla as on figure 90.

	Lpron	wpron	LFIII	LTIII	Lel	wel	Lovip
Male (n=1)	2.5	4.9	14.9	15	9.9	6.9	—
Female (n = 1)	2.9	4.4	16.4	16.3	—	—	19.8

Noctivox tzotzila Desutter-Grandcolas & Hubbell, n. sp.
(Fig. 76, 80, 84, 91)

Type locality: Mexico, Chiapas, Tuxtla Gutierrez, Sumidero.

Type material: Male holotype: Mexico Chiapas, Cerro Sumidero near Tuxtla Gutierrez, 4000 ft., 7-VIII-1953 (P. Brodkorb), in alcohol, genitalia n° 954, UMMZ. Female allotype: Same locality, same date, same collector as the holotype, dry and mounted, UMMZ. Paratype: Chiapas, 11.2 mi N of Tuxtla Gutierrez, c. 4000 ft., 3-VII-1956 (W.E. Duellman & R.E. Etheridge), 1 female, alcohol, MNHP.

Diagnosis

Species most similar to *N. sanchezi* among the species of the group, but recognizable by the following characters:

Vertex yellow between the eyes, the fastigium (back to the lateral ocelli) and the posterior margin of the vertex dark brown. Cheeks almost entirely yellow, only the posterior margin dark brown. Legs of lighter color.

Male. Elytra as on figure 80. Stridulatory file only 78 - 81 teeth (n=2).

Male genitalia (Fig. 76, 84) most resembling those of *N. sanchezi* by the epiphallic parameres (but different by C-sclerite and epiphalle) and those of *N. ocote* by C-sclerite and epiphalle (but very different by epiphallic parameres).

Female. Subgenital plate deeply indented, as in *N. sanchezi*.

Female genitalia (Fig. 91). Copulatory papilla longer and thinner at its base than that of the other species of the group.

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Male (n=1)	2.3	14.2	15	8.8	6.2	—
Females (n=2)	2.6-3	16.1-18.5	16.4-18.9	—	—	16.3-18.2

Other material observed: Mexico, Palenque, 1 male, III-IV 46 (M. del Toro), dry, MNHP. This male shows quite an important difference of size with the holotype (2.8, 18, 20.8, 11.4, 7.8 mm respectively).

Noctivox clava Desutter-Grandcolas, n. sp. (Fig. 92).

Type locality: Mexico, Chiapas, Union Juarez.

Type material: Female holotype: Mexico, Chiapas, Union Juarez, 1300 m, 3/8, 1939 (P. Brodkorb), dry, UMMZ.

Diagnosis

Species resembling *N. sanchezi* and *N. ocote*, but of smaller size and slightly lighter colour. There seems to exist a yellowish spot in the anterior angle of pronotum lateral lobe. The copulatory papilla is short, with a very large apex and a narrow base (Fig. 92). Male unknown.

Measures (in mm):

Lpron	wpron	LFIII	LTIII	Lovip
3.3	4.6	18.7	19.3	17.6

Noctivox longixipha Desutter-Grandcolas, n. sp. (Fig. 87, 93)

Type locality: Mexico, Chiapas, La Trinitaria.

Type material: Female holotype: Mexico, Chiapas, La Trinitaria, cueva de Zapaluta,1500m,16-VIII-1973(V. Sbordoni), in alcohol, UTVR.

Diagnosis

Species characterized by its very long ovipositor (compared to that of the other species of the genus). Face and cheeks similar to thoese of *N. tzotzila*, but the yellow line under the antennal pit larger. Fastigium and vertex brown yellow, except for the posterior margin of the vertex and of a line joining this margin to the eye. Subgenital plate indented on less than one third of its own lenght (Fig. 87). Copulatory papilla as on the figure 93. Male unknown.

Measures (in mm):

Lpron	LFIII	LTIII	Lovip
3	17.5	19.7	22.4

Noctivox dissimilis Desutter-Grandcolas, n. sp.
(Fig. 94, 95, 98, 100, 101)

Type locality: Mexico, Chiapas, Tila.

Type material: Male holotype: Mexico, Chiapas, Tila, cueva 1 Barrio F. Madero, 1160 m, 2-X-1975 (V. Vomero), UTVR. Female allotype: Same locality, same date as the holotype (V. Sbordoni), UTVR. Paratypes: Same locality, same date, same collector as the allotype, 1 male and 2 females, UTVR; id., 1 male and 1 female, MNHP. Chiapas, Tumbala, cueva de Cuncumpa, 1 male, 16-17-IV-1991 (V. Sbordoni), MNHP. All specimens in alcohol.

Diagnosis

In addition to the characters of the species group: Large species of light brown colour, with distinctly ringed legs. Face quite similar to that of *N. sanchezi*, but the yellow line under the antennal pit larger and not bifurcated. Cheek yellowish. Fastigium and vertex brown.

Male. Metanotal glands similar to that of *N. hubbelli* (see below). Elytra covering more than one half of the body, and not enlarged. Venation (Fig. 98): harp with 4 veins; mirror larger than long and crossed by 2 veins. Stridulatory file with 87-99 teeth (n=2).

Male genitalia as on figures 94, 95.

Female. Ovipositor quite short (see measures). Subgenital plate as on figure 100.

Female genitalia as on figure 101. Note the shortness of the thickened membrane above the copulatory papilla.

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Males	2.8-3.1	17.8-19	19.1-20.6	9.4-9.6	6.6-6.1	—
(n=2)						
Females	3-3.3	17.8-19.7	19.5-21.3	—	—	13.8-14.7
(n=3)	3.2	18.5	20.3			14.1

Noctivox hubbelli Desutter-Grandcolas, n. sp. (Fig. 96, 97, 99, 102)

Type locality: Mexico, Chiapas, Tuxtla Gutierrez, Ocozocoautla, Piedra Parada, El Ocote.

Type material: Male holotype: Mexico, Chiapas, Tuxtla Gutierrez, Ocozocoautla, Piedra Parada, El Ocote, 1028 m, 4-XI-1990, nuit, au sol dans chaos rocheux (L. Desutter). Female allotype: Same locality, same date, same collector as the holotype. Paratypes: Same locality, same date, same collector as the holotype, 860 m, 1 female. Same locality, same collector as the holotype, c. 1000 m, 6-XI-1990, dans une fente entre 2 rochers, 1 female. All specimens dry, MNHP.

Diagnosis

Species close to *N. dissimilis*, with the following differences:

On the face, yellow band under the antennal pit larger, reaching the margins of the antennal pit and of the eye. Fastigium and vertex light brown.

Male. Metanotal glands with the median elongate elements broader, and the lateral rounded elements much smaller than in *N. sanchezi*. Elytra not enlarged. Venation (Fig. 99): mirror much larger than long; cell separating the anal veins and the mirror much extended (see the position of its basal vein). Stridulatory file with 61 teeth (n=1).

Male genitalia (Fig. 96, 97) smaller than those of *N. dissimilis*, and with smaller epiphallic parameres 1 & 2. C-sclerites somewhat bigger.

Female genitalia (Fig. 102). Copulatory papilla thicher than in *N. dissimilis*.

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Males	2.7-2.9	17.6-18	19-19.4	8.4	5.7-5.9	—
(n=2)						
Females	3.3-3.5	19.7-20.1	21-21.5	—	—	15-17.5
(n=2)						

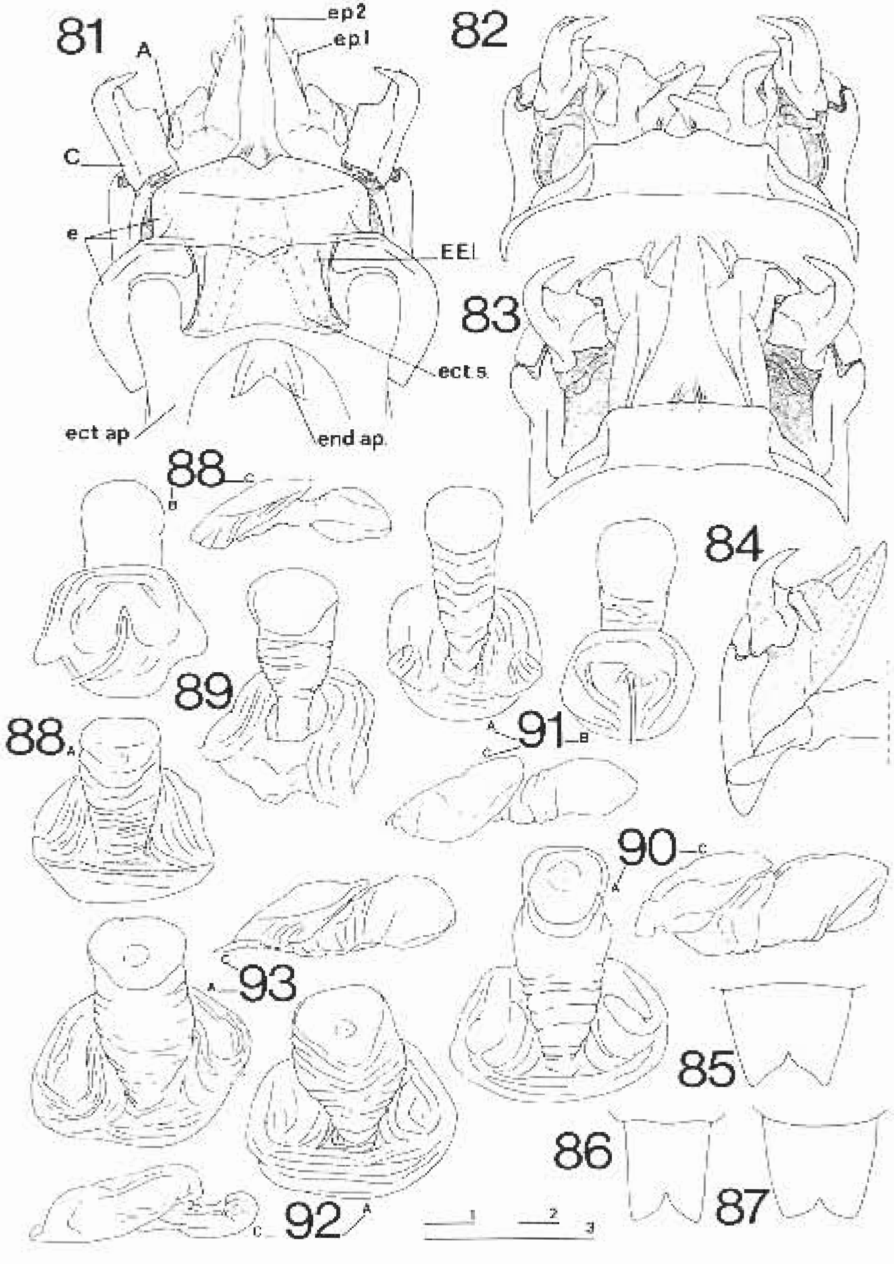

Fig. 81-93 — Genus *Noctivox*. Male genitalia (dorsal view, scale 3): Fig. 81: *N. sanchezi*, n. sp.; Fig. 82: *N. ocote*, n. sp.; Fig. 83: *N. minor*, n. sp.; Fig. 84: *N. tzotzila*, n. sp. (left half). Female subgenital plate (scale 2): Fig. 85: *N. sanchezi;* Fig. 86: *N. minor;* Fig. 87: *N. longixipha*, n. sp. Female copulatory papilla (scale 1): Fig. 88: *N. sanchezi;* Fig. 89: *N. ocote;* Fig. 90: *N. minor;* Fig. 91: *N. tzotzila;* Fig. 92: *N. clava*, n. sp.; Fig. 93: *N. longixipha.* Scales 1 mm. Abbreviations: p. 10.

7. Genus *NEMORICANTOR* Desutter-Grandcolas & Hubbell, n. gen.

Type species: *Nemoricantor maya* (Hubbell, 1938), n. comb.

Distribution: Central America, from Chiapas (Mexico) in the North to Costa Rica in the South.

Nemoricantor has been collected in tropical rainforest and premontane moist forest, at altitudes ranging from 150 to 930 m.

Diagnosis

Hindtibiae serrulated and with 4 pairs of subapical spurs. Tibiae II with 2 apical spurs. Tibiae I with only one, inner, tympanum. Hindfemora apical part filiform. First hindtarsomeres with an outer row of spines and 1 or 2 inner spines. Legs more or less clearly ringed. Hindfemora with several brown lines on their outer sides. Vertex relatively narrow. Fastigium below the level of the vertex; basal furrow more evident in females than in males, half-circled between lateral ocelli. Ocelli not reduced. Eyes protruding (Fig. 103). Pronotum bordered with a yellow band, greatly enlarged on lateral lobes (except in anterior angles, black).

Males. Elytra covering not much than half the abdomen, and with a yellow band along their outer margin (very large on lateral field). Lateral field short and with a simplified venation (R and SC only present, subdivisions of SC not clearly visible: Fig. 104). Stridulatory apparatus complete. Susanal plate posterior angles not particularly developed. Metanotal glands resembling those of *Amphiacusta*, with 2 flat light-coloured zones, at the same level as metanotal surface.

Male genitalia. C-sclerites reduced to a transversal membranous lobe. A-sclerites and the membrane separating it from epiphallic parameres forming a big, uniformely sclerotized structure. Epiphallic parameres relatively small, resembling those of *N. sanchezi* group, but the parameres 1 very short. Epiphalle without median visor or enlargement, but straight and relatively large. Ectophallic apodemes large and flat, not enlarged near the epiphalle as in the other Amphiacust genera, but with only a slightly convex part. Ectophallic arc slightly extending on the base of ectophallic fold, but not projecting. Endophallic apodemes long and divergent.

Female. Subgenital plate posterior margin straight, not indented.

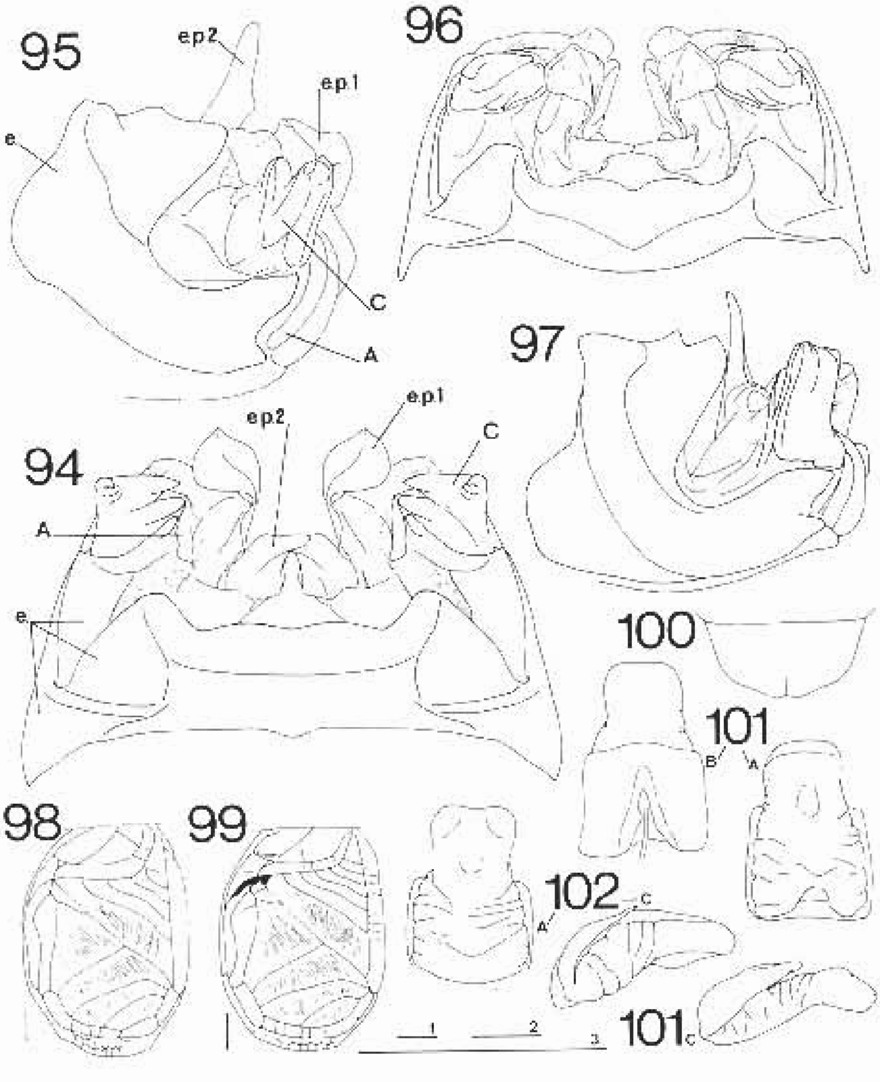

Fig. 94-102 — Genus *Noctivox* n. gen. Male genitalia (dorsal and lateral view, scale 3): Fig. 94-95: *N. dissimilis*, n. sp.; Fig. 96-97: *N. hubbelli*, n. sp. Male elytra: Fig. 98: *N. dissimilis*; Fig. 99: *N. hubbelli*. Fig. 100: Female subgenital plate of *N. dissimilis* (scale 2). Female copulatory papilla (scale 1): Fig. 101: *N. dissimilis*; Fig. 102: *N. hubbelli*. Scales 1 mm. Abbreviations: p. 10.

Female genitalia. Copulatory papilla sclerotized and very short, the base rounded and the apex narrow.

Monophyly and relationships

The monophyly of *Nemoricantor* is attested by the regression of C-sclerites, the development and modification of the membrane separating A-sclerites and epiphallic parameres (different from that of *Longuripes* group), the shape of ectophallic apodemes and that of epiphallic sclerite. Males also possess a large yellow band on elytral lateral field.

Nemoricantor shares the same apomorphous development of endophallic apodemes as *Arachnopsita* and *Mayagryllus*, and a similar C-sclerite structure (dorsally membranous and ventrally sclerotized). Together with *Longuripes, Prolonguripes, Arachnopsita* and *Mayagryllus* it has also only 2 apical spurs on tibiae II. This last character cannot however be considered as an apomorphy as it could have suffered homoplasy (see also *Amphiacusta*).

Two species are presently known in that genus: *N. maya* (Hubbell, 1938), the type species, from Honduras, and *N. aztecus* (Saussure, 1897), known from Teapa in Tabasco (type locality) and Chiapas. Other material from Guatemala, Nicaragua and Costa Rica will be studied later.

Biology

The biology of *Nemoricantor* has been shortly described by Hubbell (1938) and intensively studied by Boake (1984). This genus is nocturnal, cavicolous and gregarious. At dawn, adults and last instar larvae group in colonies in hollow trees, where mating occur at the very beginning of the day. They disperse at dusk, foraging during the night. It is unclear from Boake's paper whether foraging occurs in leaf litter or not. Young larvae are solitary.

Nemoricantor aztecus (Saussure, 1897), n. comb. (Fig. 103-108).

Endacustes aztecus Saussure, Biol. Centr. - Amer., 1897: 250.

Type locality: Mexico, Tabasco, Teapa.

Type material: Male and female types, MHNG (not examined).

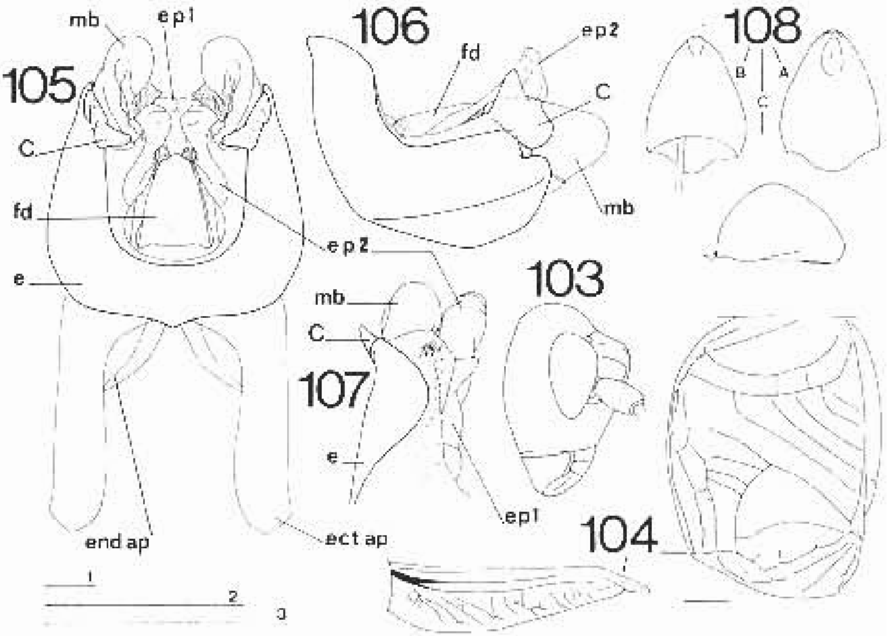

Fig. 103-108 — Genus *Nemoricantor*, n. gen. Fig. 103: Head (lateral view, scale 1) of *N. aztecus* (Saussure, 1897). Fig. 104: id., male elytra. Fig. 105-107: id., male genitalia (dorsal and lateral view and inner side of epiphallic arm, scale 3). Fig. 108: id., female copulatory papilla (scale 2). Scales 1 mm. Abbreviations: p. 10.

Diagnosis (based on specimens originating from Finca Esperanza, Chiapas)

Species quite similar to *N. maya*, but of smaller size.

Face. Yellow with longitudinal brown stripes: one stripe along the inner margin of each antennal pit, extending from the median ocellus and to the epistemal suture, thus delimiting a yellow median space, narrow under the median ocellus, larger toward the epistemal suture; a light brown fleck above the epistemal suture. Another brown stripe under the inferior tip of each eye. Mouthparts light yellow, except for the black margin of mandibles. Cheeks yellow, spotted with brown. Vertex light brown near the occiput, yellowish between the eyes, except behind lateral ocelli. Fastigium yellow, the upper part of its sides black. Space between the anterior margin of the eyes and the posterior margin of the antennal pit black and yellow.

Yellow bands on pronotal lateral lobes long and wide.

Male. Elytra (Fig. 104): venation not as clear and strong as in *N. maya*. Mirror triangular. Stridulatory file: 362 teeth (n=1).

Male genitalia. Genitalia small compared to those of *N. maya* (Fig. 105-107); epiphallic parameres 2 short and large; C-sclerites small.

Female genitalia (Fig. 108). Copulatory papilla apex quite round.

Measures (in mm):

	Lpron	LFIII	LTIII	Lel	wel	Lovip
Male (n=1)	2.1	13.9	14.7	5.5	4.3	—
Female (n=1)	2.6	15.1	16.1	—	—	13.5

Material examined: Mexico, Chiapas, Finca Esperanza, 150 m, 1 male and 1 female, 11, 27 1939 (P. Brodkorb), dry, MNHP.

KEY FOR GENERA AND SPECIES GROUPS

1 Median tibiae with 3 apical spurs (dorso-outer spur lost) 2

— Median tibiae with 2 apical spurs (dorso-outer and -inner spurs lost). 4

2 Hindtibiae with 5 pairs of subapical spurs. Male metanotal glands as on figure 72. Male genitalia: Epiphallic sclerite with a median visor. .... *NOCTIVOX* 3

— Hindtibiae with 4 pairs of subapical spurs. Male metanotal glands as on figure 1. Male genitalia: Epiphallic sclerite without a median visor. .... *AMPHIACUSTA*

3 Tibiae I with 2 tympana. Female subgenital plate longer than large, and with a deep V-shaped indentation (Fig. 85). Male genitalia: C-sclerites long and hook-like. .... *NOCTIVOX SANCHEZI* GROUP

— Tibiae I with 1 (inner) tympanum. Female subgenital plate larger than long, the apex straight or slightly bisinuated (Fig. 100). Male genitalia: C-sclerites short and stout. .... *NOCTIVOX DISSIMILIS* GROUP

4 Tibiae I without tympanum (a small inner one in *Mayagryllus yucatanus*). Males without elytra (except *Mayagryllus yucatanus*, which has very short ones) and metanotal glands. 5

— Tibiae I with 1 or 2 tympana. Males with elytra covering at least half of the abdomen; stridulatory apparatus complete 7

5 Ocelli absent or greatly reduced. Male genitalia: C-sclerites formed by a narrow plate with a lateral notch, vertically articulated on epiphallic arm and slightly inflated ventrally; epiphallic sclerite with a sharp median point. Female genitalia: Copulatory papilla very large and flat. *ARACHNOPSITA*

— Ocelli present. male genitalia: C-sclerites large, almost horizontal, dorsally membranous; epiphallic sclerite simple. Female genitalia: Copulatory papilla not flat, triangular or quadrangulate in shape. .... *MAYAGRYLLUS* 6

6 Male genitalia short and large, not particularly elongated at the apex; endophallic apodemes largely separated and divergent. Species known from Yucatan (Mexico), Belize and Guatemala. ....*MAYAGRYLLUS APTERUS* GROUP

— Male genitalia long and narrow; endophallic apodemes very close. Species known only from Chiapas (Mexico). .... *MAYAGRYLLUS TILAENSIS* GROUP

7 Tibiae I with 2 tympana. Males with rounded bumps on metanotum and first tergites. Male elytra of uniform colour. Male genitalia: C-sclerites very developed, with a vertical basal plate, a lateroventral spine and a glandular ventral pouch. Female genitalia: Copulatory papilla membranous, long and slender 8

— Tibiae I with an inner tympanum only. Male metanotal glands resembling those of *Amphiacusta* (Fig. 1). Male elytra inferior margins light-coloured. Male genitalia: C-sclerites reduced, rectangular in shape. Female genitalia: Copulatory papilla sclerotized, very short, the base rounded and the apex narrow. .... *NEMORICANTOR*

8 Male genitalia: C-sclerites ventral pouch small; aperture of lateroventral spine apical. Female genitalia: Copulatory papilla plicated, with a distinctively constricted apex. Species

from Guatemala and Honduras, brown and yellow and with normal ocelli .... *PROLONGURIPES*

— Male genitalia: C-sclerites ventral pouch very large; aperture of lateroventral spine subapical. Female genitalia: Copulatory papilla different. Species known only from Chiapas and Oaxaca (Mexico), light brown (not always ringed), with reduced ocelli. .... *LONGURIPES* 9

9 Legs ringed. Male genitalia: C-sclerites lateroventral spine large and relatively small. Species known only from Chiapas in localities from 1200 to 2380 m high .... *LONGURIPES ARGANOI* GROUP

— Legs not ringed. Male genitalia: C-sclerites lateroventral spine long and slender. Species known from Oaxaca and Chiapas, in Chiapas from localities up to 1350 m. 8

10 Male stridulatory file with more than 350 teeth. Species known only from Oaxaca. *LONGURIPES STENOPS* GROUP

— Male stridulatory file with less than 300 teeth. Species known from Oaxaca and Chiapas. .... *LONGURIPES SBORDONII* GROUP.

PHYLOGENY OF AMPHIACUSTAE

A matrix of characters states (table 1) was assembled for 11 genera, 9 Amphiacust genera (two of which are new but unknown from Chiapas, see above: List of genera and species) and 2 other

Table 1 - Matrix of the characters used for the phylogenetic analysis (list of characters in the text).

LUZARIDA	00000	00000	00000	00000	00
LERNECA	00000	00000	00000	00000	00
AMPHIACUSTA	11000	00000	00001	01110	00
LONGURIPES	11111	00002	01021	00210	11
PROLONGURIPES	11111	00002	01021	00210	11
ARACHNOPSITA	11110	00001	01011	0021?	?1
MAYAGRYLLUS	11000	00101	01011	00210	00
NOCTIVOX	11000	00100	10101	00111	00
NEMORICANTOR	11000	10110	00002	10210	00
GROUP A	11000	10110	00002	1021?	?0
GROUP B	11000	01000	10101	01111	00

Luzarine genera used as outgroups. These last genera are *Luzarida* Hebard 1928 (known from Amazonia) and *Lerneca* Walker, 1869 (widely distributed in Central and South America).

Although the subject of the present paper is limited to cave-dwelling crickets from Chiapas, the phylogenetic analysis had to treat Amphiacustae as a whole to give a sufficient phylogenetic argumentation to discuss the troglobitic evolution of this group; it could not however be much more enlarged. The analysis presented here does not include Est Indian Amphiacustae other than true *Amphiacusta*; systematic analysis of these specimens shows that they are close to *Amphiacusta*.

The study of cricket genera from the whole Neotropical Region allows to define and limit Amphiacustae as a monophyletic group (Desutter, 1990); the choice of *Lerneca* and *Luzarida* as outgroups has been directed by the fact that these genera represent 2 different major structures of male genitalia in Luzarinae (Desutter-Grandcolas, 1992c). A more extended phylogenetic analysis will be presented in another publication, dealing with Central American Phalangopsidae (Desutter-Grandcolas, in prep.).

The cladistic anlysis uses 22 characters dealing with male genitalia (characters 1 to 77) and morphology (characters 18 to 22). All characters are two-state, except for 3 trinary characters coded as additive (characters 10 and 14) or non-additive (character 18).

Concerning male genitalia characters: Each group of genera possesses a particular C-sclerite structure. I choose to code separately each of these structure as independent characters, instead of considering them as multiple states of a unique unordered character, because it is not possible to assume that these different structures are states of a unique transformation series. From outgroup comparisons, plesiomorphic state of C-sclerite can be defined as a sclerite bordering the inner margine of epiphallic arm.

Character 01. Epiphallic arm structure: C-sclerites located at the apex of epiphallic arms (B-sclerite without any particular development), from which they are distinctly separate (1); C-sclerites more directly linked to epiphallic base, the separations between the different sclerites less marked (0).

This character opposes Amphiacustae to all other known Luzarinae (Desutter-Grandcolas, 1992c and unpubl. data).

Character 02. Endophallic apodeme: medio-dorsal crest between endophallic sclerite and ectophallic fold apex lost (Desutter, 1990) (1); medio-dorsal crest present (0).

The loss of endophallic medio-dorsal crest occurs also in *Stenotes* Desutter-Grandcolas, 1992b, where endophallic apodeme differs however from that of Amphiacustae; other derived characters bring *Stenotes* close to *Luzarida* (Desutter-Grandcolas, 1992c, 1993).

Character 03. C-sclerite articulation on epiphallic arm: C-sclerite vertically articulated (articulation zone located along its lateral margin) (1); C-sclerite horizontally articulated (articulation zone located along its base) (0).

Character 04. C-sclerite differenciated and complex, comprising a thin and long plate, a lateral spine or notch, and a more or less developed ventral pouch (1). C-sclerite comprising only a basal part with or without a lateral extension (0).

Character 05. C-sclerite developing a large glandular system, formed by the ventral pouch (reservoir) and the lateral spine (draining duct), located on the outer side of epiphallic arm (1). C-sclerite without such a glandular system (0).

Character 06. C-sclerite regressed, having the form of a quadrangulate, supple lobe (1). C-sclerite not regressed (0).

Character 07. C-sclerite having the form of a strong vertical spine, not very mobile on epiphallic arm; articulation zone located at its base, and more or less quadrangulate in shape (1). C-sclerite not spine-like (0).

Character 08. C-sclerite heterogenous, with a large membranous dorsal part and a smaller, elongated and sclerotized ventral part (1). C-sclerite not presenting this character (0).

Character 09. Membrane separating C-sclerite from epiphallic parameres developed as an individualized, sclerotized structure absorbing A-sclerite, but clearly separate from epiphallic parameres (1). Membrane not forming a distinct sclerotized structure (0).

Character 10. Membrane separating A-sclerite from epiphallic parameres more or less inflated, pushing aside A-sclerite behind C-sclerite basal plate, and more or less absorbing epiphallic parameres (1). Its development may deeply modify the whole shape of epiphallic arm (2). Epiphallic arm structure unmodified (0).

Characters 9 and 10 plesiomorphic state is the absence of any particular development of the membrane separating A- and C-sclerites from epiphallic parameres, A-sclerite being thus well formed and developed, and epiphallic parameres located on the inner and dorsal sides of epiphallic arm. In Amphiacustae, that state is realised in *Amphiacusta* (and other related West Indian taxa), *Noctivox* and group B.

Character 11. Epiphallic parameres 1 & 2 having the shape of large vertical spines (1). Epihallic parameres 1 & 2 not both spine-like (0).

Character 12. Epiphallic parameres 2 elongated, bordering the whole dorsal face of epiphallic arm (1). Epiphallic parameres 2 not elongated, located near the apex of epiphallic arm (0).

Character 13. Epiphallic sclerite developing a median projection resembling a 'visor' (1). Epiphallic sclerite simple (0).

Character 14. Formation of a pair of invaginations on epi-ectophallic membrane (1), developed as 2 huge glands (2). Epi-ectophallic membrane simple (0).

Character 15. Ectophallic apodemes large and thick, with an abutment on which epiphallic sclerite leans (1); abutment regressed and laterally displaced, the ectophallic apodemes extremely thin (2). Ectophallic apodemes flat, without abutment, not particularly large or thin (0).

Character 16. Endophallic apodemes: lateral lamina of endophallic apodeme much elongated (1); lateral lamina short (0).

Character 17. Ectophallic arc extended above ectophallic fold and protruding (1). Ectophallic arc without extension (0).

Character 18. Number of apical spurs of median tibiae equal to 2 (2), 3 (1) or 4 (0). This character has been treated as non-additive, as state 1 (3 spurs) cannot be considered as an obligate intermediary state between states 0 and 2.

The vast maiority of Phalangopsidae possesses 4 apical spurs. The general reduction of their number in Amphiacustae is thus informative, even though it is not exclusive of this group.

Character 19. Inner apical spurs of hindtibiae: median spur much longer than the dorsal one (1); median spur shorter than the dorsal one (0).

Character 20. Structure of male metanotal gland as on figure 71 (1). Metanotal gland not present (?) or different (0).

Character 21. Male glands present on metanotum and on the first tergites, their shape as on figure 6 (1). Gland not present (?) or different (0).

Character 22. Hind femora very thin, even at its base (1). Hind femora much inflated at its base (0).

Cladistic structure of Amphiacustae:

Only one tree resulted from the analysis, 28 steps long, with a consistency index of 0.92 and a retention index of 0.95 (Fig. 109).

The hypothesis of Amphiacust monophyly is supported by characters 1, 2, 15 and 19, and to a lesser extent 18 (see above).

The present analysis subdivides Amphiacustae into 2 sister groups:

1. The first group comprises *Amphiacusta, Noctivox* and group B. It is defined by two synapomorphies (character 17 and state 1 of character 18), *Noctivox* and group B being sister genera (characters 7, 11, 13, and probaby 20).

2. The second group includes *Longuripes, Prolonguripes, Arachnopsita* and *Mayagryllus* on the one hand, and *Nemoricantor* and group A on the other hand. It is defined by one synapomorphy (state 2 of character 18); the subgroups are defined by 3 synapomorphies each (characters 10, 12, 14 and characters 6, 9, 15 respectively).

The regression tendencies of male genitalia in *Nemoricantor* subgroup and of morphology in *Longuripes* subgroup (troglobitic adaptations) make difficult the finding of synapomorphies between these two sets of genera. In addition to character 18 (median tibiae apical spurs number equal to 2), one might also consider the modification of the membrane separating A- and C-sclerites from epiphallic parameres, coded here as two independent characters.

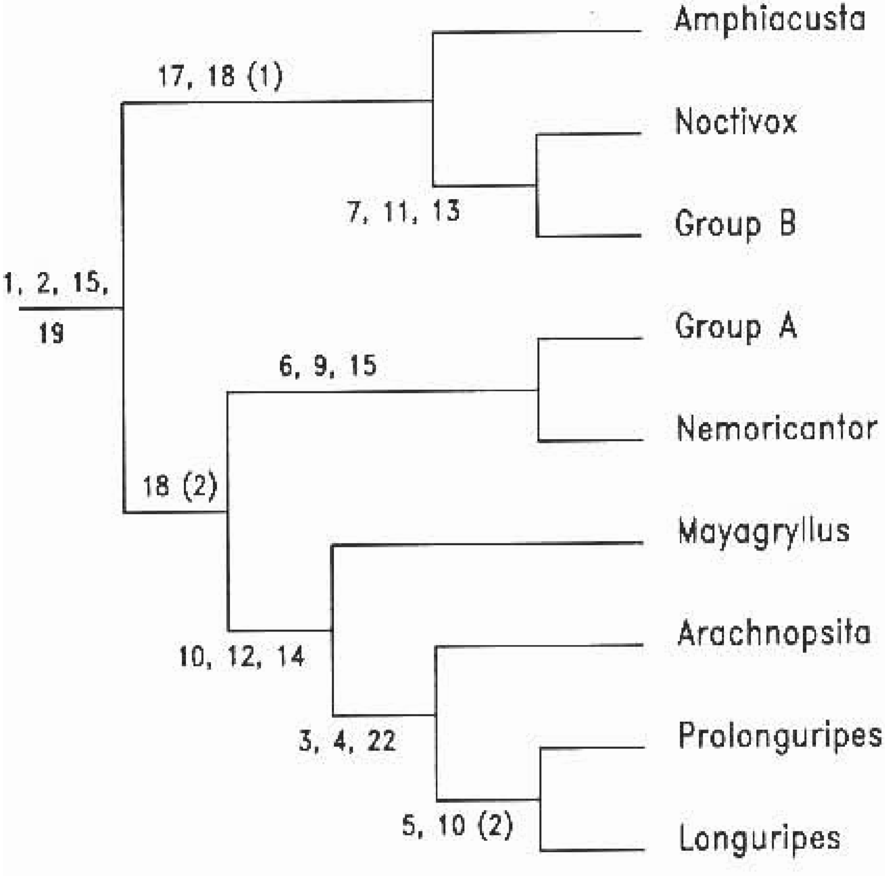

Fig. 109 — Phylogeny of Amphiacustae. Tree obtained with the ie option of Hennig 86 program.

RESULTS: COMPOSITION AND EVOLUTION OF THE FAUNA OF CHIAPAS

I will now analyze the Grylloid cavernicolous fauna of Chiapas, giving its generic composition and then trying to determine how it evolves toward cave life. It is however necessary for an outgroup comparison to summarize first what is known on Amphiacust biology (this has been argumented for each genus in the systematic analysis) and to compare these data with the biology of other Neotropical Phalangopsidae.

Biology of Amphiacustae (and other Phalangopsidae)

Amphiacustae are active at night and hide during the day, as many Phalangopsidae do. Most studied specimens found in caves were collected during the day. Except for those species which are evidently troglobitic (morphology, location deep in caves), most if not all the species studied must be cavicolous, hiding opportunistically in caves. Their natural refuges in forest are most often hollow trees, but also crevices, burrows or under dead branches.

Direct observations on activity habitat are scarse and need to be supported; it may be however hypothesized that most Amphiacustae forage in leaf litter. When observed, perching was always low on tree trunks, and almost always by singing males; no Amphiacust specimen has been observed foraging on tree trunks.

Available data do not permit to qualify non troglobitic species as troglophiles or trogloxenes, as no observations have been made on their nocturnal behavior. There exists a possibility that the presence of resources in caves could be determinant in this matter.

Most Luzarinae other than Amphiacustae live in tropical forest litter (Desutter, 1990; Desutter-Grandcolas, 1992c, 1993). They are active by day or by night. Their refuge habitat is not precisely known, but several specimens were found in thick litter, under dead palms or at plant bases. They were never encountered in hollow trees, burrows or caves.

True troglobites are known in Luzarinae outside Amphiacustae. In addition to the genera already cited for the Caribbean region, several genera exist in the southern half of South America (*Endecous* and related genera, *Strinatia* group of genera, a new genus from

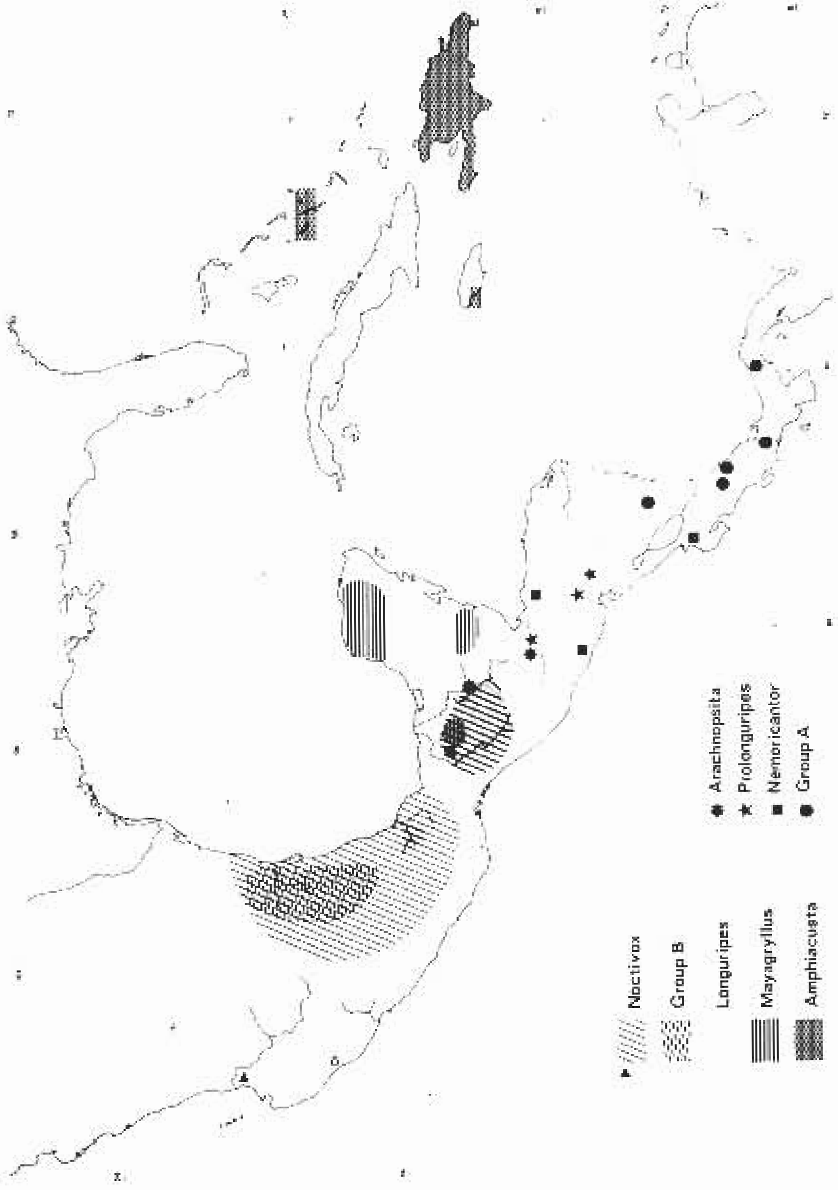

Fig. 110 — Distributions of the genera of Amphiacustae. The open triangle indicates a locality where no Amphiacustae has been found.

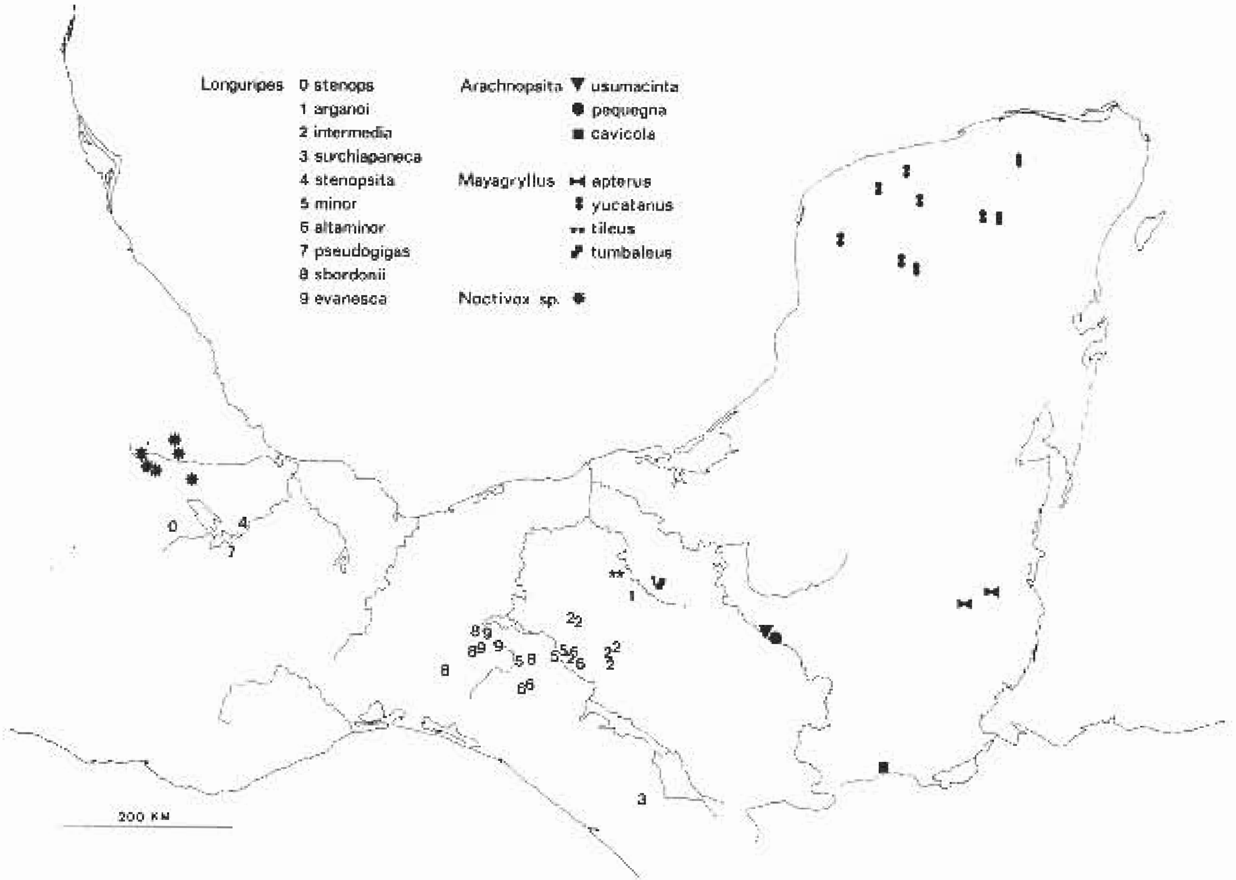

Fig. 111 — Distribution of troglobitic species of Amphiacustae.

Chile). They do not have close relationships together or with Amphiacustae (Desutter, 1990, and unpubl. data).

Cavicolous habits are more frequent in Phalangopsinae than in Luzarinae (Desutter-Grandcolas, 1992c); they are also known in Old World and Australian Phalangopsidae, although this has not been clearly studied yet (Chopard, 1924, 1969; Richards, 1965; Sinha & Agarwal, 1977). My own observations indicate that a specific set of natural cavities is colonized by each Phalangopsin tribe or group of genera; Phalangopsinae are moreover really active on arboreal structures in forests (tree trunks, lianas, ...), where they are easily observed foraging and singing (Desutter-Grandcolas, 1992c).

Among Phalangopsinae, a few genera can be encountered in caves (although none is truly troglobitic): these genera are always linked to ground level, either by their foraging activity (*Phalangopsis* and allies for example, which hide in hollow trees during the day), or by their refuge habitat (Aclodae, hiding in burrows among other cavities).

Generally speaking, Phalangopsidae are very sensitive to dessication (pers. obs. in forest regeneration in Peru and during dry season in French Guiana).

Given these data, I choose to test the following attributes in reference to phylogeny: I - troglobitic (1) *versus* non troglobitic (0); II - cavicolous (1) *versus* non cavicolous (0); III - Foraging (1) *versus* not foraging (0) in leaf litter. Their states for each genus are shown on figure 112.

Composition of the cavernicolous fauna from Chiapas

In Chiapas, the Grylloid cavernicolous fauna entirely belongs to Amphiacustae; it comprises mostly troglobitic species, but also some troglophilous/trogloxenous species.

True troglobites are known in *Longuripes*, *Arachnopsita* and *Mayagryllus*, for which no epigean species has been recorded. The distribution of these genera is centered on the Chiapanecan - Guatemalan region, extending in Yucatan (Fig. 111): *Longuripes* is distributed mainly in Chiapas, with a few species on the Oaxacan side of the Isthmus of Tehuantepec; *Arachnopsita* is know from the Mexican - Guatemalan border, and *Mayagryllus* is present in northern Chiapas and in the Yucatan peninsula.

Apart from these genera, Amphiacustae are represented in Chiapas by epigean species of *Noctivox* and *Nemoricantor*. *Noctivox* is distributed mainly in northwestern Mexico and is not known south of Chiapas; *Nemoricantor* on the reverse has his northern limit in Chiapas and is otherwise recorded farther south down to Costa Rica (Fig. 110).

The great majority of the troglobitic species recorded in Amphiacustae belongs to this Chiapanecan fauna. Outside Chiapas, only a few troglobitic species are known in Amphiacustae: they belong to the genus *Noctivox* and are quite strictly localized in Oaxaca and Veracruz (Fig. 111). Other genera are all troglophilous / trogloxenous.

This concentration of troglobitic species in Chiapas is surprising for a group whose distribution covers Central America and part of the West Indies. Although it can be logically hypothesized that all Amphiacust species are not known yet, many caves have been explored in whole Central America and in the West Indies (Bonfils, 1981; Peck, 1981 and references therein; Reddell, 1971 and references therein; Sbordoni et al., 1987 and references therein); it then does not seem justified to explain the observed pattern by data failure.

Enjalbert (1964-1967) defines three main calcareous regions in Mexico: the Sierra Madre Oriental, north of the Neovolcanic Cordillera, the Chiapanecan - Guatemalan region, extended in the Yucatan Peninsula, and the Huastecan - Oaxacan region, south of the Neovolcanic Cordillera. Each of these areas has been colonized by troglobitic Phalangopsidae: *Paracophus* in the Sierra Madre Oriental, *Longuripes* group in the Chiapanecan - Guatemalan region, and *Noctivox* p. p. in the east of the Huastecan - Oaxacan region; the western part of this last area, where no Phalangopsid troglobites has been recorded yet, is said to correspond to the Balsa basin (Enjalbert, 1964: 33), which has a drier climate (Rzedowsky, 1981).

Evolution of cavenicolous Amphiacustae

Figure 112 shows the distribution of the attributes previously defined upon the phylogeny of Amphiacustae. It allows the following remarks on the evolution of this group:

1. Although data on the habitat of Amphiacustae are still scarse, their distribution in reference to our phylogenetic hypothesis

suggests that the ancestral habitat could be characterized by foraging in leaf litter and hidding in natural cavities.

2. The adaptation to troglobitic life arose twice in Amphiacustae: once in the *Longuripes* group, evolved in Chiapas, and once in the genus *Noctivox* (p.p.) in Veracruz and Oaxaca. *Prolonguripes* returned at least partially to an epigean life.

This is the most parsimonious hypothesis of cave adaptation appearance in Amphiacustae. The other possibility would be a unique appearance of cave adaptation in the ancestor of Amphiacustae, as most other Luzarinae are litter living species (with several unrelated taxa adapted to troglobitic life) and the other Amphiacust genera are not troglobitic. This hypothesis would however imply 4 disappearances of troglobitic adaptation (i.e. 4 returns to epigean life), and 5 steps would be then necessary to report the present situation.

DISCUSSION

The following discussion will analyze our results in the light of the main theoretical developments on the evolution of life in caves. I will successively deal with the problem of «pre-adaptation» and with the nature of the determinant factors to cave adaptation.

«Pre-adaptation» (exaptation)

Cave environment has harsh characteristics that impose many constraints for an evolution toward troglobitic life (Howarth, 1980). The relatively small number of troglobitic taxa belong to phyla that are thus tradionally considered as «pre-adapted» to cave environment by their epigean ecology (Barr, 1968; Holsinger, 1998), ie. by living in obscure and humid places.

Amphiacustae are ancestrally cavicolous and leaf litter living. These two ecological features may in fact be the prerequisites to cave adaptation in Phalangopsidae.

A similar connection exists in Phalangopsinae with *Phalangopsis* and the Aclodae group, although this last group does not really forage in leaf litter, but is linked to the ground level for its refuge habitat. Data available on other Luzarinae and Phalangopsinae further support our hypothesis: taxa presenting only one of the ancestral characteristics of Amphiacustae (leaf litter living or cavicoly),

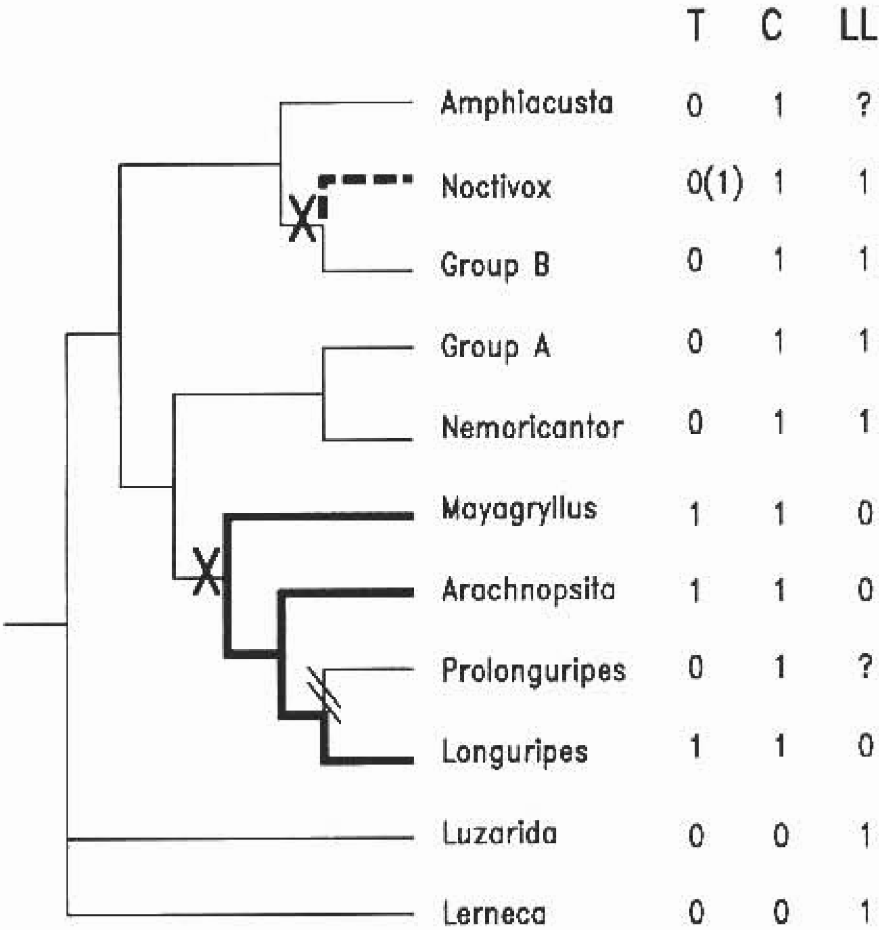

Fig. 112 — Possible scenario on the evolution of troglobitic life in Amphiacustae, and states of the attributes studied in each genus: T: troglobitic (1) *versus* non troglobitic (0); C: cavicolous (1) *versus* non cavicolous (0); LL: leaf litter foraging (1) or leaf litter not foraging (0). Thick branch: troglobitic taxa; X: troglobitic life appearance; return to epigean life.

but not both, have never been encountered in caves (Desutter-Grandcolas, in prep.).

If this hypothesis is true, cavicoly and ground / litter living could be considered as two components of an ecological niche that would have facilitated or actually made possible a passage to cave environment. This niche would consequently be an exaptation to troglobitic life (Gould & Vrba, 1982).

This hypothesis could explain why none of the other Grylloid families living in tropical forests but mostly arboreal have been able to adapt to caves, even if they hide in natual cavities such as furrows in tree bark, epiphytes, dead leaves, etc. In this respect, it would be most interesting to compare our data on Phalangopsidae with observations on the Hawaiian genus *Thaumatogryllus* (Oecanthidae, Prognathogryllini), which belongs to a vegetation living family but has diversified in lava tubes (Howarth, 1972).

Determinant factors

The theoretical framework on the origin and evolution of troglobitic faunas has been deeply modified these last twenty years, owing to an increased knowledge on temperate faunas and environments and to the developments of researches in tropical caves (Howarth, 1983; Juberthie, 1984).

The relict theory was developed in temperate areas and prevailed up to the seventies or later (Barr 1968: Vandel, 1964). It enhanced the role of external (mostly climatic) factors as the agent of a passage in the subterranean environment. Caves were refuges, where initially epigean, «pre-adapted» taxa could survive harsh environmental conditions. These relict taxa would be isolated geographically from their epigean closest relatives and would be a «blind alley of evolutionary lines» (*in* Papp, 1982).

New developments in Biospeology question these refuge and relict conceptions and develop a new approach on the role of stress factors (Juberthie, op. cit.). They tend to consider troglobites as the result of an active or passive colonization of caves by an epigean «pre-adapted» taxon. Determinant factor would no more be harsh environmental conditions, but a tentative to exploit a new set of resources (Matile, 1970; Howarth, 1987), ie. an extension of the ecological niche of the taxon. The most demonstrative studies in this domain are those on the shallow mesocavernous habitat («milieu souterrain superficiel») in temperate zones (Juberthie, 1984 and references therein) and those on the Hawaiian lava tubes (Howarth, 1991 and references therein). Howarth's analysis is the only one, to our knowledge, dealing with supraspecific evolution of troglobites in tropical caves. This author considers that troglobitic adaptation is an opportunity for a taxon to diversify its ecology; in this sense, cave adaptation would be similar to any other adaptation to a particular biotope.

Finally, Late Cenozoic climatic vicissitudes are still considered as potential determinant factors for cave colonization at least in temperate areas, even though they are not always considered as the primary factor (Juberthie, 1984; Peck 1990). Their importance in troglobitic life evolution in the Tropics is however far from ascertained. Numerous papers present elements in favor of climatic and vegetational changes in the Tropics during the Late Cenozoic, both in term of altitudinal shifts and in term of vegetational cover (van der Hammen, 1988; Villeumier & Monasterio, 1986). These changes could maybe have provoked the colonization of caves, but could also have been followed by mere diplacements of populations or by an adaptation to a new biome.

How our results on troglobitic Amphiacustae could be interpreted in this theoretical framework?

As far as the niche colonization hypothesis can be tested, it could apply to the Chiapanecan troglobitic genera. The phylogeny of Amphiacustae suggest a single appearance of troglobitic adaptation in the monophyletic group formed by these genera, *Prolonguripes* having at least partly returned to epigean life. The resource conquered in this case could be the mature karstic relief of the whole Chiapanecan - Guatemalan region; *Prolonguripes* is distributed in non calcareous areas (Butterlin, 1977). A similar hypothesis has been formulated for spider evolution (Deeleman-Reinhold, 1981).

The absence of epigean species in the Chiapanecan genera makes difficult the appreciation of a possible effect of glacial - interglacial episodes. The occurrence of climatic changes in Central America has been acknowledged on palynological, geological and botanical bases (Klaus, 1973, in Toledo, 1982; Toledo 1982, Butterlin, 1977; ...). Yet, it cannot explain how a general disappearance of epigean taxa and a general cave colonization process could have occurred in the whole distributional area of the genera concerned. The sister group relationships of these genera would moreover imply several independent cave colonization / epigean disappearance events, unless one envisages a subterranean diversification.

If the hypothesis of a single appearance of troglobitic adaptation in *Longuripes* group is accepted, one must question the mode of dispersal of these taxa. Can this dispersion have been achieved only by means of the subterranean environment or not? and if not, is it possible to hypothesize epigean dispersions during some peculiar climatic episodes?

The existence and phylogenetic position of epigean *Prolonguripes*, the distribution of *Longuripes* species groups (at least partially distributed along an altitudinal gradient) would support an epigean dispersal. Howart (1980, 1982) compares the climatological environments of caves in temperate and tropical areas and emphasizes the limiting effect of water evaporation in the development of terrestrial troglobitic life; this effect would be more pronounced in the Tropics, owing to higher general temperatures, frequent winter effect and karst geomorphology. This author also mentions migrations of troblobites within caves according to humidity changes (Howarth, 1982, 1987). Extending these observations on a larger time scale, it could be hypothesized that movements outside caves would be possible providing that evaporation remains low. Klaus (1973, in Toledo, 1982) attests the occurrence of alternate cold/dry, cold/wet, warm/dry and warm/wet climatic phases in the Latest Cenozoic of Mexico. Climatic fluctuations are also deduced from the mixed composition of Central American vegetation, with tropical and boreal floristic elements, both in the mountains and in the lowlands (Rzedowsky, 1981; Toledo, 1982). Epigean dispersal by troglobites is not a commonly observed phenomenon (Howarth, 1983). Such an hypothesis has however been proposed and argumented by Peck (1978, 1990).

The comparison of Chiapanecan troglobitic genera first with other Amphiacustae living in caves, and second with other Central American troglobitic Luzarinae gives further information on the evolution of cave adaptation in this group.

Outside Chiapas, troglobitic Amphiacustae are represented by a few species of *Noctivox*, distributed in high altitude areas of the Veracruz province of Mexico, near Cordoba and Orizaba, and partly sympatric with epigean species. In this area, it can be hypothesized that glacial episodes had a greater influence on the appearance of troglobitic life, comparable to what is known in temperate areas.

The colonization of subterranean environment could have occurred during unfavourable conditions, while epigean, troglophilous / trogloxenous, species could extend the distributional area of the genus during favourable climatic episodes.

Three other points should be mentioned: first, except for the monospecific *Tohila* and the Chiapanecan genera, troglobitic genera have both troglobitic and epigean species, mostly distributed sympatrically. Second, as already mentioned, all the main calcareous areas of Mexico and Central America (Enjalbert, 1964, 1967) have supported the evolution of Phalangopsid troglobites: *Paracophus* in Northern Sierra Madre Oriental, *Noctivox* in Southern Sierra Madre Oriental, *Longuripes, Arachnopsita* and *Mayagryllus* in Chiapanecan - Guatemalan region, *Mayagryllus* and *Tohila* in the Yucatan Peninsula; the only exception according to available data would be in the southwest of the Neovolcanic Cordillera (probably for climatic reasons). Third, troglobites belonging to different genera are almost always distributed in separate areas; this is even true for the troglobitic species of those genera which epigean species are sympatrical (*Noctivox* and *Paracophus*). In all the material studied, the presence of different genera in one cave has been recorded only twice: *Longuripes arganoi* and *Mayagryllus tumbalaensis* in the cueva de Cuncumpa, near Tumbala in Chiapas and *Mayagryllus* and *Tohila* in Yucatan (Hubbell, 1938).

What scenario for troglobitic adaptation in Amphiacustae can then be hypothesized on the base of available data?

The evolution of troglobitic life in Amphiacustae may have been made possible by combined characteristics of their ancestral ecology. Troglobitic adaptation itself could have been the result of an ecological shift toward caves exploitation whenever it was possible, ie. whenever non preoccupied caves were encountered. The actual effects of climatic fluctuations could have been different according to the localisation of the taxa: isolation of troglobitic species (as in *Noctivox*) or epigean dispersal of troglobitic taxa (as in *Longuripes* group).

CONCLUSION

The present study on the cavernicolous Grylloid fauna of Chiapas has resulted in a phylogenetic definition of this fauna and on preliminary hypotheses on its evolution. Many points are still not established with certainty. Thus detailed analysis on the ecology of each Amphiacust genus are needed to define precisely their habitats: these data would allow in turn an improved definition of the ancestral ecological characteristics that could have facilitated troglobitic adaptation.

Similarly, the evolution of other biological features should be studied, to offer a more complete idea of what troglobitic adaptation implies for species survival. Such is the case for example of mating behavior. Boake (1984) showed that *Nemoricantor* gathers in colonies in tree trunks, and that male singing repertoire lacks a real calling song: gregariousness could have been associated with an apparent «simplification» of communication behavior. What is the situation in troglobitic genera? It is impossible by now to say if troglobitic adaptation influence mating behavior, and if it ever does so, how. The divergent morphology of *Longuripes* and *Noctivox* on one hand, and of *Arachnopsita* and *Mayagryllus* on the other hand would tend to indicate that different mating behaviors exist in troglobitic Amphiacustae, and that their evolution could be independent of troglobitic adaptation. That however remains to be tested.

Finally, the Grylloid family Phalangopsidae presents several cases of cave adaptation in different not related groups of genera. This offers a set of non homologous situations which can be compared (Desutter-Grandcolas, in prep.) and permits to test hypotheses in a monophyletic phylum for which phylogeny is accessible.

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