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

Laure Desutter-Grandcolas *

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 clearly 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 Amphiacustae is then analyzed. Available data on the biology of Amphiacustae 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

addressed the origin of cave life 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 opportunity 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 Hubbell 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 homoplastic 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 epiphalle 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 cladogram 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)

   
   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

   Distribution: Guatemala, Honduras

   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.

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

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.
5. *Noctivox clava* 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*)


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 caviculous, 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


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; Le: 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.  

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
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 epiphthallic parameres not inflated. Epiphthallic parameres 1 and 2 lobeshaped and more or less sclerotized, without protruding highly sclerotized parts (compare to Noctivox for example). Ectophthallic arc extended above ectophthallic fold by a pair of protruding, long and thin sclerites. Ectophthallic fold generally short. Ectophthallic apodemes not particularly enlarged at their bases. Endophthallic 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 ectophthallic extensions above ectophthallic fold. An extension of the ectophthallic 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 epiphthallic 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*). Epiectophallic 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*, *Arachnopsis* 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 *Arachnopsis*, *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 glands 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):

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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, Ocozocoautla, 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):

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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 epiphalllic sclerite not so protruding; dorsal edge of epiphalllic 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 length of the ovipositor and of the copulatory papilla in the females. The two species are sympatric.

Measures (in mm):

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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);

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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. stenopsis*, 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. stenopsis*; Fig. 24-25: *L. minor*; Fig. 26: *L. altaminor*. Female subgenital plate: Fig. 27: *L. stenopsis*; Fig. 28: *L. minor*; Fig. 29: *L. altaminor*. Female copulatory papilla (scale 1); Fig. 30: *L. stenopsis*; 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 Balnearo, 10 mi NE Tuxtla Gutierrez, 2690 ft., 1 male and 1 female, 18-V-1972 (D. McKenzie), 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 easing surrounding the base of the papilla distinctively inflated (Fig. 31).

Measures (in mm):

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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 Gutierrez 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, Ocozocoautla, 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-ectophageal 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):

<table>
<thead>
<tr>
<th></th>
<th>Lpron</th>
<th>LFIII</th>
<th>LTIII</th>
<th>LeI</th>
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<th>Lovip</th>
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</thead>
<tbody>
<tr>
<td>Males</td>
<td>1.6-1.8</td>
<td>12.8-14.7</td>
<td>15-16.5</td>
<td>6.5-7.1</td>
<td>4.3-4.5</td>
<td>—</td>
</tr>
<tr>
<td>(n=3)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>2.2</td>
<td>17.1</td>
<td>19.7</td>
<td>—</td>
<td>—</td>
<td>10.4</td>
</tr>
<tr>
<td>(n=1)</td>
<td></td>
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</table>

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 joining the inner chord and the mirror lacking. File with 171-188 teeth (mean number: 179, n = 3). Dorsal bumps present on metanotum and tergite 1 (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. surchitaapaneca*, 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.):

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<tr>
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<th>Lpron</th>
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<td>13.6-14.2</td>
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<td>6.6-2</td>
<td>4-4.4</td>
<td>—</td>
</tr>
<tr>
<td>(n=3)</td>
<td>1.8</td>
<td>(n=2)</td>
<td>(n=2)</td>
<td>6.1</td>
<td>4.2</td>
<td>—</td>
</tr>
<tr>
<td>Females</td>
<td>2.2-2.5</td>
<td>13.6-15.9</td>
<td>14.3-17.3</td>
<td>—</td>
<td>—</td>
<td>9-10.3</td>
</tr>
<tr>
<td>(n=4)</td>
<td>2.4</td>
<td>15.1</td>
<td>16.5</td>
<td>—</td>
<td>—</td>
<td>9.8</td>
</tr>
</tbody>
</table>

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):

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<tbody>
<tr>
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<td>2-2.4</td>
<td>17.9-18.1</td>
<td>15.4-20.7</td>
<td>6.7-8.5</td>
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<tr>
<td>(n=2)</td>
<td>2.3</td>
<td>(n=2)</td>
<td>17.9</td>
<td>15.4</td>
<td>6.7</td>
</tr>
</tbody>
</table>

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. sur-chiapanae*, and with slight differences on median lophi, C-sclerites basal plate and spine (Fig 34, 35).
Female genitalia (Fig. 40, 41). Copulatory papilla slightly narrowed before the apex; apex clearly narrower than the base, slightly or not bisinuated (not bilobated as in *L. arganoi*).

Measures (in mm):

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<tr>
<th></th>
<th>Lpron</th>
<th>LFIII</th>
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<th>Lei</th>
<th>wel</th>
<th>Lovip</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>1.8-2</td>
<td>12.6-15.7</td>
<td>13.9-17</td>
<td>5.9-6.8</td>
<td>3.8-4.1</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>1.9</td>
<td>14.2</td>
<td>15.5</td>
<td>6.2</td>
<td>4</td>
<td>—</td>
</tr>
<tr>
<td>Females</td>
<td>2.4-2.6</td>
<td>16.4-17.2</td>
<td>17.9-19</td>
<td>—</td>
<td>—</td>
<td>9.8-10.3</td>
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<tr>
<td></td>
<td>(n = 3)</td>
<td>(n=2)</td>
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</table>

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 co-
vered with long setae. Dorsal bumps present on metanotum and ter-
gites 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 ge-
nus; basal plates not enlarged at the apex; lateroventral spines long
and thin. Glands formed on epi-ectophallic membrane resembling a
simple pouch, without an individualized 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):

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<th>Lpron</th>
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<th>LTIII</th>
<th>LeI</th>
<th>wel</th>
<th>Lovip</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>2.2-2.1</td>
<td>16.8-18.8</td>
<td>20.2-24</td>
<td>8.9-9</td>
<td>5.6-5.7</td>
<td>—</td>
</tr>
<tr>
<td>(n=3)</td>
<td>2.1</td>
<td>17.6</td>
<td>22.1</td>
<td>9</td>
<td>5.6</td>
<td>—</td>
</tr>
<tr>
<td>Females</td>
<td>2.5-2.8</td>
<td>19-20</td>
<td>22.3-25.5</td>
<td>—</td>
<td>—</td>
<td>13.6-13.9</td>
</tr>
<tr>
<td>(n=3)</td>
<td>2.6</td>
<td>19.5</td>
<td>23.6</td>
<td>—</td>
<td>—</td>
<td>13.8</td>
</tr>
</tbody>
</table>

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


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.** Sustal 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).


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. usumacinta; Fig. 54: A. cavicola, female copulatory papilla (scale 1); Fig. 55: A. usumacinta; 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 midlength of the sclerite (not at its base) and short; no ventral pouch clearly distinguishable. Epiphallus 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 bini- nuated.

**Measures (in mm):**

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<th>LTIII</th>
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<td>13.9</td>
<td>—</td>
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<td><strong>Females</strong></td>
<td>2.9-3.3</td>
<td>16.1-19</td>
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<td>10.7-11.4</td>
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<td>(n=3)</td>
<td>3.1</td>
<td>17.4</td>
<td>20.5</td>
<td>11</td>
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</table>

**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, in alcohol, MNHP. 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, UTVR; id., 1 male and 1 female, 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):

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<td></td>
<td></td>
</tr>
<tr>
<td>n(=2)</td>
<td>1.8-1.9</td>
<td>11.2-11.3</td>
<td>12.5</td>
<td>—</td>
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<tr>
<td>Females</td>
<td>2.5-2.6</td>
<td>14.5-15.3</td>
<td>16.1-16.4</td>
<td>8.7-8.9</td>
</tr>
</tbody>
</table>

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

Arachnomimus cavicola Saussure, 1897, Biol. Centr.-Amer.: 251.

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, slightly narrowed toward the apex (but not as in the other species); apex almost straight.

Measures (in mm):

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<th>LTIII</th>
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<td>12.7-15.1</td>
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<td>9.3-11.4</td>
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</table>

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 serrated 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 epiphalic arm); Fig. 61-62: M. tilaensis, n. sp. (dorsal and lateral view); Fig. 63-64: M. tumbalaensis, n. sp. (lateral and dorsal view of epiphalic 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 epiphallus 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 epiphallus parameres with distinct furrows. Epiphallus parameres 2 similar to those of Arachnopsita, but the free still more developed. Endophallus apodemes elongate.

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

**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. Endophallus 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. Endophallus 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):

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</table>

*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):

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<td>16.8</td>
<td>19.5</td>
<td>10.7</td>
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</table>

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):

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<tr>
<td>(n=2)</td>
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</table>

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.


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-like; 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 pattern 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 episternal 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):

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*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). Epiphallus parameres 2 shorter than in *N. sanchezi*; C-sclerites and epiphallus visor slightly different (compare the figures).

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

Measures (in mm):

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<tr>
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<td>19.8</td>
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*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. ocole*, n. sp.; Fig. 75: *N. minor*, n. sp.; Fig. 76: *N. tzotzila*, n. sp. Male elytra: Fig. 77: *N. sanchezi*; Fig. 78: *N. ocole* (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.

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</table>

*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):

<table>
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<tr>
<th></th>
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<tr>
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</table>

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):

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<td>18.7</td>
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<td>17.6</td>
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*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
those of \textit{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 length (Fig. 87). Copulatory papilla as on the figure 93. Male unknown.

Measures (in mm):

\begin{tabular}{cccc}
\text{Lpron} & \text{LFIII} & \text{LTIII} & \text{Lovip} \\
3 & 17.5 & 19.7 & 22.4 \\
\end{tabular}

\textit{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 I 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.

\textbf{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 \textit{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 \textit{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.
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. sanchezii*. 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):**

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<tr>
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</tr>
<tr>
<td>Females</td>
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<td>21-21.5</td>
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</tbody>
</table>
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.

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).


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 epiphallus 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 epistomal suture, thus delimiting a yellow median space, narrow under the median ocellus, larger toward the epistomal suture; a light brown fleck above the epistomal 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):

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</table>

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)  
   — 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*  
   — 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

6. 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*

7. Ocelli present. Male genitalia: C-sclerites large, almost horizontal, dorsally membranous; epiphallic sclerite simple. Female genitalia: Copulatory papilla not flat, triangular or quadrangular in shape.

8. 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.

9. 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.

10. 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 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).

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</table>
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 cavedwelling 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 analysis 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 margin 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 Luzarineae (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 differentiated 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 para-
meres (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), *Notivox* and group B.

**Character 11.** Epiphallic parameres 1 & 2 having the shape of large vertical spines (1). Epiphallic 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 epiectophallic membrane (1), developed as 2 huge glands (2). Epiectophallic 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 majority 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 probably 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 scarce 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 Amphicustae. The open triangle indicates a locality where no Amphicustae has been found.
Fig. 111 — Distribution of troglobitic species of Amphipodidae.
They do not have close relationships together or with Amphiacustae (Desutter, 1990, and unpubl. data).

Cavicole 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 its 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 scarce, their distribution in reference to our phylogenetic hypothesis
suggests that the ancestral habitat could be characterized by foraging in leaf litter and hiding 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 Amphiacustae 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 traditionally considered as «pre-adapted» to cave environment by their epigean ecology (Barr, 1968; Holsinger, 1998), i.e. 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.

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<td>Amphiacusta</td>
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<td>1</td>
<td>?</td>
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<tr>
<td>Noctivox</td>
<td>0(1)</td>
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<td>Group B</td>
<td>0</td>
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<tr>
<td>Group A</td>
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<td>Nemoricantor</td>
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<td>Mayagryllus</td>
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<td>Arachnopsita</td>
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<td>Prolonguripes</td>
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<tr>
<td>Longuripes</td>
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<td>Luzarida</td>
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<td>Lerneca</td>
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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 natural 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 displacements 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 im-
ply several independent cave colonization/epigean disappearance events, unless one envisions 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 troglobites 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 argued 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, i.e. 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 Arachnopsis 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 Gryllloid 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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The second occurrence of the troglobic shrimp
Macrobrachium microps Holthuis
(Crustacea, Decapoda, Palaemonidae), in Samoa

Alexander J. Bruce * and Thomas M. Iliffe **

SUMMARY

A single example of Macrobrachium from an anchialine lava tube on Upolu, Samoa, is described and illustrated. The specimen is referred to M. microps Holthuis, 1978, but shows some differences that may be of specific value, which are discussed. The troglobic species of Macrobrachium are reviewed.

In the Indo-West-Pacific region the species rich genus Macrobrachium, abundant in tropical fresh waters, is represented by very few troglobic species. The first to be described, M. cavernicola (Kemp, 1924) is known only from Assam, India. M. microps was described by Holthuis in 1978, from New Ireland, Papua New Guinea, and the only other species, M. poeti Holthuis (1984), is known only from central Java, Indonesia. A further addition to this sparse and scarce record is therefore of some interest.

Palaemonidae

Macrobrachium microps Holthuis, 1978


Material examined.

1 male, stn.88-36, Ana Pe'ape'a, at Tafetafe, Upolu, Western Samoa, leg. S. Sarbu and T.M. Iliffe, 19 April 1988, by dip net, from bare rock bottom in 0-80 cm depths of an anchialine pool.

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Description.

A small shrimp of slender, glabrous, smooth, subcylindrical body form.

Rostrum short, about 0.4 of carapace length, straight, horizontal, extending to about middle of distal segment of antennular peduncle, slightly upturned distally, about 5.0 times longer than deep, dorsal carina with 4 acute teeth, with 6 postorbital acute teeth, first tooth at about 0.45 of carapace length, first 3 teeth articulated, with short simple setae laterally, anterior teeth non-articulate, separated by rows of short plumose median setae, ventral margin feebly convex, with 4 small acute teeth, separated by medial row of short plumose setae, proximal tooth situated anteriorly to eighth dorsal tooth, proximal ventral margin with submedian rows of short plumose setae; orbit feebly developed, inferior orbital angle slightly produced, antennal spine large, acute, slightly postmarginal, with short carina, hepatic spine well developed, articulate, rigid, well below level of antennal spine, branchiostegal suture distinct, anterolateral angle of carapace bluntly obtuse.

Abdomen with sixth segment about 3.0 of carapace length, 1.2 times longer than deep, 1.4 times longer than fifth segment, posterolateral and posteroventral angles acutely produced, pleura of first three segments broadly rounded, fourth and fifth strongly acutely produced posteroventrally, ventral margins with plumose setae, sternite of first segment with acute median tooth, smaller teeth on second and third sternites. Telson about 0.5 of carapace length, 0.6 times sixth segment length, 3.0 times longer than wide, with two pairs of small dorsal spines, at 0.4 and 0.6 of telson length, posterior margin about 0.3 of anterior margin width, angularly produced, with acute median point, with two pairs of posterolateral spines, lateral spines small, short, about 0.5 of dorsal spine length, medial spine long, about 0.11 of telson length, 2.0 times dorsal spine length, far exceeding tip of telson, central posterior margin with 9 long subventral plumose setae, with few shorter simple setae dorsally.

Eye strongly reduced, with small well pigmented cornea, about 2.0 times wider than deep, 0.5 of stalk width, oblique, stalk swollen, 2.0 times wider than deep, compressed, eye reaches to about 0.4 of length of proximal segment of antennular peduncle.

Antennule with proximal segment about 1.4 times longer than central width, ventromedial margin without acute tooth, lateral
Fig. 1 — *Macrobrachium microps* Holthuis, male, Upolu, Samoa. Scale divisions in millimetres.
margin sublinear, anterolateral angle strongly produced, with long slender acute distolateral tooth reaching easily to level of distal margin of intermediate segment of peduncle, anteromedial margin smoothly concave, setose, stylocerite slender, reaching to about 0.6 of proximal segment length, statocyst present, statolith feebly developed; intermediate segment about 0.5 of proximal segment length, 1.4 times longer than wide, with large oblique articulation with distal segment; distal segment about 1.3 times length of intermediate segment, 2.0 times longer than proximal width; upper flagellum biramous, 5 proximal segments fused, shorter ramus about 0.75 of carapace length, 10 times fused portion length, longer ramus subequal to shorter ramus length (?, tips missing).

Antenna with basicerite with strong slender lateral tooth, with small subacute ventrolateral carina; ischiocerite and merocerite normal; carpocerite short, extending to about distal end of proximal segment of antennular peduncle, 0.3 of scaphocerite length, about 3.0 times longer than wide, flagellum well developed, long slender, about 4 times carapace length (?, distal portion missing); scaphocerite with lamella distinctly exceeding antennular peduncle, distolateral spine slightly exceeding peduncle, lamella about 3.6 times longer than width, width maximal at 0.3 of length, lateral margin straight, with strong distolateral tooth, well exceeded by angular, bluntly rounded distal lamella.

Ophthalmic somite with small rounded bec ocellaire, with small median pigment spot. Epistomal region without special features. Labrum with anterior median carina.

Mandible (right) with corpus stout, with slender, 3-segmented palp, with numerous short simple spines and setae, segment lengths in ratio 1.6:1.0:1.8; molar process robust, truncate distally, with 4 blunt peripheral teeth, 1 trullate tooth posteriorly, incisor process short, broad, with 3 stout acute teeth distally, central tooth slightly smaller than outer teeth. Maxillula with palp deeply bilobed, upper lobe elongate, slender, with numerous short simple setae, lower lobe short, tapering, with single simple distodorsal seta, non-setose distoventral tubercle; upper lacinia slender, tapering, distally truncate, with about 12-13 simple spines, with numerous finely serrulate spiniform setae distally and ventrally, sparse simple setae along dorsal margin; lower lacinia tapering, distally subacute, with numerous finely serrate setae. Maxilla with tapering, distally acute palp with single short
simple preterminal seta, with several short plumose setae proximolaterally, basal endite with 2 elongate lobes, upper lobe slightly longer and broader than lower, with numerous short simple setae distally, with similar setae along dorsal margin of upper and ventral margin of lower lobe, coxal endite obsolete, medial margin feebly bilobed; scaphognathite well developed, about 3.0 times longer than wide, posterior lobe large, anterior lobe narrow, medial margin deeply emarginate. First marilliped with elongate, slender palp with long preterminal seta, several short setae on proximal medial margin, basal endite large, broadly rounded, with straight densely setose medial margin, distinctly demarkated from coxal endite, medial margin thickened, setose, exopod well developed, flagellum with numerous long plumose setae distally, caridean lobe normal, epipod bilobed, distal lobe larger than proximal. Second maxilliped normal, with endopod normal, dactylar segment 2.6 times longer than wide, with numerous robust simple spines medially, propodal segment broadly rounded distomedially, with long slender simple spiniform setae distomedially, carpus with distomedial angle acutely produced, basis feebly excavate medially, exopod well developed, with numerous plumose setae distally, coxa with medial margin broadly rounded with numerous slender simple setae, with small rounded epipod laterally, with small podobranch. Third maxilliped with endopod slender, reaching anteriorly to about end of antennular peduncle, ischiomer al segment completely fused to basis, combined segment about 5.7 times longer than distal width, bowed, slightly expanded and flattened distally, medial and lateral margins setose, penultimate segment about 0.6 of proximal segment length, 5.0 times longer than proximal width, with numerous long simple spiniform setae, terminal segment about 0.75 of penultimate segment length, slender, about 6.5 times longer than proximal width, tapering to acute point distally, with numerous simple spiniform setae, exopod well developed, reaching to about 0.75 of proximal segment length, with numerous plumose setae distally, coxa feebly produced medially, sparsely setose, with small oval lateral plate, larger lower and smaller upper arthrobranchs laterally.

Thoracic sternites 1-3 broad, with low transverse ridges, 4 unarmed, without median process, 5-8 narrow, unarmed.

First pereiopod very slender, exceeding carpocerite by distal merus, rostrum by 0.6 of carpus; chela with palm about 2.6 times longer than central depth, subequal to length of fingers, fingers
slender, dactyl 7.0 times longer than proximal depth, with entire cutting edges and small acute hooked tips; carpus about 1.9 times chela length, about 10 times longer than distal width, slightly tapering proximally; merus about 0.85 of carpus length, 8 times longer than proximal width, slightly expanded and setose proximomedially, ischium subequal to chela length, 0.6 of meral length, medially setose; basis normal; coxa with small distoventral lobe.

Second pereiopods subequal, similar, slender, smooth, exceeding rostrum by carpus, chela and distal sixth of merus; chela with palm subcylindrical, slightly swollen centrally, smooth ?, 2.9 times longer than deep, fingers slender, 1.45 times palm length, dactyl 8.5 times longer than proximal depth, with 3-4 very small low teeth proximally, rest of cutting edge sharp, entire, with small acute hooked tip, fixed finger similar, with single small tooth proximally; carpus about 1.25 times palm length, subequal to length of fingers, 6.0 times longer than distal width, slightly expanded distally, unarmed; merus 1.1 times carpus length, 11 times longer than central width, slightly expanded distally, unarmed; ischium about 0.6 of meral length, unarmed; basis and coxa without special features.

Ambulatory pereiopods slender, third exceeding carapace by dactyl, propod and carpus; third pereiopod with dactyl compressed, about 0.3 of propod length, 5.5 times longer than proximal depth, feebly curved, with acute tip, unguis not distinct, corpus with 4 groups of short spiniform setae dorsolaterally, 2 pairs of setae ventrally and distoventral group of longer setae; propod about 0.44 carapace length, 16.5 times longer than central width, subuniform, with 10 small ventral spines, 2 small distoventral spines, sparsely setose; carpus about 0.65 of propod length; merus 1.2 times propod length, 9.5 times longer than central width, sparsely setose ventrally, devoid of spinules, unarmed; ischium about 0.4 of merus length; basis and coxa without special features; fourth pereiopod similar to third; fifth pereiopod with propod 1.5 times length of third propod, with 10 small ventral spines, smaller spines on dorsal margin, 5 transverse rows of setae distoventrally, without distoventral spines.

First pleopod with basipodite 2.2 times longer than broad; endopod about 0.6 of basipodite length, 3.5 times longer than proximal width, distinctly curved medially, distomedial third and distolateral two third of margin with short finely plumose setae, proximal medial margin with numerous short slender spiniform setae, 5 longer coarsely plumose setae, exopod 2.0 times endopod length. Second
pleopod with basipodite 2.2 times longer than wide, 1.1 times first
pleopod basipodite length; endopod 1.3 times basipodite length, appendices at 0.3 of medial margin length, appendix masculina long, slender, subcylindrical, about 13 times longer than central width, feebly tapering distally, reaching to about 0.75 of endopod length, with about 15 transverse rows of slender simple spiniform setae ventrally, appendix interna about 0.5 of appendix masculina length, reaching to 0.5 of endopod length, with few distal cincinnuli; endopod 6.5 times longer than wide, 1.4 time basipodite length.

Uropod with protopodite with strong acute distolateral process; exopod subequal to telson length, 2.5 times longer than wide, lateral margin straight, with acute distolateral tooth at about 0.75 of length, with small mobile spine medially; endopod subequal to exopod length, 3.3 times longer than wide.

Habitat

Ana Pe'ape'a at Tafetafe is an anchialine lava tube cave located about 1 km inland from the coast of Upolu at Tafetafe village. In Polynesian, «ana» is the word for cave, while «pe'ape'a» refers to the cave swallow. This cave has a total length of 1,572 m, of which 102 m is an underwater passage (Fig. 6). Ana Pe'ape'a has only a single entrance with passages trending in opposite directions. Downstream (in relation to the direction of the lava flow which formed the cave), a 5 m wide by 2 m high gallery reaches a subterranean lake after a distance of 200 m. The water in the lake gradually deepens until the passage becomes totally submerged. This water is very clear, with underwater visibility in excess of 30 m. Salinity (measured with a calibrated refractometer) and water temperature were 1ppt and 23°C respectively. The bottom consisted of bare lava rock with only a small amount of silt and a few small pieces of wood apparently washed into the cave. The underwater tube was blocked at its terminus by a large boulder cemented into place by the lava. Peering through a small hole, it was possible to see the passage continuing south toward the coast past the obstruction. Several small, reddish to clear coloured atyid shrimps were also collected from the cave.

Upolu is a volcanic island of Pliocene age located in the central South Pacific at about 14°S and 172°W. Pleistocene to Holocene age eruptions along the central spine of the island have produced lava flows that spread out as fans to reach the coast.
MACROBRACHIUM MICROS IN SAMOA

Systematic remarks

Assessment of the correct systematic position of the specimen under consideration presents some difficulties. Like the original material of *Macrobrachium microps*, only a single male specimen is available. While it is evident that the holotype of *M. microps* is a fully developed male, the developmental status of the Samoan specimen is uncertain, making a full comparison difficult. The separation *Macrobrachium* males when only not fully developed males are available is notoriously uncertain. The Samoan specimen presents a number of differences from the New Ireland specimen that might suggest that separate taxa are involved, a possibility that is increased by the considerable geographic separation of the sites of collection. Although many anchialine shrimps, of marine origin and presumably with planktonic larval stages, are of very wide geographical distribution, this is much less marked in freshwater troglobic forms.

The present specimen has a rostrum that is slightly shorter than the antennular peduncle, and has only 10 dorsal and 4 ventral teeth, whereas the *M. microps* holotype has 11 dorsal teeth and 3 ventral teeth, with the rostrum reaching to the end of the peduncle. In the Samoan specimen the first three dorsal teeth are articulated, with simple setae lateral to the tooth, with the more distal teeth separated by a median row of plumose setae. This arrangement is not evident in the holotype. The antennal spine appears longer and more acute in the Samoan specimen. The Samoan specimen has the distolateral angle of the proximal segment of the antennular peduncle with a more strongly acute tooth, with the medial margin deeply concave, rather than convex as in the holotype. The second pereiopods in the two specimens are markedly different, but the slender gracile from of the Samoan specimen could be only undeveloped from of the New Ireland specimen, or of something quite different. The ambulatory pereiopods in the Samoan specimen are distinctly more slender than in the New Ireland specimen, with the third propod about 16 times longer than the central width, as opposed to 10.75 times and with propod 3.5 times the dactyl length as opposed to 2.75 times. The ventral surface of the merus is without spinules, which are present in the holotype.

Holthuis (1986) listed only 6 stygiobiont species of *Macrobrachium*, together with an additional 12 stygiophile and stygoxene...
Fig. 6 — Map of Ana Pe'ape'a at Tafetafe, Upolu, Western Samoa.
species. Since that date no further stygiobiont species have been described. Three species are known from the Indo-West Pacific region and three from the Central American-Caribbean region. There results are summarized on the following table.

The Stygiobiont Species of *Macrobrachium* Bate, 1868 (after Holthuis, 1986)

<table>
<thead>
<tr>
<th>Species</th>
<th>Region</th>
</tr>
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<tbody>
<tr>
<td><em>M. cavernicola</em></td>
<td>India</td>
</tr>
<tr>
<td><em>M. villalobosi</em></td>
<td>Mexico</td>
</tr>
<tr>
<td><em>M. lucifugum</em></td>
<td>Curacao, Bonaire, Santo Domingo, Jamaica, Cuba</td>
</tr>
<tr>
<td><em>M. acherontium</em></td>
<td>Mexico</td>
</tr>
<tr>
<td><em>M. microps</em></td>
<td>New Ireland</td>
</tr>
<tr>
<td><em>M. poeti</em></td>
<td>Java</td>
</tr>
</tbody>
</table>

**ACKNOWLEDGEMENTS**

Biospeleological investigations in Western Samoa were part of a year long expedition studying the fauna of anchialine caves in the South Pacific. This research was supported by grants from the National Science Foundation (BSR-8700079) and the National Geographic Society (3412-86). Mr Dan Sua, of the Western Samoa Department of Fisheries, provided considerable logistical assistance. Serban Sarbu and Yolanda Iliffe aided with the cave collections.

**REFERENCES**


Harpacticoida (Crustacea, Copepoda) from subterranean waters of Bue Marino cave, Sardinia, and St. Barthélémy cave, Corsica, and description of three new species *

Vezio Cottarelli ** and Maria Cristina Bruno **

SUMMARY

Three new species of harpacticoid copepods are described and discussed. Nitocrella beatricis n. sp. has been collected in different hyporheic sites in Sardinia and in two caves («Bue Marino» cave in Sardinia and «St. Barthélémy» cave in Corsica); Elaphoidella janas n. sp. and Parastenocaris triphyda n. sp. have been collected only in «Bue Marino» cave. Some considerations concerning the ecology and biogeography of the three species are also presented.

INTRODUCTION

During a faunistic research carried out in 1992, the impressive karstic system of «Bue Marino» cave (12 SA/NU, Dorgali, Cala Gonone) and the small «St. Barthélémy» cave, near Bonifacio town, Corsica, were explored. In these caves some samples of phreatic fauna, containing several rare or undescribed stygobiont harpacticoid copepods, were collected (1). In this paper the results of the research concerning the material collected in these caves and during other expeditions in Sardinia are explained and discussed.

* Research supported by grants from M.U.R.S.T. (60%) and C.N.R.
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1) All the material listed in this paper has been collected using the Karaman-Chappuis method and a particular hand-pump (Vigna Taglianti et al., 1969).
Fam. AMEIRIDAE Monard, 1927; Lang, 1948
Gen. Nitocrella Chappuis, 1923
Nitocrella beatricis n. sp.

Material

33 ♀♀, 18 ♂♂, R. Argano, V. Cottarelli legg., 21.VI.1970, in the hyporheic water bed of Liscia river (Sassari province), at about 200 m from the bridge where the trunk-road N. 133 crosses the river. 8 ♀♀, 6 ♂♂, V. Cottarelli, B. Deriu legg., 14.V.1978, in the hyporheic water bed of Cedrino river (Nuoro province), near the bridge where the trunk-road N. 125, km 224.8, crosses the river. 9 ♀♀, 7 ♂♂, V. Cottarelli leg., 6.V.1984, in the hyporheic water bed of Quirra river (Cagliari province), near the trunk-road N. 125, km 83.8. 3 ♀♀, V. Cottarelli, E. De Matthaeis legg., 1.VI.1992, «Bue Marino» cave (Nuoro Province), inside the sandy-shore of the first freshwater lake in the southern drift of the cave, at about 600 m from the entry. 6 ♀♀, 2 ♂♂, M. Cobolli, V. Cottarelli, E. De Matthaeis legg., 3.VI.1992, «St. Barthélemy» cave (Bonifacio, Corsica), in the sandy-shore of a little freshwater basin formed by the spring gushing from the bottom of the cave.

Types

Holotype: a female from Liscia river, completely dissected and mounted on a slide labelled N. beatricis ht. Paratypes: 20 ♀♀ and 15 ♂♂ (25 dissected), mounted on slides labelled N. beatricis pt. with the indication of the collecting place, numbered from 1 to 35. The material of the typical series, as well as all the other Nitocrella preserved in alcohol, are temporarily deposited at the «Dipartimento di Scienze Ambientali, Università della Tuscia», Viterbo (Cottarelli collection).

Diagnosis

A Nitocrella of the vasconica group Petkovski, 1976, characterized by the combination of the following features: first segment of the P2 - P4 endopods unarmed; second article with one, two, one setae, respectively; P5 baseoendopod with three inner setae; P5 exopod with four setae; distal margin of the anal operculum with a row of spinules.
Description of the holotype

Body elongated, subcylindrical, without eyes or pigment; length, from the rostrum to the apex of the furcal rami, 0.678 mm. Thoracic somites without ornamentation; first and second abdominal somite merged. Each abdominal segments with a posterior row of small hairy spinules; anal somite (Fig. 1) with a dorsal row of spines in the central share and a second row of larger spines surrounding the somite. Anal operculum (Fig. 1) convex, with five strong spines aligned along the margin. Furcal rami (Fig. 1): subconical, short; the outer margin with a spine at about 2/3 of the length; dorsal margin with a long outer seta and a spiniform inner seta; four setae apically inserted; the medial distal seta is the longest and it is of different size, the inner one is about twice as much the length of the outer one; at the basis of the principal apical seta there are three spinules.

Rostrum very small. Antennule (Fig. 4): eight-segmented: aesthete on fourth segment a little longer than the tip of the distal segment.

Antenna (Fig. 5): exopod one-segmented, armed with three distal setae, the inner one is the longest.

Mandible (Fig. 6): praecoxa with a bi-dentate pars incisiva; two-segmented palp: the second article with five distal setae.

Maxillule (Fig. 8): arthrite of the praecoxa with four distal spines; coxa with two setae; basipod with two distal and a lateral seta.

Maxilla (Fig. 7): syncoxa with an endite bringing three apical setae; endopod reduced to a tubercle with two setae.

Maxilliped (Fig. 9): shown in figure.

P1 (Fig. 12): three-segmented exopod, long as much as the first two segments of the corresponding endopod; all the segments of the exopod with one seta on the distal outer corner; third segment with three strong apical setae, the outer one is the shortest. Endopod three-segmented, the first one is the biggest and has a long seta at about 3/4 of the inner lateral margin. Distal segment with two long apical setae, the longest one geniculated, and with a little spine.

P2 (Fig. 13): second segment of the exopod with one seta on the inner distal corner; third segment with four apical setae. Second segment of the endopod with only one long distal seta; the endopod is shorter than the first two segments of the corresponding exopod.

P3 (Fig. 14): exopod as in P2; second segment of the endopod
Figs. 1-4 — *Nitocrella beatricis* n. sp. 1,4: holotype ♀; 2,3: paratype ♂. 1, last somite, anal operculum and caudal ramus, dorsal view; 2, last somite, anal operculum and caudal ramus, dorsal view; 3, antennule; 4, antennule.
Figs. 5-19 — *Nitocrella beatricis* n. sp. 5,6,7,8,9,10,12,13,14,18: holotype ♀, 5, antenna; 6, mandible; 7, maxilla; 8, maxillule; 9, maxilliped; 10, P4; 11, P5 ♀ (Bue Marino Cave); 12, P1; 13, P2; 14, P3; 15, P5 ♀ (Cedrino River); 16, P5 ♀ (St. Barthélémy Cave); 17, P5 ♀ (Quirra River); 18, P5; 19, P5 ♀ (Concas River).
short, with a slender, curved seta on the distal inner corner, and a spinulate apical seta.

P4 (Fig. 10): third segment of the exopod with six setae. The endopod is a little longer than the first segment of the corresponding exopod. Second segment with a spinulate seta.

P5 (Fig. 18): baseoendopod with a long seta on the distal outer corner. The internal lobe with three setae. Exopod rounded, with one long and slender seta on the distal outer corner, three apical setae, the medium one is the shortest, and some spinules on the inner margin.

The setal formula of legs from 1 to 4 is listed below:

<table>
<thead>
<tr>
<th></th>
<th>Exopod</th>
<th>Endopod</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1</td>
<td>0</td>
<td>0,2,0</td>
</tr>
<tr>
<td>P2</td>
<td>0</td>
<td>0,1,0</td>
</tr>
<tr>
<td>P3</td>
<td>0</td>
<td>0,1,0</td>
</tr>
<tr>
<td>P4</td>
<td>0</td>
<td>0,1,0</td>
</tr>
</tbody>
</table>

**Description of the male**

Length, measured as in the female: 0.650 mm. Morphology and ornamentation of the anal operculum and furcal rami with little differences from the female’s ones, as shown in figure 2. Antennule (Fig. 3): eight-segmented, the fourth and the fifth one strongly enlarged. Antenna, mouth parts, maxillipeds, legs P2-P4 (Figs. 21, 22, 23) as in the female.

P1 (Fig. 20): as in the female but the inner spine of the baseoendopod is transformed as is usual in the genus.

P5 (Fig. 25): baseoendopod less developed than in the female, with only two setae on the inner lobe; exopod rounded with four setae, the inner one is the longest.

P6 (Fig. 26): reduced to a little plate with two distal setae.

**Variability**

A female collected in Rio Concas with two inner setae on P5 baseoendopod (Fig. 19) instead of three; the number of spines on the anal operculum varies between five and seven. The other features considered are constant in all the specimens. Figures 11, 15, 16, 17 illustrate the P5 of specimens from different sampling sytes.
Figs. 20-26 — *Nitocrella beatricis* n. sp. 20, 21, 22, 23, 24, 25, 26: paratype ♀. 20, P1; 21, P2; 22, P3; 23, P4; 24, antenna; 25, P5; 26, P6.
Derivatio nominis

The new species is dedicated to Mrs. Beatrice Deriu, as a friendly acknowledgement of the help she gave to V. Cottarelli for some sampling, and the hospitality she offered him in Sardinia.

Affinities

_N. beatricis_ n. sp. fits well with the species group _vasconica_ Petkovski, 1976, to which all the species showing the last segment of exopod P4 with six setae belong. In this group, _N. vasconica_ Chappuis, 1937, found in Spain, seems to have some affinities with the new species.

We notice moreover that _N. beatricis_ n. sp. is the first species belonging to _vasconica_ group known in the Sardinian fauna until now.

Fam. CANTHOCAMPTIDAE Sars, 1906; Monard, 1927; Lang 1948
Gen. _Ceuthonectes_ Chappuis, 1923
_Ceuthonectes pescei_ Cottarelli & Saporito, 1985

Material

1 ♂ adult, M. Cobolli, V. Cottarelli, E. De Matthaeis legg., 1.VI.1992 collected with the same method and in the same station of the «Bue Marino» cave indicated before.

Remarks

The specimen from the «Bue Marino» cave certainly belongs to _Ceuthonectes pescei_. Up to now this species was only known from its type locality: a well not so far from the «Bue Marino» cave (Cottarelli & Saporito, 1985). This is the second male specimen ever found. We provide therefore pictures of the P2 endopod (Fig. 27), P3 (Fig. 28), P4 (Fig. 30), P5 (Fig. 31), P6 (Fig. 33), anal operculum (Fig. 32), maxilla (Fig. 29). This last appendix is different from the original description because the second endite is armed with three setae instead of two.
Figs. 27-33 — Ceuthonectes pescei, ♂. 27, P2 endopod; 28, P3 endopod; 29, maxilla; 30, P4 endopod; 31, P5; 32, anal operculum; 33, P6.
Gen. *Elaphoidella* sensu Apostolov, 1985

*Elaphoidella janas* n. sp.

**Material**

5 ♀♂, (2 ovigerous), 3 ♂♂, 1 female copepodite, M. Cobolli, V. Cottarelli, E. De Matthaeis legg., 1.VI.1992, collected with the same method and in the same station of the «Bue Marino» cave indicated before.

**Types**

Holotype: a mature female, dissected and mounted on a slide labelled *E. janas* ht. Paratypes: the remaining specimens, mounted on slides labelled *E. janas* pt., numbered from 1 to 7. The material of the typical series is temporarily deposited at the «Dipartimento di Scienze Ambientali, Università della Tuscia», Viterbo (Cottarelli collection).

**Diagnosis**

An *Elaphoidella* of the *gracilis* group Apostolov, 1985, characterized, among other things, by the combination of the following features: ornamentation of P2 and P3 endopods and of anal operculum, shape and chaetotaxy of furcal rami.

**Description of the holotype**

Body somewhat slender, subcylindrical, posteriorly tapering, depigmented and without photoreceptors. Length, from the rostrum to the apex of the furcal rami, 0.693 mm. Body with a row of spines on the ventral and distal margin of genital, postgenital and terminal somites.

Distal margins of the thoracic somites dorsally denticulated; the denticulation is also present along the distal margins of the abdominal somites. Anal somite (Fig. 34) with a transverse row of spines aligned ventrally at about half of the length; 3 - 4 spines inserted near the basis of each furcal ramus (Fig. 34); remaining ventral and dorsal ornamentation is shown in figures.

Anal operculum (Fig. 34): convex, with 18-20 «tubercles» aligned along the margin. Furcal rami (Fig. 34): cone-shaped and elongated (length/width ratio: 2,2); outer margin with a seta and three spines;
Figs. 34-43 — *Elaphoidella janas* n. sp. 34, 35, 36, 37, 39, 42, 43: holotype ♂. 38, 40, 41: paratype ♀. 34, last somite, anal operculum and caudal rami, dorsal view; 35, mandible; 36, maxilliped; 37, maxilla; 38, P5; 39, last somite and caudal rami, ventral view; 40, antennula; 41, last somite, anal operculum and caudal rami, dorsal view; 42, antennule; 43, maxillule.
three apical setae: the medial seta is the longest, the outer seta is three times as long as the corresponding inner one; a last dorsal composite seta, longer than the furcal ramus, is inserted near a chitinous protrusion.

Antennule (Fig. 42): eight-segmented; aesthete on fourth segment not much exceeding the tip of the distal segment.

Antenna: allobasipod unarmed; one-segmented exopod with two distal and two subdistal spinulose setae.

Mandible (Fig. 35): praecoxa with a bi-dentate pars incisiva; two-segmented palp: the first article unarmed, the second one has three distal setae, a proximal seta and a spinula.

Maxillule (Fig. 43): arthrite of the praecoxa with four distal spines; coxa with two setae; basipod with two distal and five lateral setae.

Maxilla (Fig. 37): syncoxa with two endites, bringing two setae each one; endopod represented by two setae.

Maxilliped (Fig. 36): basipod with a distal row of spinules; first article of the endopod with a line of setulae; second article with a strong, recurved thorn and a little spine.

P1 (Fig. 52): both rami are three-segmented; endopod longer than the corresponding exopod; the first segment of the endopod is as long as the first two segments of the corresponding exopod, with a seta on the inner margin; second segment also armed with a seta; third segment with three setae, the longest one is geniculated. Second article of the exopod with a strong inner seta; third segment armed with two spinulose and two geniculate setae.

P2 (Fig. 50): endopod two-segmented; first segment with a thin seta; the second one has two inner-lateral and two apical setae. Third article of the exopod with five setae.

P3 (Fig. 45): endopod two-segmented, the first one unarmed, the second one with three distal setae. Distal segment of the exopod with six setae.

P4 (Fig. 44): endopod two-segmented; first article unarmed, the second with three apical setae. Distal article of the exopod with six setae.

P5 (Fig. 46): exopod approximately quadrangular and provided with a strong distal spinulose seta and two subdistal short setae; the outer margin with a spinule. The inner lobe of the baseoendopod has three long spinulose setae.
Figs. 44-52 — *Elaphoidella janas* n. sp. 44,45,46,50,52: holotype ♀; 47,48,49,51: paratype ♂. 44, P4; 45, P3; 46, P5; 47, P4; 48, P3; 49, P2; 50, P2; 51, P1; 52, P1.
The setal formula of the legs from 1 to 4 is listed below:

<table>
<thead>
<tr>
<th></th>
<th>Exopod</th>
<th>Endopod</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>P2</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>P3</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>P4</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

Description of the male

Length, measured in the same way as in the female, 0.664 mm. Rostrum, A2, mouthparts, maxillipeds, body ornamentation and anal operculum as in female. The chaetotaxy and the shape of P1 (Fig. 51), P2 - P4 exopods and furcal rami are also similar to the female's one, apart from some little differences regarding the size and length of setae and spines.

Antennule (Fig. 40): seven-segmented and haplocer; aesthete on third segment a little longer than the tip of the distal segment.

P2 (Fig. 49): endopod two-segmented; second article with three setae.

P3 (Fig. 48): three-segmented endopod; first article unarmed; medial segment with a long, lanceolate apophysis; distal segment with two setae of different length.

P4 (Fig. 47): endopod biarticulated, with the same ornamentation as in the female but shorter.

P5 (Fig. 38): baseoendopod bare; exopod little, suboval, with a strong apical seta and two small ones.

Anal operculum and furcal rami (Fig. 41).

Etimology

The word janas refers to «Domus de janas», in the Sardinian language a common name of the caves, which means «sorceress's house».

Variability

The features considered above appear to be constant in all the specimens of the typical series. Females are always bigger than males.
Affinities

*E. janas* n. sp. belongs to *gracilis* group of *Elaphoidella* as defined by Apostolov, 1985. Within this group, the new species resembles both *E. damianae* Kiefer, 1967, from Rumanian groundwaters, and *E. proserpina* Chappuis 1934. However, the new species resembles more *E. federicae* Pesce & Galassi, 1988, from the phreatic waters of Corsica; the armature of the exopods P1, P3, P4, P5 and P2 in both sexes are shared with these species. *E. janas* n. sp. differs from the former species in the shape and ornamentation of the body somites, the anal operculum, the caudal rami and the P2 endopod in both sexes, armed with four and three apical setae respectively, instead of three and two setae. The mouthparts cannot be compared, because they are undescribed in *E. federicae*. Finally, it may be interesting to observe that the new species has very few affinities with *E. nuragica* Pesce & Galassi, 1986, 1988, the only *Elaphoidella* described until now from groundwater of Sardinia.

Fam. PARASTENOCARIDIDAE Chappuis, 1933  
Gen. *Parastenocaris* Kessler, 1913  
*Parastenocaris triphyda* n. sp.

Material

6 ♀♀ and 4 ♂♂ V. Cottarelli leg., 1.VI.1992 collected with the same method, in the same station of the «Bue Marino» cave before indicated.

Types

Holotype: 1 ♂, completely dissected and mounted on a slide labelled *P. triphyda* ht. Paratypes: all the other specimens, mounted on slides labelled *P. triphyda* pt., numbered from 1 to 9.

Diagnosis

A *Parastenocaris* of the *minuta* group Lang, 1948, mainly characterized by the combination of the following features: peculiar morphology and ornamentation of P3 legs, P4 endopods of the males and furcal rami of both sexes.
Description of the holotype

Body cylindrical and lengthened, depigmented; no photoreceptors. Length, from the rostrum to the apex of the furcal rami, 0.330 mm.

The ventral surface of the last abdominal somite with two groups of spinules near the median line (Fig. 67).

Anal operculum (Fig. 67): with semicircular distal margin.

Caudal rami (Fig. 67): much longer than the last abdominal somite, approximately cylindrical, very long and slender; length/width ratio = 7.2. Ornamentation represented by three apical setae, three spinules ventrally inserted; three little setae originate sub-apically from the outer lateral margin; a last composed seta is inserted dorsally.

Rostrum (Fig. 68): little and triangular, with two sensillae. Antennule (Fig. 68): seven-segmented; the first segment unarmed, the second one with a proximal plumose seta and four distal setae; third segment with four distal setae too; fourth segment, not very enlarged, armed with two long and a short setae and a big aesthete; fifth segment with a single distal seta; the sixth segment, prolonged distally into a sharpened aphophysis, is moreover unarmed; the seventh segment brings seven setae and an apical aesthete.

Antenna (Fig. 63): one-segmented little exopod with an apical spinulose seta; allobasipod unarmed; distal segment of the endopod with five setae, one modified and two geniculate ones and a spine, distally inserted.

Mandible (Fig. 62): one-segmented palp with two setae.

Maxillule (Fig. 61): difficult to observe; the praecoxal arthrite with three distal spines; the coxa is armed with a short distal seta; basipod with two distal setae.

Maxilla (Fig. 64): syncoxa with an endite bringing a seta; basis prolonged into a distally curved tip; endopod represented by a little tubercle with only one seta.

Maxilliped (Fig. 57): lengthened; second segment with a spinulose thorn.

PI (Fig. 53): exopod three-segmented, shorter than the endopod; distal segment with a subapical outer seta and three apical ones, two of which are geniculate. Endopod two-segmented: the first segment with two groups of lateral spinules; the second segment with two lateral spinules and two apical setae; the longest one is geniculate.
HARPACTICOIDA FROM SUBTERRANEAN WATERS

Figs. 53-65 — Parastenocaris triphyda n. sp. 53,54,55,57,60,62,63,64: holotype ♂; 56,58,59,65: paratype ♀. 53, P1; 54, P2; 55, P4; 56, P4; 57, maxilliped; 58, P2 endopod; 59, P3; 60, P5; 61, maxillule; 62, mandible; 63, antenna; 64, maxilla; 65, P5.
P2 (Fig. 54): exopod three segmented, ornamentation is shown in figure; endopod represented by a little cylindrical segment with three apical spinules and one seta.

P3 (Fig. 66): quite long and slender; basis with a long external seta followed by a series of spinules; endopod reduced to a stick-like appendix. The first segment of the exopod, slender and slightly curved, has a tubercle on the proximal side of the inner margin; two groups of spiniform setae are inserted on the outer margin. The segment ends into a long spoon-like and very sharpened apophysis. The second exopodial segment has a peculiar morphology: it is represented by a narrow and sinuous appendix, distally ending in three tips.

P4 (Fig. 55): exopod three segmented, chaetotaxy shown in figure. The endopod, as long as the first segment of the exopod, is represented by a segment with a sharpened extroflession coming from the distal outer corner; the segment continues into a narrow, spinulate lamina. Near the basis of the endopod two strong curved thorns and a spinula are inserted.

P5 (Fig. 60): represented by a quite rectangular plate with a long and slender seta on the distal outer corner, a short spinula and two setae on the distal margin; the distal inner corner is prolonged into a slightly curved tip.

Description of the female

Length, measured in the same way of the male: 0.322 mm. Rostrum, A2, mouth appendages, maxillipeds, P1, P2 and P4 exopods, ornamentation of the last abdominal somite and furcal rami, as in the male.

Antennule (Fig. 69): seven-segmented; aesthete of the fourth segment smaller than in the male.

P2 (Fig. 58): endopod similar to the male’s one, but a little longer, with an additional apical spinula.

P3 (Fig. 59): endopod represented by a narrow and sharpened spinulate segment, shorter than the first segment of the exopod; four little spinules are aligned near the base of this appendix. Exopod two segmented, ornamentation as in figure.

P4 (Fig. 56): cylindrical endopod, shorter than the first segment of the corresponding exopod, armed with two distal spinules and a small seta.
HARPACTICOIDA FROM SUBTERRANEAN WATERS.

Figs. 66-70 — *Parastenocaris triphyda* n. sp. 66, 67, 68, 70: holotype ♂; 69: paratype ♀.
66, P3; 67, last somite and caudal rami, lateral view; 68, antennule, 69, antennule; 70, last somite, anal operculum and caudal rami, dorsal view.
P5 (Fig. 65): ornamentation represented by a long seta which originates from the distal outer corner; distal margin provided with two setae; distal inner corner extended into a curved tip.

**Etimology**

The latine adjective *triphyda* is referred to the particular shape of the second exopod-segment of the male’s P3.

**Variability**

The features considered above appear to be constant in all the specimens of the typical series. Females are always smaller than males.

**Affinities**

*P. triphyda* n. sp., because of the construction and ornamentation of both the endopod and basis of P4 in male, well fits the *minutata*-group of species sensu Lang, 1948. Within this group the new species resembles *P. trinacriae* Pesce et al., 1988, from Sicily, but resembles even more *P. nertensis* Rouch 1990, from the Nert brook underflow of the Pyrénées (France). However, *P. triphyda* n. sp., is easily recognizable from the above species and from all the other species of the group, because of the characteristic morphology of P3 in males and the considerable length of the furcal rami in both sexes.

**REMARKS**

Sardinia is covered for about 1/10 of its surface by calcareous formations (2250 square km): some are typical paleo-Karst formations from the Cambrian but mostly from the Mesozoic period (From Cassola, 1978).

The «Bue Marino» cave is a calcareous cave from medium Jurassic in Orosei gulf, with three distinct entrances; it extends for about 4,5 km with two main branches: a northern fossil one, equipped for turist visits, and a southern one, active, not equipped for tourists, which can be crossed partly on foot and partly with the aid of row-boats (Casale, 1972). The cave is well known by the biospeleologists because it has been explored several times: the first
faunistic researches were carried out by Saverio Patrizi in 1955 (Cassola, 1978). It is also well known because it is inhabited by many terrestrial troglobionts of great interest; and it is also one of the few caves in Sardinia where aquatic fauna has been collected (Lindberg, 1956; Stella, 1957). Cassola (1978) and Casale (1972) provide a complete list of the terrestrial and aquatic taxa known for the «Bue Marino» cave. The most interesting elements of aquatic fauna are two Ciclopoids: *Speocyclops sardus* Lindberg, 1956, an endemic stygobiont, and *Dyacyclops crassicaudis cosana* Stella & Salvatori, 1954, a stygophile or eustygophile. As far as Harpacticoids, Lindberg (1956) mentions three stygoxene species from brackish or marine waters, and Stella (1957) mentions marine Harpacticoids sampled at the entrance of the cave, in marine water.

Actually, periodical researches of the Crustacean fauna of the subterranean waters of Sardinia (more recently concerning the minor Islands as well), have been carried out for more than twenty years by the senior Author. This effort has allowed us to get many results which are particularly interesting for their taxonomical and biogeographical aspects.

At the beginning, these researches have dealt with the «superficial» water-bearing stratum, especially the hyporheic habitats. Then, it became necessary to explore the «deep» water-bearing stratum, sampling in wells and caves. The first results, some of them still unpublished (Cottarelli, in litteris), seem to confirm that «the interstitial habitats, previously considered as homogeneous compared to epigean biotopes, are now recognized as heterogeneous, mainly because of the influence hydrology exerts on the physical, chemical and biological structure of the system» (Dole-Olivier et al., 1993).

Considering only the Sardinian fauna (data concerning Corsica are still insufficient), it can be observed that some genera (*Nitocrella, Parastenocaris, Elaphoidella*), have been found both in superficial and deep strata. Nevertheless, while the only *Nitocrella* ever sampled in all these habitats are *N. beatricis* n. sp. and *N. stammeri* Chappuis, 1938, the genera *Elaphoidella* and *Parastenocaris* are represented by different species. *P. ima* Cottarelli, 1989 and *P. triphyda* n. sp. are specific of deep waters, all the other *Parastenocaris* known in Sardinia have never been found in wells or in cave (Cottarelli, unpublished data).

Finally, *Ceuthonectes*, present in Sardinia with *C. pescei*, seems to be confined to the wells and to the subterranean cave waters.
Similar considerations can be applied to other groups of Crustaceans. An example is provided by the Syncarida, present in Sardinia with the species *Sardobathynella cottarellii* Serban, 1973, and two undescribed species of *Exobathynella*, found in hyporheic waters and in artesian strata, and *Meridiobathynella* which instead seems typical of wells.

Besides the faunistical, taxonomical and ecological interest, the distribution of *N. beatricis* n. sp., is of zoogeographical interest; this species, present in Sardinia and Corsica, could be one of the few endemic Corsica-Sardinia elements which are in counterposition with «the high discordance index between the two islands» (Cassola, 1978). *E. janas* n. sp. which has a great affinity with a corsican congeneric species, seems to be another example of this kind. Finally, as far as *Parastenocaris* is concerned, many of the Sardinian species, including the species described here, show affinities with pyrenaic and provençal ones. This genus, too, could belong to those taxa present in Sardinia, Southern France, Maritime Alps and Eastern Spain, but absent in Corsica for various reasons (following submersions, quaternarian ice-ages, the «solco di Terranova» effect).

**ACKNOWLEDGEMENTS**

We thank Professors Marina Cobolli, Elvira De Matthaeis, Augusto Vigna Taglianti from «Università degli Studi di Roma La Sapienza» and Professor Achille Casale from «Università degli Studi di Sassari», for participating to the researches and contributing to the sampling. We are also grateful to A. Vigna Taglianti and A. Casale for exchanging useful opinions and informations. Particular thanks are due to the Municipality and to the speleologists of Dorgali who kindly offered us the row-boats and part of the speleologic equipment.

**REFERENCES**


Comparative performances of non-visual food search in the hypogean cyprinid *Phreatichthys andruzzii* and in the epigean relative *Barbus filamentosus* *

Roberto Berti ** and Luca Masciarelli **

SUMMARY

The anophthalmic hypogean cyprinid *Phreatichthys andruzzii* Vinciguerra shows a more efficient food searching behaviour than blinded specimens of the epigean species *Barbus filamentosus* Cuvier and Valenciennes. This difference seems to be related to a tendency to swim near the bottom of the aquarium and the behavioural stereotypes in food localization and intake. Both in *P. andruzzii* and in the blinded *B. filamentosus* food search is guided by chemical stimulation. Other data indicate that mechanical stimulation could play an important role in the feeding behaviour of the hypogean form. The behavioural analogies in food localization between *P. andruzzii* and the cave forms of the characid *Astyanax fasciatus* Cuvier are briefly discussed.

INTRODUCTION

Fish adaptation to a subterranean life is characterized by a clear evolutionary convergence in regressive features such as eye and optic lobe regression and pigment reduction. Besides these regressive traits, which are common to almost all the subterranean fish (Thinès, 1969), a few forms also show some constructive traits. These appear as a result of natural selection based on the scarce supply of trophic resources, which generally characterizes the subterranean waters (Poulson, 1963; Barr, 1968; Culver, 1982; Wilkens, 1988). An example is represented by the characid *Astyanax fasciatus* Cuvier, where constructive features shown by the cave dwelling

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populations involve an improved efficiency in feeding behaviour, in resisting starvation and in energy economy (Wilkens, 1988). Moreover the constructive traits show some variability in intensity according to the degree of cave adaptation shown by each population. Similar relationships have been pointed out in amblyopsid fish such as *Chologaster agassizi* Putnam, *Typhlichthys subterraneus* Girard, *Amblyopsis spelaea* Dekay and *A. rosae* Eigenmann which are differently adapted to cave life (Poulson, 1963).

The cyprinid *Phreatichthys andruzzii* Vinciguerra, a phreatic species from Somalia closely related to the genus *Barbus*, is thought to represent (Vandel, 1965) one of the forms of most ancient adaptation to the subterranean habitat as shown by the importance of both regressive and constructive features. Scales and pigmentation are fully absent (Vinciguerra, 1924), and the anophthalmia, accompanied by the loss of the optic nerves, is complete (Ercolini and Berti, 1975). A strong reduction of the entire encephalon, and in particular of the optic lobes, is also present (Ercolini and Berti, 1975). The high degree of adaptation to a subterranean life is also confirmed by the presence of an extremely reduced metabolic rate, as seen by comparing closely related epigean and hypogean cyprinids (Ercolini et al., 1987).

In such a well adapted hypogean form, the existence of other evolutionary constructive traits appeared very probable. The aim of the present study was to verify if adaptation to hypogean life has been accompanied, in *P. andruzzii*, by an increase in the efficiency of food searching behaviour and intake of necessity based on and coordinated by non-visual sensory stimulation.

**MATERIALS AND METHODS**

For the present study a group of *Phreatichthys andruzzii* Vinciguerra (Pisces Cyprinidae), collected in December 1982 in a well at Gheriale (4°07′N - 46°29′15′′E; Central Somalia), and a group of *Barbus filamentosus* Cuvier and Valenciennes, bought in November 1987 from a dealer, were used. The latter species belongs to the epigean genus considered the closest to *Phreatichthys* (Vinciguerra, 1924).

In order to test the basic hypothesis, the efficiency of the non-visual feeding activity of both species has been compared. In the
epigean fish, any optic-motor coordination was excluded not only during the tests but also for a long period before the experiments. Such a pre-experimental treatment appeared essential to permit the fish to be accustomed to finding food without the aid of sight and to allow any possible sensory-motor coordination, based on non-visual stimulation, to be enhanced.

One year after that the _B. filamentosus_ were purchased, twenty of them, with an equal number of _P. andruzzii_, were anaesthetized with Ms 222 and subjected to surgery. The _B. filamentosus_ were blinded by removing the eyeballs, whereas the _P. andruzzii_ were lanced on both sides of the head in the areas corresponding _Barbus_ eyes, so as to cause trauma as similar as possible to that experienced by _B. filamentosus_. Both the trauma of the operation and the effects of the anaesthesia were quickly overcome. Regular feeding was observed four days after the operation, when food was given for the first time. For the three following months nourishment consisted of dried food commonly used for tropical ornamental fish and thawed chironomid larvae. Later only the larvae were supplied. Food was supplied daily, in a single dose. After a few hours any remaining food was removed. The aquaria were kept in a room weakly illuminated by orange lights so as to enable spot checks and routine maintenance. Light was kept continuous and constant.

Approximately six months after surgery, 16 fish were randomly chosen from each of the two groups. The 32 specimens were distributed in four aquaria so as to make four experimental groups: a monospecific group of 8 _P. andruzzii_, a monospecific group of 8 _B. filamentosus_ and two mixed groups, each of 4 _P. andruzzii_ and 4 _B. filamentosus_. The test aquaria (100 × 40 × 50 cm) were subdivided in two sections. A carbon filter and a heating system were installed in the smaller section (20 × 40 × 50 cm) whereas the fish were placed in the larger compartment (80 × 40 × 50 cm). Water depth was 40 cm, water temperature 27 °C. Four horizontal

1 Alternative procedures that excluded surgical injuries were considered. The only one which appeared able to meet the basic requirement of the experimental design (i.e. the exclusion of any optic-motor coordination in the epigean fish during both the tests and the pre-experimental training) was to keep and test fish in complete darkness, using an infra-red night-sight device for both tests and maintenance operations of the aquaria. The procedure was unworkable: the infra-red apparatus, perfectly fit to carry out the experiments, was not suitable for the routine maintenance operations.
layers 10 cm thick were indicated by thin strips of coloured tape applied to the aquaria walls.

The observations started about three months from the formation of the four groups, nine months after surgery. These were conducted using a method similar to the one already adopted in a study of the food finding ability of the hypogean and epigean forms of the characid Astyanax fasciatus Cuvier (Hüppop, 1987).

Each group of fish was starved for a 24 hr period, and then single chironomid larvae were successively offered. A time interval of 10 minutes was strictly kept between an eaten larva and the next one supplied. Each larva was offered in such a way as to ensure that it would sink to the bottom of the aquarium and not float on the water surface. The latency, from the moment the larva was introduced in the aquarium to the moment it was eaten, was recorded. If the larva was eaten before hitting the bottom of the tank, the layer in which it had been taken was registered. Obviously in the mixed fish groups the species that ate the prey also was recorded. At the end of each experimental session all fish were fed ad libitum.

From September to October 1989, during a four week period, 24 experimental sessions were carried out with each group. During each experimental session a total of 16 larvae were successively supplied, giving a total of 384 food tests performed with each group.

RESULTS

Observations conducted on both the monospecific and mixed groups revealed a greater efficiency in food localization in the hypogean form.

Quantitative results of the tests carried out on the monospecific groups are shown in Table 1. In 384 food tests, food was eaten before hitting the bottom 23 times by Phreatichthys andruzzii and only twice by Barbus filamentosus. The mean latency of the fish feeding on the sunken larvae was of 33.6 sec for the former group and of 76.5 sec for the latter, a 1:2 ratio. The one-tailed Kolmogorov-Smirnov test for large samples (Siegel, 1956) was used for the statistical analysis of the latency distributions. The test shows a highly significant difference (D=.604; p <.001) between the two species.

The data relative to the test conducted on the mixed groups are shown in Table 2, and substantially confirm the results obtained
with the monospecific groups. Once again, better performances were revealed by the hypogean fishes as compared to the blinded epigean ones. In the 768 food tests, conducted on the two mixed groups, sinking food was eaten 39 times by *P. andruzzii*, 3 times by *B. filamentosus*. Of the 726 sunken larvae, 714 were eaten by the former species and only 12 by the latter. While the mean latency of feeding on the bottom recorded for *P. andruzzii* is substantially similar to the one registered during the tests conducted on the monospecific group, the mean latency for *B. filamentosus* was greatly reduced and appears equal to that recorded for the hypogean species. An hypothetical improvement in the food finding

Table 1 — Comparative food finding performance in *Phreatichthys andruzzii* and blinded *Barbus filamentosus* (monospecific groups). Number of larvae presented to each group: 384.

<table>
<thead>
<tr>
<th>Water layer</th>
<th>Height above bottom (cm)</th>
<th><em>Phreatichthys andruzzii</em></th>
<th><em>Barbus filamentosus</em></th>
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<tbody>
<tr>
<td></td>
<td>No. of eaten food items</td>
<td>Mean time of intake (sec)</td>
<td>No. of eaten food items</td>
</tr>
<tr>
<td>IV</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>III</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>II</td>
<td>18</td>
<td>17.3</td>
<td>714</td>
</tr>
<tr>
<td>I</td>
<td>361</td>
<td>33.6</td>
<td>382</td>
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</table>

Table 2 — Comparative food finding performance in *Phreatichthys andruzzii* and blinded *Barbus filamentosus* (mixed groups). Total number of larvae presented to the two groups: 768.

<table>
<thead>
<tr>
<th>Water layer</th>
<th>Height above bottom (cm)</th>
<th><em>Phreatichthys andruzzii</em></th>
<th><em>Barbus filamentosus</em></th>
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<tr>
<td></td>
<td>No. of eaten food items</td>
<td>Mean time of intake (sec)</td>
<td>No. of eaten food items</td>
</tr>
<tr>
<td>IV</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>III</td>
<td>6</td>
<td>5.8</td>
<td>1</td>
</tr>
<tr>
<td>II</td>
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ability of *B. filamentosus* due to the interspecific competition can be excluded as an artefact of the testing procedure. In fact, in consequence of the greater capacity in food finding shown by the hypogean species, almost all the food items were consumed by the *P. andruzzii* specimens and the epigean fishes could eat only when they exceptionally localized the prey during the earlier phases of the test. Since the probability that a similar event could happen is evidently very low, both the remarkable decrease of the mean latency and the very small amount of food items eaten appear fully explained. Given the great differences in performance registered between the two species, a statistical analysis of the data appeared to be superfluous.

No particular tendency to occupy the lower part of the aquarium was shown by the blinded *B. filamentosus*. Generally the fish swam in each layer with the same frequency and only in some cases a single specimen would swim near the bottom of the tank, skimming it ventrally. Food presence was detected at mid-water by crossing the odorous trace left by the sinking larva and a sudden increase in swimming movements was generally registered. The whole group was then seized with a frantic locomotory activity, characterized by horizontal and non-orientated movement patterns and by sudden short vertical excursions. Food search would start when one individual, later followed by other specimens, swam towards the bottom. At this point the fish would start to swim frequently touching the ground with the tip of their snouts and interrupting their locomotory activities with quick snappings, in the course of which their body axis was considerably inclined to the bottom. As the search proceeded the initially rare snappings would become more frequent and would be characterized by larger angles of inclination. Near the food a long series of snappings would be performed by the fish, while maintaining a steep angle of about 90° with the bottom rotating around their body axis. Food intake seemed to depend on a largely random contact between the lips and the larva. Sensorimotor coordinations did not seem very effective and sometimes food was hit or moved by the fish's snout without being eaten.

The tendency of *P. andruzzii* to swim near the bottom of the aquarium and to skim it ventrally was greater than in *B. filamentosus*. Consequently food presence was traced not only at mid-water by crossing the odorous trace left by the sinking larva but also by passing near the point where the larva had hit the bottom surface.
In this second case, once the fish had realized the presence of food, it would suddenly slow down its swimming movements. Then the fish would proceed slowly skimming the ground with the ventral parts of the head forming a 20° angle and frequently it would change direction. The search for food lasted a few seconds and seemed to pinpoint the prey's location given that ingestion did not necessarily involve prior contact with the larva itself. When, instead, food presence was detected at mid-water by crossing the scented track left by the sinking larva the fish would change direction abruptly and spiral almost vertically down around the scent, often capturing the larva before it reached the bottom. A great sensory capacity and sensori-motor coordination was demonstrated by the fact that the fish, swimming along the bottom of the aquarium at a certain distance from a food item placed laterally, would suddenly stop and rapidly turn towards the food without missing the mark. If the fish causally encountered the spot where the food was present, it could be ingested even before it was contacted. The food intake by a fish was usually followed by a sudden increase in the locomotory activity of its tank mates which converged on the spot and started an intense food search.

DISCUSSION

The greater efficiency in food search shown by Phreatichthys andruzzii as compared to the blinded Barbus filamentosus indicates that adaptation to the hypogean habitat was accompanied, in this species also, by the acquisition of behavioural constructive traits. The better performances of the hypogean form do not seem to be due to a precocious discovery of the food presence, which took about the same time in both species. The higher ability shown by P. andruzzii to find food seems to be mainly related to its tendency to occupy the lower levels of the tank and to swim along the bottom surface, as well as to its greater efficiency in locating and grabbing the prey. In the blinded B. filamentosus the polarisation of the locomotory activity on the bottom of the aquarium, registered in blinded B. conchonius (Heuts and Thinès, 1971; Thinès and Capon, 1975), did not appear. B. filamentosus rarely swims along the bottom surface and in this way differs greatly from P. andruzzii. Consequently, while in P. andruzzii food search on the bottom starts immediately
after the discovery of its presence, in *B. filamentosus* a certain amount of time elapses between the two events.

In the blinded *B. filamentosus* specimens an important role for food localization seems to be played by the direct contact of the fish's snout with the ground surface. This is achieved by a strong inclination of the fish's body axis with the bottom. The headstanding position, a feeding behavioural pattern previously described for other epigean species experimentally deprived of visual coordination (Schemmel, 1967; Glaser, 1968; Heuts and Thinès, 1971; Thinès and Capon, 1975; Hüppop, 1987), probably facilitates the perception of chemical stimulation through taste (Schemmel, 1980).

In *P. andruzzii* food localization does not seem to depend on the contact of the fish's mouth with the bottom surface, which is merely skimmed even when the fish's body axis tends to lean, and appears to be characterized by a small inclination of the body axis with the bottom. The searching behaviour is substantially similar to the one shown by the cave dwelling populations of the characid *Astyanax fasciatus* (Schemmel, 1980; Hüppop, 1987). Also the latter forms show, as compared to the relative epigean populations, a clear reduction of the subtended angle, which seems to be related to the great improvement of their taste apparatus (Schemmel, 1980). As in *A. fasciatus* (Schemmel, 1967), the adaptation of *P. andruzzii* to cave life is not associated with an improvement of the olfactory organ (Delfino et al., 1981). No data regarding the development of the taste apparatus of *P. andruzzii* are at present available, but the fact that both hypogean forms have a much more efficient food finding behaviour than the relative epigean forms and that an extraordinary similarity between their food localization behavioural patterns is shown, suggests that in *P. andruzzii* also the gustatory equipment is particularly developed.

The similar behavioural stereotypes that characterize food search in *P. andruzzii* and in the cave populations of *A. fasciatus*, two species rather far apart from a systematical point of view, represent a clear example of evolutionary convergence. The fact that the angles subtended by the fish's body axis with the bottom surface are much smaller in *P. andruzzii* than in the hypogean populations of *A. fasciatus* suggests that the behavioural divergence from the corresponding epigean form appears to be larger in the former than in the latter. This suggests that adaptation to subterranean life is
characterized, from a behavioural point of view, by some variability related to the phylogenetical age of cave colonization.

Both in the blinded *B. filamentosus* and in the anophthalmic *P. andruzzii* food search seems to be released and guided only by chemical stimulation. But other considerations make us hypothesize that mechanical stimulation may play an important role in the feeding behaviour *sensu lato* of the hypogean form. In fact, both the immediacy and the simultaneity with which the group converges on the spot where the food item was eaten on the ground indicates that the response is presumably guided by mechanical stimulations released by the fish when ingesting the prey. The ingestion of a prey clearly signals the presence of a potential food source. The acquisition of a behaviour that facilitates its immediate exploitation has a highly adaptive significance in a habitat, so poor in food as the subterranean one. Moreover, the accuracy shown in converging on the spot seems to indicate a highly efficient mechanoreceptor apparatus. Only future observations with live prey will be able to clarify the role played by mechanical stimulation in food localization.

REFERENCES


Habitat use and gas bubble disease in southern cavefish (Typhlichthys subterraneus) *

Alex L.S. Schubert **, Carl D. Nielsen **, and Douglas B. Noltie ***

SUMMARY

In situ observations of habitat use by southern cavefish (Typhlichthys subterraneus) in a Missouri, U.S.A. spring suggest that groundwater discharge and zones of substrate which have large interstitial spaces that fish can enter may be important components of the species' habitat. Such substrates may also facilitate small-scale dispersal. In addition, we document the first recorded case of gas bubble disease in a laboratory-held speciem of this species. Cavefish may be particularly susceptible to this malady, and the conditions under which it occurred are important to avoid should captive maintenance or propagation of this or related species be attempted.

INTRODUCTION

The southern cavefish (Amblyopsidae: Typhlichthys subterraneus) is a small, troglobitic species which occurs in karstic areas of central North America (Woods & Inger, 1957). Its subterranean existence has made investigation of its ecology challenging. The resulting lack of information about the species constrains efforts to protect it, Missouri populations having been designated as «watch-listed» (Missouri Department of Conservation, 1991). In collecting specimens for a research project (Schubert, 1993), we made observations of in situ habitat use which, because of their relative scarcity in the recent literature, we document herein. The subsequent maintenance-related difficulties which arose are reported because of their relevance to researchers wishing to study captive individuals of this and related species.

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**MATERIAL, METHODS AND RESULTS**

*Habitat use*

*Capture Site:* A single field collection was made via dip net on 11 April 1991 from a boxed spring (Spring No. 1) on the property of Ozark Fisheries, Inc. of Camden County, near Camdenton in central Missouri (SW 1/4, NE 1/4, SW 1/4, Sect. 25, T37N, R15W). Individuals had not been seen here previously, but an adjacent spring (Spring No. 2) ca. 150 m north has continuously yielded sightings of southern cavefish for decades (Smith, 1980; D.E. Figg, Endangered Species Coordinator, Missouri Department of Conservation, pers. comm.). There is no evidence to suggest that fish from Spring No. 1 constitute other than a naturally-occurring population. Only three specimens were removed from the site, leaving others behind. The sizes of two of the collected individuals were 0.98 g/47 mm Total Length and 3.2 g/66 mm TL, respectively. The third fish was similar in size to the larger of the other two, but was not measured directly because after collection it contracted a severe fungal infection (identified as *Saprolegnia*) and was submitted immediately post-mortem (20 April 1991) for necropsy/histopathology.

Spring No. 1 is fed diffusely (Fig. 1), with palpable groundwater discharging into the spring from at least five distinct substrate areas of clean, loosely-aggregated chert gravel (3-5 cm diameter) having large interstitial spaces. In contrast, non-discharge areas were overlain by a heavy layer of readily-suspended silt. The spring outflow was estimated at 0.35 m$^3$/s and measured 14.4°C during the collection. The spring’s volume was estimated at 45 m$^3$. The water chemistry of adjacent springs that presumably share this aquifer has been characterized by Smith (1980).

*Observations:* SCUBA gear was used during the three hours time spent submerged in Spring No. 1. Silt suspension allowed only 30 minutes of completely unobstructed observation, however. During the time below, 8 separate individuals spanning a size range of 40 to 65 mm estimated TL were censused. Within the water column, undisturbed individuals occupied positions close to the bottom (within 0.5 cm) at depths of 1.2 to 2.0 m below the water surface (1.7 to 2.5 m below grade). Individuals forayed higher into the water
Fig. 1 — Schematic diagram of side view (A) and top view (B) of Spring No. 1. Placement and orientation of cavefish is as seen at the initial opening of the spring access door.
column only when over silt substrate areas and when being followed by the observer.

With respect to the substrate, undisturbed individuals seldom strayed from the positions they held atop the mound of substrate immediately «downstream» from the central zone of groundwater discharge (Fig. 1). Our capture attempts prompted these individuals to orient to and move towards the various groundwater discharge areas, and to disappear into the substrate therein, subsequently entering and exiting the gravel interstices periodically. Fish movements between substrate patches involved exiting the substrate and traversing the interjacent silted areas (Fig. 1). Neither prey capture attempts by the fish nor prey organisms were observed over either the gravel or silt substrate areas.

**Gas bubble disease**

*Laboratory Holding Conditions:* The three field-caught individuals were relocated immediately to a holding facility at the U.S. Fish and Wildlife Service’s National Fisheries Contaminant Research Center (NFCRC) in Columbia, Missouri. Transport was accomplished by placing the specimens in a 90 l insulated picnic cooler half-filled with ca. 45 l of Spring No. 1 water. A snug-fitting layer of 3 cm thick styrofoam insulation set at the water’s surface prevented sloshing (see Bechler, 1983). Additional aeration was not supplied. All three specimens were briefly (1/2 hr) immersed in a 200 ppm formalin bath on arrival as a prophylactic measure (Piper et al., 1982:275). To this time, none of the specimens exhibited problems maintaining equilibrium or position within the water column.

Each fish was maintained in an individual 77 l aquarium (79 cm long × 32 cm wide × 30.5 cm deep) filled to 20 cm depth and 2/3 submerged in a darkened large-volume water table. Part-volumes (1.5 l) of the aquarium water were automatically replaced each quarter hour from a pressurized pipe. Water bath temperatures were maintained at 15°C by a cooling unit. The source for the aquarium replacement water was a 202 m deep on-site well, the flow from which is pumped atop a 12 m tower for aeration through a series of baffles and for subsequent distribution. The chemistry of the water has been well characterized (Hunn & Greer, 1991) and closely resembled that of the fish’s spring water (Smith, 1980). During the first two weeks of holding, none of the specimens exhibited problems
maintaining equilibrium or water column position. All three successfully made the transition to cultured, live food (Amphipoda: *Hyalella azteca*) provided in abundance.

**Disease Occurrence:** On the morning of the 16th day of holding (26 April 1991), we decided to enhance water circulation in the two remaining fish's aquaria by introducing a single air-stone delivering compressed atmospheric air. On checking the animals about 12 h later, the larger of the two was found floating upright at the surface, its dorsal surface protruding when at rest. This fish was bloated and its attempts at submergence were ineffective: depths of only ca. 2 cm were reached, but just for brief periods after much effort and vigorous but erratic swimming. Its bulging swim bladder, visible through the body wall, suggested overinflation. The aeration of both aquaria was halted immediately. Eight hours later, the affected individual had partially recovered. After 16 more hours, it had reassumed the appearance and behavior it displayed preceding this occurrence. The individual remains alive to this day.

The well water supplying the fish's aquaria routinely carries dissolved nitrogen at levels between 100 and 105% saturation at 18°C, occasionally rising to 110-115% when water temperatures are increased to 25°C (I.E. Greer, NFCRC, pers. comm.). Greer also reports that dissolved oxygen levels averaged 8.0 mg/l over the period 1982-1987, an 82% saturation level at 15°C determined using methods described in Colt (1984: 37) and APHA (1989: 4-155) and correcting for the NFCRC's benchmarked altitude (252 m above sea level). On repeating the events described above (*sans* fish) on 29 May 1991, similar levels of supplementary aeration raised measured dissolved oxygen concentrations from 8.2 to 9.3 mg/l at 15°C water temperature and that day's 980 mbar median air pressure (climatological data and conversions provided by NOAA/NWS Columbia Airport station; station altitude 273 m above sea level). This change represented an increase in oxygen saturation from 84% to 95%. Other gases were not measured. When gas measuring equipment became available (21 January 1993), the dissolved gas saturation of the influent water measured 106.2% nitrogen, 83.1% oxygen, and 101.3% total gas pressure (Weiss saturometer, Eco-Enterprises, Model ES-3; Yellow Springs Instruments, Model 54ARC).
DISCUSSION

Habitat use

Our observations that undisturbed southern cavefish seldom strayed far from zones of substrate that both have large interstitial spaces and that discharge groundwater indicates that such features may be important elements of appropriate southern cavefish habitat. That disturbed individuals sought these areas directly suggests that shelter is one benefit they might provide. A variety of authors, including Eigenmann (1909: 72,73) and Bechler (1980), record Typhlichthys sheltering below rocks, and Bechler (pers. comm. in Brown & Willis, 1984) makes mention of their ability to burrow in interstitial spaces.

The fish's orientation and movement directly towards the groundwater discharge zones indicates that the southern cavefish in this population may be positively rheotactic, as was observed by Poulson (1960, 1963), Bechler (per. comm. in Brown & Willis, 1984), and has been seen in related cavefish species (Layne & Thompson, 1952; Poulson, 1963; Weise, 1957). This response may serve to guide individuals towards the shelter of the vesicular substrates commonly associated with discharge areas. Likewise, the occupation of positions low in the water column, also observed in Typhlichthys by Eigenmann (1909: 80), Poulson (1963), and Armstrong & Williams (1971), may aid in maintaining their proximity to substrate shelter.

Because we observed neither prey nor prey capture attempts, we could not ascertain whether a relationship between habitat use and prey availability existed. However, vesicular substrates may harbor more, more accessible, or choicer food organisms, the fish's rheotactic responses maintaining their spatial association with such productive foraging areas. Foraging at the substrate has been observed in Typhlichthys by Poulson (1960). Foraging by the related cavefish Amblyopsis rosae also occurs at and within the substrate (Poulson 1960), and time spent foraging by A. spelaea within the substrate is related to forage availability (Mohr & Poulson, 1966).

It is interesting that southern cavefish had not been previously reported from Spring No. 1, despite its long history of use. Given the proximity of the historical population in nearby Spring No 2, the invasion of Spring No. 1 via subterranean dispersal seems a likely scenario (see Poulson, 1960; Woods & Inger, 1957). Movements of a simi-
lar distance have been recorded for normally epigean species (Nelson & Paetz, 1974) under similar circumstances.

The observation of only post-juvenile-sized individuals in Spring No. 1 suggests (1) that they represent older individuals that have exited a larger population more extensively distributed below ground, (2) that outflows had removed young from the system, (3) that the young present were simply hiding or too small to be noticed, or (4) that young previously produced there had been prompted to move elsewhere. Adults in Typhlichthys populations do tend to dominate the population structure (Poulson, 1963). Furthermore, one would anticipate a population of emigrants from a larger population to be composed mainly of adults (Poulson, 1960, 1963). Nonetheless, young should have been observable had they been present given the time of year the sampling occurred (Poulson, 1963). The reason for their absence remains uncertain, and further monitoring of the structure and dynamics of this population seems warranted.

Gas bubble disease

Diagnosis and Causation: As in many cases of suspected gas bubble disease, we were alerted to the problem post facto by the symptoms the stricken individual exhibited (Bouck et al., 1980; Marking, 1987). Our decision to ultimately endorse this diagnosis is based on the following.

First, the onset and termination of symptoms occurred with the addition and then withdrawal of supplementary aeration, respectively. While the rarity of these organisms prevented us from attempting to repeat the occurrence, gas bubble disease has been induced in a similar fashion in tank-held channel catfish (Ictalurus punctatus) (Bowser et al., 1983; Jones & Lewis, 1976). Recovery on immersion in equilibrated water has likewise been recorded (Crunkilton et al., 1980; Dawley et al., 1976; Schiewe, 1974).

Second, the dissolved nitrogen levels which characterize NFCRC well water are frequently in excess of saturation levels, a necessary and often sufficient condition for the development of gas bubble disease. Interestingly, the symptoms in the affected fish arose during a period of rapidly declining atmospheric pressure when saturation conditions may have been exacerbated. With the passage of a storm front, barometric pressures dipped to 968 mbars during the occurrence (26/27 April 1991), the lowest level they had
attained since the fish's capture (NOAA/NWS Columbia Airport station pressure). Alderdice & Jensen (1985) have suggested that changing weather conditions may influence the onset of gas bubble disease symptoms.

Third, although the levels of supersaturation involved were probably not excessive, the occurrences of gas bubble disease at relatively low supersaturation levels is known (Bouck, 1980; Colt, 1986; Cornacchia & Colt, 1984; Harvey & Cooper, 1962; Jensen et al., 1985; Shrimpton et al., 1990b; Weitkamp & Katz, 1980). Nitrogen is typically the offending gas in situations involving the extraction of water from deep well sources (Harvey, 1975; Matsue et al., 1953; Satomi, 1955; Weitkamp & Katz, 1980). The aeration tower at the NFCRC does reduce the water's nitrogen content. However, in similar aeration towers, aeration commonly increases oxygenation levels and the nitrogen excess is not totally reduced (D'Aoust, 1989; Machado et al., 1987), potentially aggravating any incipient supersaturation problem. In addition, the positive buoyancy that affected fish exhibit forces them to respire the supersaturated water at the air-water interface (Johnson & Katavic, 1984; Kramer & Mehegan, 1981), which may complicate matters further (Alderdice & Jensen, 1985; Johnson & Katavic, 1984; Weitkamp & Katz, 1980).

Finally, symptoms consistent with those we observed (swim bladder hyperinflation, excessive buoyancy, difficulties swimming) have been reported for a number of other fishes where supersaturation of the medium occurred and a diagnosis of gas bubble disease was made (Alderdice & Jensen, 1985; Chamberlain et al., 1980; Cornacchia & Colt, 1984; Crunkilton et al., 1980; Dannevig & Dannevig, 1950; Egusa, 1959; Hauck, 1986; Henly, 1952; Jensen, 1988; Nash et al., 1977; Renfro, 1963; Rukavina & Varenika, 1956; Shrimpton et al., 1990 a,b; Stround et al., 1975). These symptoms are consistent with Fidler's (1984) «Type 1» or Alderdice & Jensen's (1985) «chronic» from of gas bubble disease/trauma (note: most of the literature cited herein does not distinguish between the potential forms).

**Alternative Diagnoses:** Another possible diagnosis fitting some of the observed symptoms is «swimbladder stress syndrome», attributable to a stress-induced malfunction of the swimbladder (Bagarinao & Kungvankij, 1986; Clary & Clary, 1978; Johnson & Katavic, 1984; Kolbeinshavn & Wallace, 1985). Elevated stress levels might
have resulted from treating the affected fish for a *Saprolegnia* infection during the three days preceding this occurrence, the treatment involving immersion for 20 minutes in a separate 3 ppm potassium permanganate solution each day. Given the fish's rapid recovery on the cessation of aeration, and the elevated nitrogen saturation levels typifying the NFCRC water source, a stress-related diagnosis seems less appropriate.

We also discount the suggestion that the affected fish was exhibiting decompression-related effects, some of which resemble the symptoms of gas bubble disease (Bishai, 1961; Feathers & Knable, 1983; Tsvetkov et al., 1972). Such a diagnosis would not be consistent with the fish's collection from a shallow spring, or with the development of symptoms more than two weeks thereafter, since the effects of decompression typically manifest themselves more rapidly. We are familiar with the symptoms of decompression in southern cavefish, these having been observed in two specimens brought by divers to the surface from depths of 13 and 18 m respectively during a 30 June 1991 collection at another Missouri site. These effects were consistent with the descriptions of decompression-related difficulties encountered by other species (Bishai, 1961; Feathers & Knable, 1983; Hauck, 1986; Tsvetkov et al., 1972). One of these cavefish did not survive the trauma and succumbed on 4 July 1991. The other individual recovered, however, and remains alive to the present.

**Implications:** No previous report of cavefish exhibiting gas bubble disease could be found in the literature, despite others having maintained wild-caught individuals in captivity (Poulson, 1960, 1963), some using aerated well water (e.g. Bechler, 1983). Cavefish may be particularly susceptible to this problem, given that selection for tolerance of fluctuating saturation levels should be weak in the relatively constant conditions that typify groundwater and/or cave system (Brown & Willis, 1984). The relatively shallow water depths these fish occur at in nature probably reduce the $\Delta P_{\text{Uncomp}}$ (Colt, 1986) these fish experience to levels less than zero, suggesting that their exposure to supersaturated conditions would be rare in any event.

In addition, *T. subterraneus* possesses a large swim bladder (Putnam, 1875) and is a physoclistous species (Regan, 1929), the adults lacking a pneumatic duct joining the swim bladder and the gastro-intestinal tract which would help vent gas accumulations.
This may also render them more susceptible to the effects of decompression (Bishai, 1961). In the related spring cavefish (Chologaster agassizii), individuals exhibited preferences for oxygenation levels in excess of a particular threshold, but did not discriminate between levels above that threshold (Hill, 1966, 1968). A similar lack of discrimination may prevent Typhlichthys from avoiding supersaturated conditions when they arise. Finally, that it was the larger cavefish specimen that developed gas bubble disease is consistent with other findings regarding the susceptibility of larger individuals within other species (Alderdice & Jensen, 1985; Dawley et al., 1976; Marsh & Gorham, 1905; Meekin & Allen, 1974; Rucker, 1975; Shirahata, 1966). Because the southern cavefish is a species at risk, and thus a candidate for captive maintenance and/or artificial propagation, future culture personnel need to be aware of this susceptibility to gas bubble disease.

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REFERENCES


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