

# The spiny devil katydids, *Panacanthus* Walker (Orthoptera: Tettigoniidae): an evolutionary study of acoustic behaviour and morphological traits

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**Abstract.** A cladistic analysis and systematic revision of the genus *Panacanthus* accompanies the description of three new species, with calling songs reported for four species. The evolutionary origin of spines is considered as a defensive mechanism in *Panacanthus*; both morphological and behavioural (i.e. acoustic) traits allow inferences about relationships. Phylogenetic analysis produced one most parsimonious cladogram eighty-two steps long, with the ensemble consistency index = 0.84. *Panacanthus cuspidatus* and *P. pallicornis* (formerly *Storniza* Walker 1869, *Martinezia* Bolivar 1881) are properly incorporated in *Panacanthus*. On morphology, *Panacanthus* is more related to the Neotropical *Copiphora* and *Lirometopum* than to the Old World *Lesina*. Character analysis reveals that in *Panacanthus* the ancestral condition of calling song resonance (the production of musical sounds) has given rise to a more nonresonant (transient) stridulation. A correlation between the production of more complex sound waves and spinous protection of the body (especially the pronotum) is noted. Because early workers grouped *Panacanthus* with other spiny genera, based on pronotal morphology, we present a critique of the evolutionary and ecological implications of the development of defensive spines in this genus. This approach may be applied to other taxa using a similar protective mechanism. We advise against arrangement of the pronotal, cephalic and femoral armature as a homologous characteristic across subfamilies. Several pronotal processes and modifications evolved independently in other genera of Conocephalinae, Hetrodinae, Pseudophyllinae and Phaneropterinae. The pronotal structure of *Panacanthus* is unique and may be taken as a synapomorphic characteristic of all its species and as an autapomorphic feature of the genus.

## Introduction

Resembling creatures summoned from science fiction, Neotropical katydids of the genus *Panacanthus* exhibit an astonishing appearance: robust spines, some branching, adorn their head, pronotum and legs (Gurney, 1976). References to the species occur in the context of morphological and behavioural defensive adaptations (Belwood, 1990;

Hogue, 1993; Nickle & Castner, 1995; Castner, 2000). An older taxonomic literature addressing this genus (Walker, 1869; Redtenbacher, 1891; Karny, 1912) has been supplemented by recent reports of undescribed species in Colombia (Montealegre-Z., 1996, 1997).

Five species of *Panacanthus* are currently recorded in the literature: *P. cuspidatus* (Bolivar), *P. pallicornis* Walker, *P. tuberculatus* Redtenbacher, *P. spinosus* Redtenbacher and *P. varius* Walker. Using the pronotal structure and the presence or absence of prosternal spines, Walker (1869) erected two genera: *Panacanthus* and *Storniza*. He indicated great similarity between these taxa, but emphasized differences in the construction of the prothorax: *Panacanthus*

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with a strongly spinose pronotum and unarmed prosternum, *Storniza* with a 'granulate' pronotum and bispinose prosternum. The type specimen of each genus, *P. varius* (from Ecuador) and *Storniza pallicornis* (from Colombia) is a single male and a nymphal female, respectively.

Bolivar (1881), apparently unaware of Walker's earlier publication, established the genus *Martinezia* on a single species, *M. cuspidata*, from Ecuador, described from an immature female, distinguished by a 'granulate' pronotum. Redtenbacher (1891) grouped *Martinezia* and *Storniza* under *Panacanthus*, and described two more species, *P. tuberculatus* (from Colombia) and *P. spinosus* (from Panama). He listed four species: *P. varius* Walker, *P. (Martinezia) cuspidatus* Bolivar, and his two new species, but failed to mention *P. pallicornis*. Karny (1912) followed Redtenbacher's classification but included all five described species. Here we add three new species, and synonymize *P. tuberculatus* under *P. pallicornis*, thereby increasing the number of species to seven (see Results).

Detailed diagnoses of *Panacanthus* were provided by Redtenbacher (1891) and Karny (1912) and they grouped *Panacanthus*, *Rhynchocerus* Karsch 1896 and *Lesina* Walker 1869 (= *Eumegalodon* Brogniart) on the basis of the possession of pronotal spines (see definitions below). Although *Panacanthus* is readily separable from these genera using Redtenbacher's and Karny's descriptions, the descriptions present problems if using the presence or absent of pronotal spines to attribute monophyly to the several taxa.

Special pronotal processes have been noted within a variety of Old and New World katydids, but were not used satisfactorily by the earlier taxonomists. For that reason, we venture here a comparative study of the morphological variation and taxonomic relationship of pronotal spines in Old and New World katydids, and assess whether the pronotal spines of *Panacanthus* and *Lesina* are homologous.

#### *Behavioural characters*

Morphology can be a reliable source of information for reconstructing phylogenies (Sanderson & Donoghue, 1989) and the use of behavioural traits in phylogenetic analysis surveys has become common (McLennan *et al.*, 1988; Wenzel, 1992). But, as behaviours are not easily observed and coded into character states, most people conducting systematic analyses prefer not to use them (see Wenzel's 1992 arguments on this topic). The phylogeny of any taxa may help to understand the evolved behaviour of individuals and other associated traits. In the present paper, our behavioural characters are physical measures of the sounds produced by stridulation.

#### *Stridulation in phylogenetic reconstruction*

Stridulation (sound production by friction; Ewing, 1989) is a common feature of animals with an exoskeleton. It usually involves moving a ridge (scraper) situated on one body region to and fro along a line of cuticular teeth (file)

located on another: the resulting shocks give energy to adjacent sound-radiating surfaces. Tegminotegminal stridulation is a synapomorphy for Gryllidae and Tettigoniidae (Gwynne, 1995). A transversely running vein on one forewing is modified as a file and engaged by an upturned region (scraper) on the anal edge of the other wing; modified wing cells serve as radiators.

This mechanism generates sounds in two basic ways, designated by Elsner & Popov (1978) as resonant and non-resonant. The former involves the production of sound pulses that are sinusoidal, musical, approximating pure tones and with narrow-peaked (high-Q) spectra; the latter involves the production of complex-wave transient pulses, noisy, characterized by broad-band (low-Q) spectra (Montealegre-Z. & Morris, 1999; Morris, 1999). (Q is an index of the central tendency of a spectral peak; Ewing, 1989).

Cricket calling songs appear to be universally pure tones (Alexander, 1956; Leroy, 1966; Otte, 1992), i.e. the product of resonant sound generation. Resonance generation in crickets is largely understood through experimental studies of mole crickets (Bennet-Clark, 1987, 1989, 1999) and field crickets of the genus *Gryllus* (Elliot & Koch, 1985; Koch *et al.*, 1988; Stephen & Hartley, 1995; Prestwich *et al.*, 2000). Koch and his coworkers describe a clockwork model, in which the advance of the plectrum from tooth to tooth down the file is gated by the simple harmonic oscillation of the cell radiators, a harp in each forewing. A relationship of 1:1 between the tooth contact rate and the generated sine wave is maintained.

Based upon observed broad-band spectral output, non-resonant mechanisms occur commonly in Tettigoniidae, e.g. Phaneropterinae (Heller, 1988). However, among Pseudophyllinae, many spectra indicate resonant mechanisms, and these range to much higher dominant carrier frequencies than observed among crickets (Morris & Beier, 1982; Morris *et al.*, 1989, 1994; Montealegre-Z. & Morris, 1999).

Orthopteran calling song evokes species-specific pairing responses, consistent with a role in premating isolation (e.g. Walker, 1957; Morris *et al.*, 1978). Song features, for example, pulse repetition rate, functioning in this way will separate species taxonomically. Although such acoustical features are distinct from each other intraspecifically, they may contain phylogenetic information. Acoustic (vibrational) signals in other insects have been a source of characteristics for successful diagnosing of a group of species (e.g. Neuroptera, Henry *et al.*, 1999): Henry found models of characters that did not vary and characters that showed informative variation congruent with the phylogenetic hypothesis for the group.

Most studies of stridulatory mechanisms in Tettigoniidae have concerned single, unrelated species (Broughton, 1964; Morris & Pipher, 1967, 1972; Bailey, 1970, Bailey & Broughton, 1970), but others involve complete lineages or generic groups (see, e.g. Walker, 1975; Heller, 1990; Naskrecki, 2000b). From these works it is apparent that the mechanics of stridulation (wing movement patterns, the physical behaviour of wing membranes that radiate the sounds, etc.), can provide phylogenetic information.

Regarding song evolution in *Panacanthus*, we are particularly interested in both mechanisms of sound production, resonant and nonresonant, which occur in species of this genus. We find that resonant generation is not inevitably a derived condition, as some species in the *Panacanthus* lineage have reverted to nonresonance.

#### *Combination of behavioural and morphological characters*

Whether behavioural and morphological characters should be combined is controversial (Donoghue *et al.*, 1995; Huelsenbeck *et al.*, 1996). Huelsenbeck *et al.* (1996) favoured examining the data using an incongruence length test to identify incongruencies between data partitions. However, this does not distinguish whether the incongruence is distributed over all of the partition or concentrated in a certain taxon or taxa (Kluge & Wolf, 1993).

De Queiroz & Wimberger (1993), who incorporated acoustic parameters of Anurans in their datasets, asked if behavioural data showed levels of homoplasy similar to those found in other types of data and found no evidence of consistent performance differences. We apply the total evidence criteria because such an approach provides a rigorous hypothesis in simultaneously considering character state distributions and is the best measure of the congruence of characteristics (Kluge & Wolf, 1993).

Here we use four behavioural attributes combined with thirty-five morphological traits, but many additional characters should become available as more acoustic information is discovered (experimentally) for some taxa (the actual number of taxa studied acoustically in any detail is six, including two of the outgroup).

## Methods

### *Fieldwork*

Colombian species of *Panacanthus* were collected in three field trips (1996, 1997, 2000). In the main areas of distribution in Colombia in the Departamentos Valle del Cauca (Bosque de Yotoco) and Nariño (RN La Planada), specimens were collected from understory vegetation at night along forest footpaths with the aid of headlamps. Occasional collection trips were made in 1998 and 1999 to forest belonging to the municipality of Bitaco, where we followed a long transect in the Simon Bolivar Road (see below).

### *Colombian locations*

*Bajo Anchicayá.* Situated on the extensive coastal plain between the eastern slope of the eastern cordillera and the Pacific Ocean. Chocó is a Departamento of Colombia, lying immediately north of Valle del Cauca. However, Chocó as a biogeographical region refers to Colombia's Pacific coastal rainforest, a forest extending from Ecuador to Panama.

Bajo Anchicayá is undisturbed tropical rainforest on the Pacific side of the Departamento del Valle del Cauca, within the municipality of Buenaventura (3°30'N, 76°50'W; 300–350 m elevation); reached via Simon Bolivar Road from Cali to the village of Buenaventura. Rainfall can exceed 7000 mm per year with peaks of precipitation in March to May and October to November. Several small communities, referred to here as Bajo Anchicayá, occur along the Simon Bolivar Road: vereda Bellavista and the vereda El Danubio.

*Reserva Forestal Bosque de Yotoco.* Forest preserve of subtropical wet forest (3°52'N, 76°23'W; 1400–1600 m elevation) on the eastern slope of the western cordillera in the Departamento Valle, 50 km north of Cali, near Buga, between the municipalities of Yotoco and Restrepo. The village Yotoco is the nearest settlement. Annual rainfall is 1000–2000 mm.

*Reserva Natural La Planada.* Very humid premontane (subandean) forest within the Departamento de Nariño (southwest Colombia) at approximately 1°12'N, 78°01'W. The closest town is Ricaute some 7 km away. The forest elevation here varies between 1200 and 2100 m and our fieldwork occurred at approximately 1780 m. The average temperature is 19 °C and rainfall regularly exceeds 5000 mm per year.

### *Ecuadorian locations*

*Mishaualli.* East of the Andes in the upper basin of the Amazon, 17 km east of Tena in the province of Napo, at the junction of the Rios Misahualli and Napo (1°2'S, 77°40'W; 400 m elevation) within lowland rainforest.

*Jaguar.* A hotel in Napo province is in mostly undisturbed lowland rainforest on the north bank of the Rio Napo, 2 h down river from Misahualli by canoe (0°59'S, 77°30'W, 300 m).

*Tinalandia.* A small private forest preserve in the province of Pichincha, southwest of Quito, 112 km from Via Santo Domingo de los Colorados; 16 km southeast of Santo Domingo (0°19'S, 79°3'W; ~600 m elevation). The vegetation is lowland rainforest, typical of the western slopes of the Andes, with faunal affinities extending into Colombia (e.g. Bajo Calima, see above).

### *Acoustic analysis*

Males of *Panacanthus* spp. were located by their loud calls. Females were collected in association with males or occasionally by searching understory vegetation with headlamps. Some specimens were recorded in the field with audio-limited equipment, others were transported to the University of Toronto where their songs were recorded

using equipment that permitted a wide assessment of the sound frequency range, from 1 to 100 kHz.

Audio range (1–20 kHz) field recordings were made with a Sony Walkman WM D6C Professional cassette tape recorder and ECM 909 microphone. Ambient air temperatures were taken using either an Omega HH23 digital thermometer or an alcohol thermometer. Full frequency range recordings in the laboratory employed Brüel & Kjær equipment: a 1/4" (4135) condenser microphone was connected to a sound level meter (2204). Each insect sang from an individual small cylindrical cage, pinned to a base of sound-absorbent material; the cage was constructed of aluminium screen (mesh size six per cm). The output from the sound level meter went to a Racal instrumentation tape recorder running at 30's<sup>-1</sup> or was digitized (Tucker Davis, System II) at a sampling rate of 180 kHz and stored to the hard disk of a computer. Digitized signals were low-pass filtered at 90 kHz to avoid aliasing. Subsequently, the signals were analysed with DADISP 4.1 software. Sound levels (re 20 µPa) were measured with the 2204 sound level meter (Fast or Impulse/Hold as indicated), usually at a distance of 10 cm between the microphone tip and the dorsum of the katydid singer. The long axis of the microphone was normal to the longitudinal axis of the insect with the microphone covered. Scanning electron micrographs were obtained using a Hitachi S-2500 microscope belonging to the Department of Zoology, University of Toronto. External structures were drawn by photographic microscopy and camera lucida; internal structures were determined by dissection.

#### *Depositories*

Academy of Natural Sciences of Philadelphia (ANSP); Natural History Museum, London (British Museum) (BNHM); Entomological Museum, Utah State University (EMUSU); Instituto Español de Entomología (IEE); Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (ICN); Museo de Entomología Universidad Nacional sede Medellín (MEUNM); Museo de Entomología Universidad Nacional sede Palmira (MEUNP); Museo de Entomología de la Universidad del Valle, Cali (MEUV); Museum of Zoology of the University of Michigan (MZUM); Naturhistorisches Museum, Wien (NMW).

### **Cladistic analysis**

#### *Character evolution*

The optimality criterion used here was that of maximum parsimony. The genera *Copiphora* (Serville 1831) and *Lirometopum* (Scudder 1875) were chosen as outgroups because they share with *Panacanthus* some synapomorphies involving the fastigium, male cercus; characteristics of the eyes and optic lobes (Appendix 1). However, although these two taxa are related to *Panacanthus*, it is possible that they are not its sister groups (see Discussion). *Lesina* Walker

1869 was also included because, by virtue of its pronotal armature, it has been regarded historically as related to *Panacanthus* (Redtenbacher, 1891; Karny, 1912). All characters were treated as nonadditive. Nine of the characters were uninformative (autapomorphic, Appendix 1), but some were useful in the diagnostic taxon presenting them. Unknown characters were coded as '?' and multistate taxa were coded as polymorphic. The data matrix is provided in Appendix 1.

All parsimony analyses were carried out using PAUP 4.0b2\* (Swofford, 1998). The small number of taxa allowed exhaustive searches to be carried out. The proportion of missing data was low, 3.5% in general (see Appendix 1). On some occasions, data were missing for certain acoustic characters of *Lesina* and *P. lacrimans*. This resulted in 16 and 19% missing characters for each taxon, respectively.

MACCLADE version 3.0 (Maddison & Maddison, 1992) was used to assemble data and to examine character evolution. Outgroup taxa were assigned (see above) and used for rooting. Nodal support was conducted by decay analysis (also called Bremer support) with PAUP.

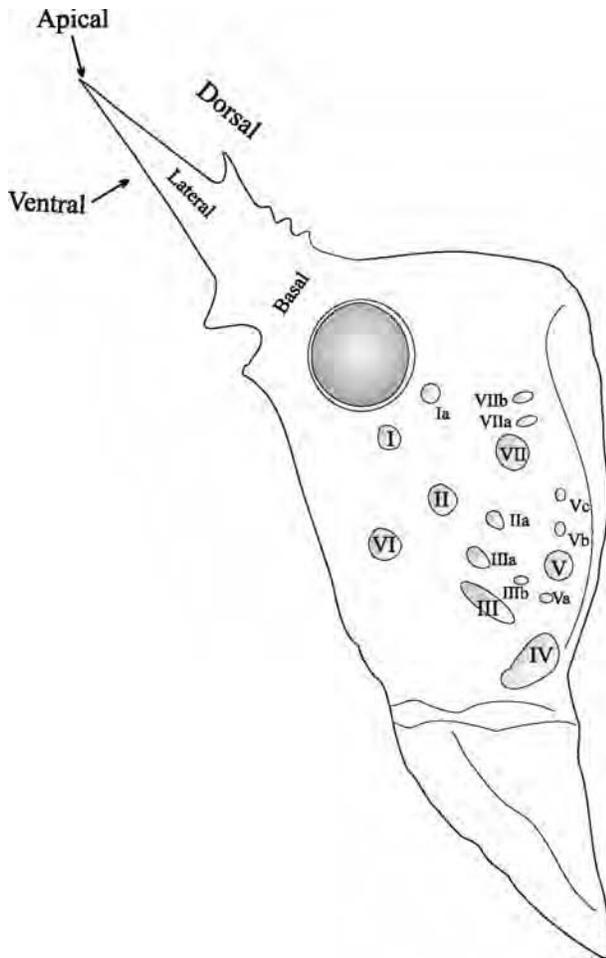
#### *Character explanation (optimization)*

The data matrix includes thirty-nine variable characters among *Panacanthus* spp. and the outgroups. Independence of the characters was assumed. However, independence was not always clear. For traits that were not applicable (i.e. not comparable because they do not exist in the outgroup), we used functional outgroup comparison to polarize the states. If a character was polymorphic but the phylogenetic analysis showed the common state to be ancestral and the other state autapomorphic, the taxon was scored as showing only the ancestral state. The phylogenetic importance of individual characters was assessed using their consistency index (ci) on the most parsimonious trees. 'Good' characters were arbitrarily defined as those with ci > 0.70. Analyses were run including and excluding behavioural traits to evaluate possible differences in topology, and as no differences were found, the discussion is based on the total evidence analysis. Acoustic characters were included in the final analysis and studied on the final tree to evaluate the likely evolutionary pathway of the mode of sound production (resonant vs nonresonant) used.

#### *Special characters*

Definitions and explanations of all characters used in this analysis are presented in Appendix 2. Here follows a short description of the more important.

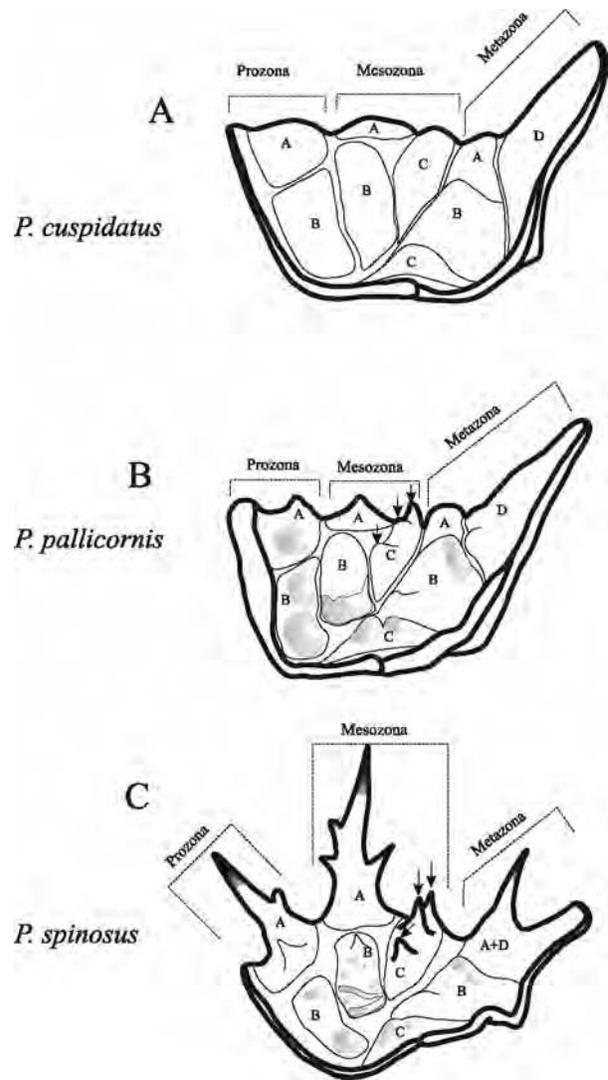
*Head.* Gena: we present a general map (model) of the distribution of tubercles and spines on the genal region (Fig. 1). The relative location of these projections is consistent across all species, and these structures range in size from very reduced tubercles in *P. intensus* to very robust spines in *P. cuspidatus*. The map of facial processes is based



**Fig. 1.** Proposed map of facial projections based upon *Panacanthus varius*. The main area of each tubercle is indicated with a Roman numeral and the largest tubercle in each area is suggested as the main one. Small tubercles surrounding a main tubercle are called subtubercles, indicated with the respective Roman numeral together with a letter in lowercase.

on *P. varius* because this species has the highest number of these of any known *Panacanthus* spp. We indicate the area for each tubercle with a Roman numeral and name the largest tubercle in each area as the main one; its closest (but smaller) tubercle is termed a subtubercle and is indicated with the respective Roman numeral with a letter in lower case. The proposed distribution map is arbitrary and is presented to facilitate the description of facial process distribution. Tubercles termed longitudinal are single, basally elongate, projections that seem not to be the fusion of two or more processes.

**Thorax.** Pronotum: one can achieve a clear allocation of taxa on the basis of the pronotal structure, but in the absence of an existing description of this body region, we propose the following model (Fig. 2). In this genus, two transverse sulci, one anterior and one posterior, always



**Fig. 2.** Standard model of the pronotum of *Panacanthus* spp., showing the main areas and their modifications. A, The simplest pronotal structure, *P. cuspidatus*; B, the tubercular state, *P. pallicornis*; C, the basic pattern for species with pronotal thorns, *P. spinosus*. Arrows indicate the development of tubercles in area C (mesozona).

divide the pronotal disk into three main regions: prozona, mesozona, metazona. The anterior transverse sulcus continues anteroventrad on to the lateral lobe. All *Panacanthus* species have these regions, but in this lineage they have been modified in a sequential way. Each pronotal area is indicated with a letter code: the prozona is subdivided into two (A, B), the mesozona into three (A, B, C) and the metazona into four areas (A–D) (Fig. 2).

Three main states occur in the pronotal structure: smooth, tubercular and spinose. In descriptions in this paper the number of processes is indicated for only one side of the pronotum (i.e. due to their bilateral symmetry) (Fig. 2). Tubercles are small blunt projections on the

pronotal surface. They are conspicuous in *P. pallicornis* (Fig. 2B) but reduced and/or modified in other species of the genus. There are no tubercles on the pronotum of *P. cuspidatus*: the areas where they might occur are swollen but the surface is smooth. Tubercles appear in all areas of *P. pallicornis*. They are modified as spines in all other species (see the Discussion for evidence of homology in those structures). Callosities are thick swollen lumps (irregular in shape) produced perhaps by the fusion of two or more tubercles. They are indicated in the pronotal map in area B of both the meso- and metazona (Fig. 2B). The term *process* embraces tubercles, callosities and spines.

It is easy to find primary homology among the smooth regions represented in Fig. 2A and those presented in the other species (Fig. 2B, C). The condition in Fig. 2A is also presented by two outgroup genera (*Copiphora* and *Lirometopum*), and we therefore have evidence to polarize this character by outgroup comparison. However, the pronotal structure of the other outgroup member (*Lesina*) has no particular applicable characteristic at this transformation series, although topographical correspondence of the spines in *Lesina* spp. is presented in area A of the prozona and the metazona. We define this state as 'rack'. Therefore, several options are available: option 1: assume all pronotal regions as one character and code no spines as (0), tubercles as (1), branched spines as (2), smooth spines as (3) and the presence of a 'racklike structure' as a separate state (4), then run the analysis with this character unordered. Option 2: code each area of the pronotum (see Fig. 2) as an independent character with states: smooth (0), tuberculate (1), and spinose (2). Such areas are recognizable in the genus *Lesina*. Therefore, the character will be coded as (4) for that taxon; this analysis has to be run as unordered. Option 3: use the state 'rack' as a separate character; this will immediately produce an uninformative autapomorphy for *Lesina*. Comparing the first two options, we based our analysis on option 1 because option 2 implies that each pronotal area is an independent trait.

We compared the pronotal structure of *Panacanthus* with that of other species having pronotal processes. The presence of pronotal processes was confirmed in twenty-two genera of Pseudophyllinae, four genera of Conocephalinae, four genera of Hetrodinae and four genera of Phaneropterinae (see Discussion). For some of these genera, additional information is taken from the literature.

### Measurements

The following conventions for length measurement are used: body, apex of fastigium to last abdominal tergite (ovipositor not included in females); fastigium, basal ventral tooth to apex; pronotum, in dorsal view, midline from anterior to posterior margin; legs, measurements of the femora exclude the coxa and trochanter, those of the tibia exclude the tarsi; ovipositor, apex of subgenital plate to apex of ovipositor.

Attributes of the stridulatory file are described as if the left forewing was laterally extended, putting the file parallel to the body axis.

### Behavioural characters

The determination of plesiomorphic and apomorphic behavioural characters used the genera *Lirometopum* and *Copiphora* as outgroups. Both genera are closely related to *Panacanthus* (Naskrecki, 2000b). However, it is unclear whether either of them is its sister group. We used acoustic characters for both *Copiphora* and *Lirometopum*. *Copiphora* is a genus with twenty-four described species (Naskrecki, 2000a) for which the song of seven is known: *C. cultricornis*, *C. hastata*, *C. brevicauda*, *C. rhinoceros*, *C. brevirostris*, *C. cf. gracilis* (Morris, 1980; Belwood & Morris, 1987; Morris *et al.*, 1994; Naskrecki, 2000a; Morris & Montealegre-Z., unpublished). We have no information for the remaining twelve species, but the morphology of their stridulatory organ is very similar to the species mentioned above (i.e. the stridulatory structures of the species whose song is unknown are similar to those whose song has previously been reported). Therefore, we suppose the production of sinusoidal pulses (pure tones) to be a highly conservative characteristic in *Copiphora*. *Lirometopum* is a small genus with only two described species; the song of one, *L. coronatum*, is known and it is a pure tone (Naskrecki, 2000a; Naskrecki, pers. comm.). For the genus *Lesina* there is no acoustic behavioural information. Therefore, we code them as '?'. However, due to the size of the species, their armature (see Discussion), stridulatory file morphology and observations by other scientists (K.-G. Heller, University of Erlangen-Nürnberg, pers. comm.), it is quite probable that species of this genus use nonresonant stridulation.

The acoustic characters (characters 36–38) are qualitative; two of them were binary. The kind of sound production mechanism used (character 36) is a complex trait with two types: the production of pure-tone song and broadband song. Both mechanisms seem to have evolved independently several times in Tettigoniidae. We coded the condition of pure-tone singing as (0) because it is present in *Copiphora* and *Lirometopum* and this coding agrees with the topology obtained excluding behavioural traits. For character 37 (pulse infrastructure), infrastructure is present in pulses of *P. gibbosus* and *P. intensus* and, according to their file morphology, the species *P. spinosus* and *P. varius* should present the same condition; but this character is not present in the most basal species (*P. cuspidatus* and *P. pallicornis*). Therefore, this character was coded upon the basis of a tree constructed with only morphological traits (assigning (0) when absent or (1) when present). Character 38 was coded in the same way.

Rearing of the anterior half of the body with lateral extension of the forelegs (Cohn, 1965; Kaltenbach, 1990; Castner, 2000) is called a 'deimatic reaction' (character 39) by Maldonado (1970). This display, which may give the impression of increased size, is observed in several

orthopteroid taxa, including twenty-one species of Peruvian rainforest katydids (Nickle & Castner, 1995). We used it as a character (character 39), but as the feature occurs widely among some higher-category orthopteroids, it will probably result in a number of homoplasies. In the present analysis, we confined it to a lower categorization, including only species and related genera. The behaviour occurs in two forms: type I involves only the lateral extension of the forelimbs, whereas in type II, leg extension occurs together with a rearing of the forepart of the body. We coded this character as (0) if absent, (1) if present as type I and (2) if present as type II.

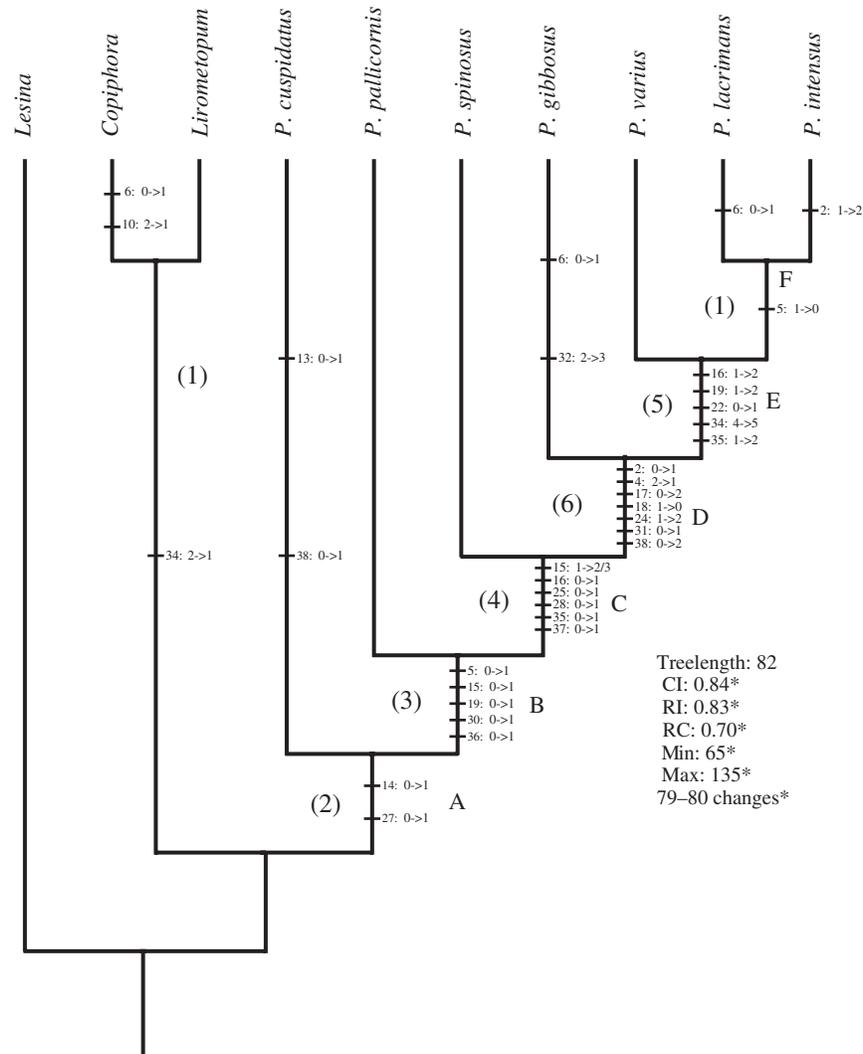
## Results

### Cladistic analysis

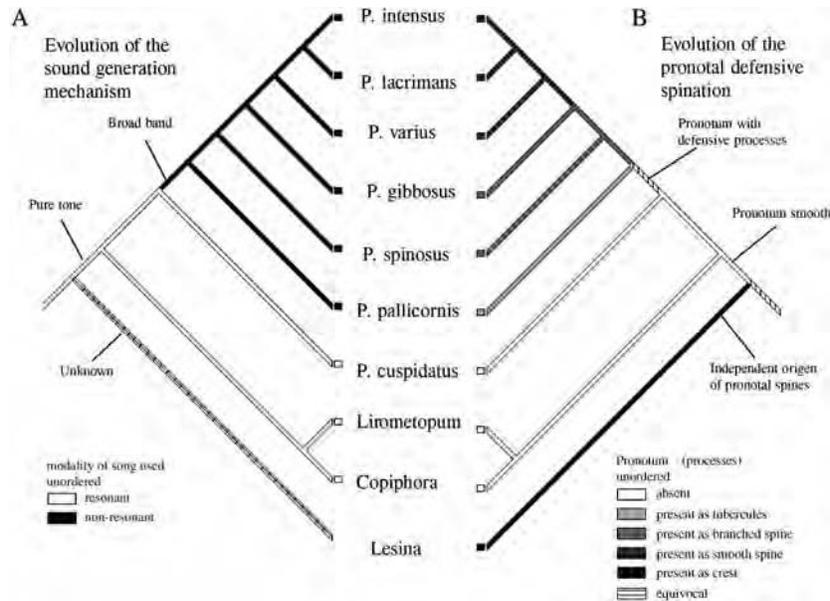
*Characters and character states.* Analysis of the dataset including all taxa resulted in a single most parsimonious

tree (Fig. 3). On this tree (eighty-two steps long, ensemble consistency index (CI) = 0.84), *Copiphora* and *Lirometopum* each appear as a monophyletic group, related to *Panacanthus* by the following characteristics: fastigium acuminate and elongate, gena tuberculate, optic lobes of the brain modified, eyes strongly protruding, mandibular molar area conspicuously developed, anal margin of wings pigmented, and male genitalia (cerci and titillators) modified.

The results show that there is no internal division constrained by characters that divides the ingroup into independent monophyletic groups. Therefore, the tree does not show a separate monophyly of *P. pallicornis* and *P. cuspidatus* (initially described, respectively, as *Storniza* Walker 1869 and *Martinesia* Bolivar 1881), although they are the most basal taxa on the tree and the two are closely related. A single tree (length = 44 steps, CI = 0.91) resulted when *Lesina*, *Copiphora* and *Lirometopum* were excluded from the analysis and *P. cuspidatus* and *P. pallicornis* chosen as



**Fig. 3.** Phylogeny of the genus *Panacanthus* (single most parsimonious tree) obtained with thirty-five morphological and four behavioural characters.



**Fig. 4.** Parsimonious evolutionary scenarios. A, Sound-generating mechanism; B, pronotal armature in *Panacanthus* (using MACCLADE). Note that the type of song is unknown for species of the genus *Lesina*.

functional outgroups. This cladogram is identical to that shown in Fig. 3 (in which *Lesina*, *Copiphora* and *Lirometopum* were excluded); the ingroup does not include any internal clade. Similarly, when characters 15 and 36 were excluded from the analysis, one tree resulted in each case. This exclusion had no effect on the tree topology shown in Fig. 3, showing seventy-five steps and  $CI = 0.84$  (when excluding character 15) and seventy-three steps and  $CI = 0.83$  (when excluding character 36).

Nodal support, as measured by the decay index (DI), is very high for nodes A–E (Fig. 3). The number of equally parsimonious cladograms increases very quickly with each additional step. The monophyly of the genus collapses after two additional steps. Nodes C–F show persistence after three additional steps; but the largest node supported by relatively high DI values (node D) includes four terminal taxa which are definitely similar in several respects (the most obvious is the cryptic coloration). The three terminal taxa (the lowland–Pacific species *P. varius*, *P. intensus* and *P. lacrimans*) at node E are also strongly supported. This clade, which collapses with five additional steps, includes very similar species but they are separable by facial colour pattern (not included in the data matrix) and the structure of the female's subgenital plate. Other characters will also serve for this: for example, the detailed composition of the male cerci (not included in the data matrix). Using *ci* as reference, thirty phylogenetically important characters ( $ci \geq 0.7$ ) were found. Twenty-nine characters presented maximal *ci* ( $ci = 1.0$ , see Appendix 2).

**Character evolution.** To address whether the pronotal spines are homologous and whether resonant generation is apomorphic or plesiomorphic, it is necessary to study the

evolution of characters 15 and 36, respectively (see Appendices 1 and 2). Evolutionary study of character 15 shows that spines in *Panacanthus* are part of a transformation series in which the plesiomorphic condition is smooth, with tuberculated and spinose apomorphic. Conversely, the pronotal armature in *Lesina* evolved independently. Analysis of character 36 shows that the condition of resonance in *Panacanthus* is plesiomorphic to broad-band sounds (Fig. 4A).

This study is consistent with a possible correlation (at least in *Panacanthus*) between the mechanism of sound production (resonant vs nonresonant) and the development of body armature, especially on the pronotum. There is no armature on the pronotal area when the mechanism of sound production used is resonant, but when the mechanism used is nonresonant, pronotal defensive spines appear (Fig. 4).

#### Taxonomy

This survey revealed three new species. We redescribe the genus, based on relevant characters. Most taxa were originally described based on one sex, and the previously unknown sex is now included for all of them; measurements for all specimens are summarized in Table 1.

#### *Panacanthus walker*

*Panacanthus* Walker, 1869: 332; Redtenbacher, 1891: 328, 334; Kirby, 1906: 229; Karny, 1912: 8  
*Martinezia* Bolivar, 1881: 494; Bolivar, 1884: 82; Kirby, 1906: 229; Karny, 1912: 8

Table 1. Measurements (in mm) of some morphological structures of *Panacanthus* species.

Structure	<i>P. cuspidatus</i>			<i>P. pallicornis</i>			<i>P. gibbosus</i>			<i>P. varius</i>			<i>P. lacrymans</i>			<i>P. intensus</i>			
	Male	Female	n = 1	Male	Female	n = 1	Male	Female	n = 1	Male	Female	n = 1	Male	Female	n = 1	Male	Female	n = 1	
Body	57	69.1	68–70.4	42.5	38–45.6	43.7	43.5–44	39.7	46.7	29.2	27.6–30.6	30.9	29.8–32.3	42.2	44.8	43.1	54.6	56.7	54–60
Fastigium	5.7	6.5	6.2–6.6	5.7	5.3–6.2	6.4	6.3–6.4	6.6	6.8	5.1	4.7–5.3	5.4	5–5.8	4.0	5.0	4.6	4.6	5.0	4.5–5.2
Pronotum	12	12.6	12.3–13	10.4	10.1–10.6	9.4	9.4–9.5	13.0	12.9	9.8	9.5–10.5	7.9	7.6–8.2	9.9	10.4	10.8	11.8	12.3	12–12.7
Tegmen	35	45.0	44.3–46	25.4	23.2–27.9	24.0	24–24.7	20.6	13.9	13.5	12.5–14.4	7.2	6.9–7.5	26.0	27.8	27.6	35.5	38.1	36–39
F-femur	16	18.7	18–19.3	11.3	10.8–11.7	13.1	13–13.2	13.2	15.1	9.6	8.8–10.9	10.6	9.7–11.3	12.0	13.4	14.3	14.0	15.1	15–15.5
M-femur	12	15.8	15.5–16	8.9	8.2–9.4	11.0	10.9–11	12.3	13.3	9.0	8.2–9.6	9.9	9–10.4	12.0	13.5	13.5	14.3	14.6	13.3–16
H-femur	22	27.8	26.5–28.8	16.2	15.6–17.3	19.9	19.9–20	20.9	25.1	18.2	17.6–19	20.1	18–21.2	22.6	25.2	26.7	26.9	28.8	27–31
F-tibia	18	22.6	22–23.7	13.8	12.5–14.8	16.0	16–16.1	15.9	17.5	11.3	10.8–11.5	11.9	11.2–13.1	14.4	16.5	15.9	16.3	18.1	17–19
M-tibia	15	19.1	18.6–19.5	10.6	10.1–11.9	12.9	12.9–13	14.2	15.8	10.0	8.7–10.7	11.8	11–12.7	13.3	13.2	15.1	15.3	17.2	16.5–18.2
H-tibia	24	31.7	30.8–33.1	18.2	17.8–19.2	22.4	22.5–22.5	24.5	28.0	19.6	18.3–20.5	22.2	19.4–23.4	25.0	29.8	28.9	29.7	30.6	29–32
S-plate	5.4	4.4	4–4.6	3.2	3.2–3.3	3.6	3.5–3.7	3.9	3.3	2.1	2–2.2	2.3	2.3–2.4	4.3	3.7	3.1	5.8	5.2	5.1–5.2
Cercus	3.6	–	–	2.7	2.5–2.9	–	–	2.4	2.4	–	–	–	–	2.8	–	–	4.0	–	–
Ovipositor	–	51.1	50–52.3	–	–	39.8	38.6–41	–	42.1	–	–	29.6	28–32.1	–	58.3	47.0	–	63.7	60–66

F, fore; M, mid; H, hind; S, suggestinal plate.

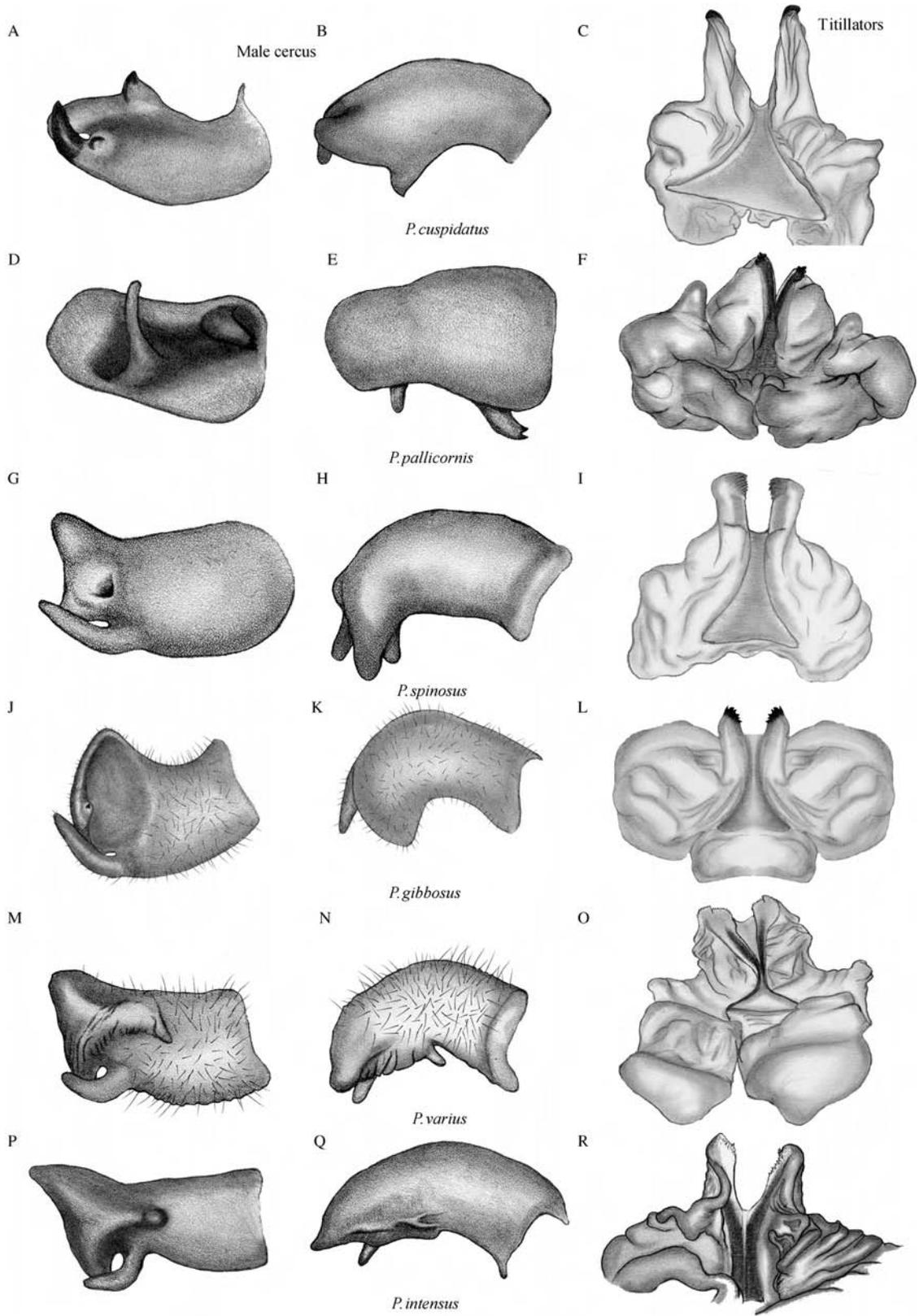
*Storniza* Walker, 1869: 333; Kirby, 1906: 229; Karny, 1912: 8  
Type species: *Panacanthus varius* Walker, 1869 (by monotypy).

**Diagnosis (based on synapomorphic traits).** Fastigium elongate, acuminate, dorsally bispinose (character 3). Areas A of prozona and mesozona, C of mesozona, D of metazona, varying through smooth, tuberculate and spinose (Fig. 2, character 15). Mandibles with apical tooth conspicuously developed (character 12). Fore tibia dorsally strongly armed with stiff spines (character 27). Posterior ventral angle of lateral lobes of pronotum markedly upturned, leaving prothoracic spiracle partially exposed in lateral view (Fig. 2, character 14). Sclerotized part of titillators bent, divergent apically, denticulate (Fig. 5, character 33). Type II deimatic defensive display (lateral extension of forelegs without exposing ventral abdomen).

**Redescription. Head:** Eyes strongly protruding. Fastigium noticeably elongate (Table 1), directed forward, acuminate bifurcate, medially with 2 spines projecting anterodorsally (character 3), with ventral tooth remote from frontal fastigium. Gena either with some tubercles or conspicuously spinose. Vertex bears 2 rows of small tubercles (moderately directed forward) which extend to fastigium; distal pair of these protuberances wholly developed as spines (character 3). **Thorax:** Pronotal zones clearly subdivided. Spines, if present, in area A of both prozona and mesozona and area D of metazona (Fig. 2). Anterior pronotal margin moderately rounded, its posterior rounded or truncate. Humeral sinus poorly defined. Hind ventral angle abruptly upcurved, leaving prothoracic spiracle partially exposed in lateral view. Prosternum may be bispinose; these processes may be reduced to prominent flat, stalklike tubercles or be elongate, acicular. Armature of sternites varies from triangular lobes at metasternum to spinous processes at mesosternum. **Legs:** Fore- and midlegs nodulate. All femora usually dorsally armed; only posterior femur of *P. cuspidatus* unarmed. **Abdomen:** Cercus of male thick, with apical ventral tooth directed inwards, usually with a dorsal tooth downcurved inward (Fig. 5). Titillator bears medially a slot, reinforced by sclerotized cuticle; dorsally divergent apically and denticulate (Fig. 5). Male subgenital plate with short style, medio-apically incised; this incision varies from minutely to broadly U-shaped (Fig. 6). Female subgenital plate wide, distally biacuminate, ovipositor long, and moderately slightly upcurved mediolaterally, ending in 2 elongate sharp projections (Fig. 6).

### *Panacanthus cuspidatus* (Bolivar) (Figs 2A, 5A–C, 6A–C, 7A–C, 8A, 9)

*Martinezia cuspidata* Bolivar, 1881: 489, holotype ♂ (lost), Ecuador: Baeza? (IEE).



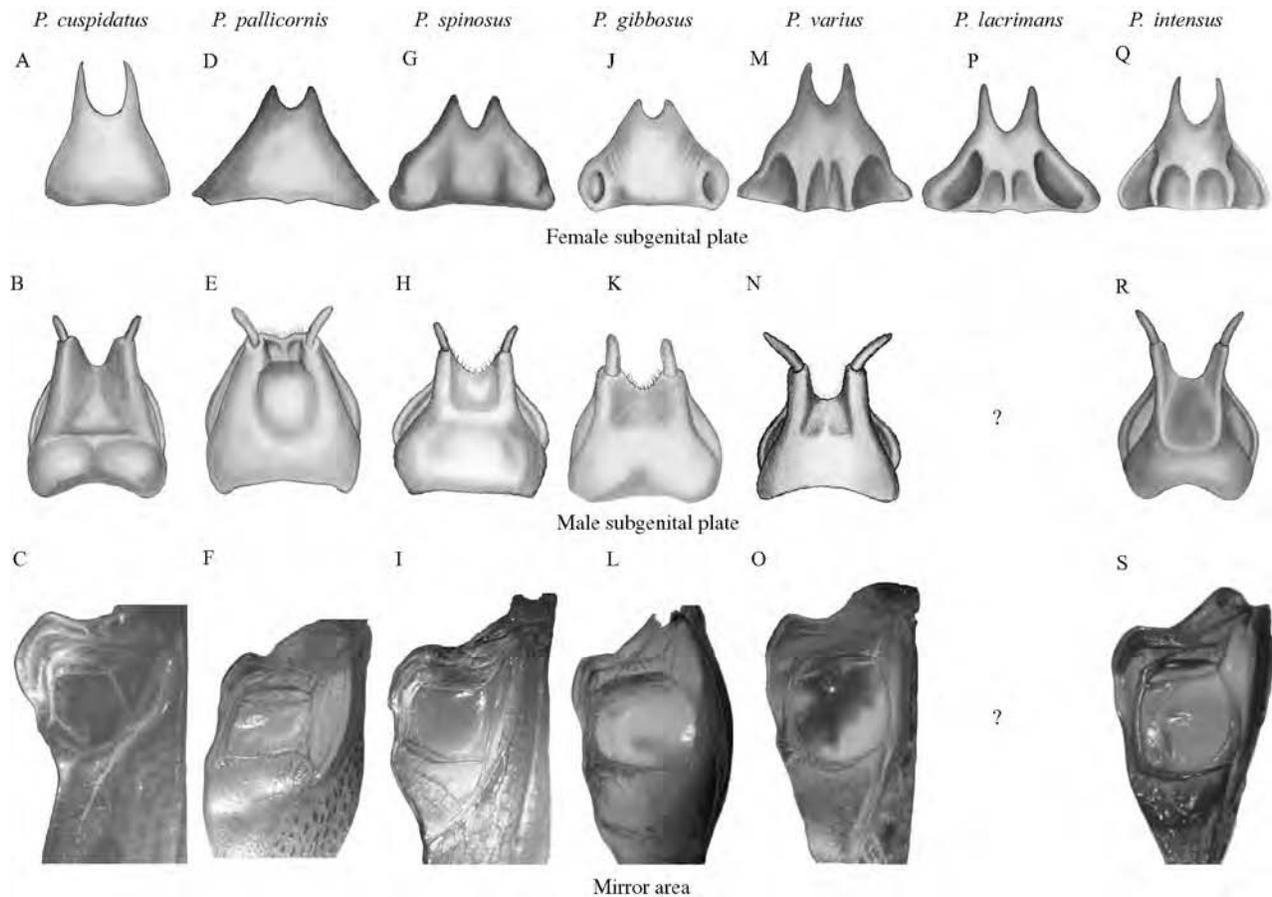
**Fig. 5.** Male genitalia. First column, left cercus, left internal view; second column, right dorsal view; third column, titillators, posterior view.

*Panacanthus cuspidatus* Redtenbacher, 1891: 336; Gigliot-  
Tos, 1898: 85; Kirby, 1906: 229; Karny, 1912: 9

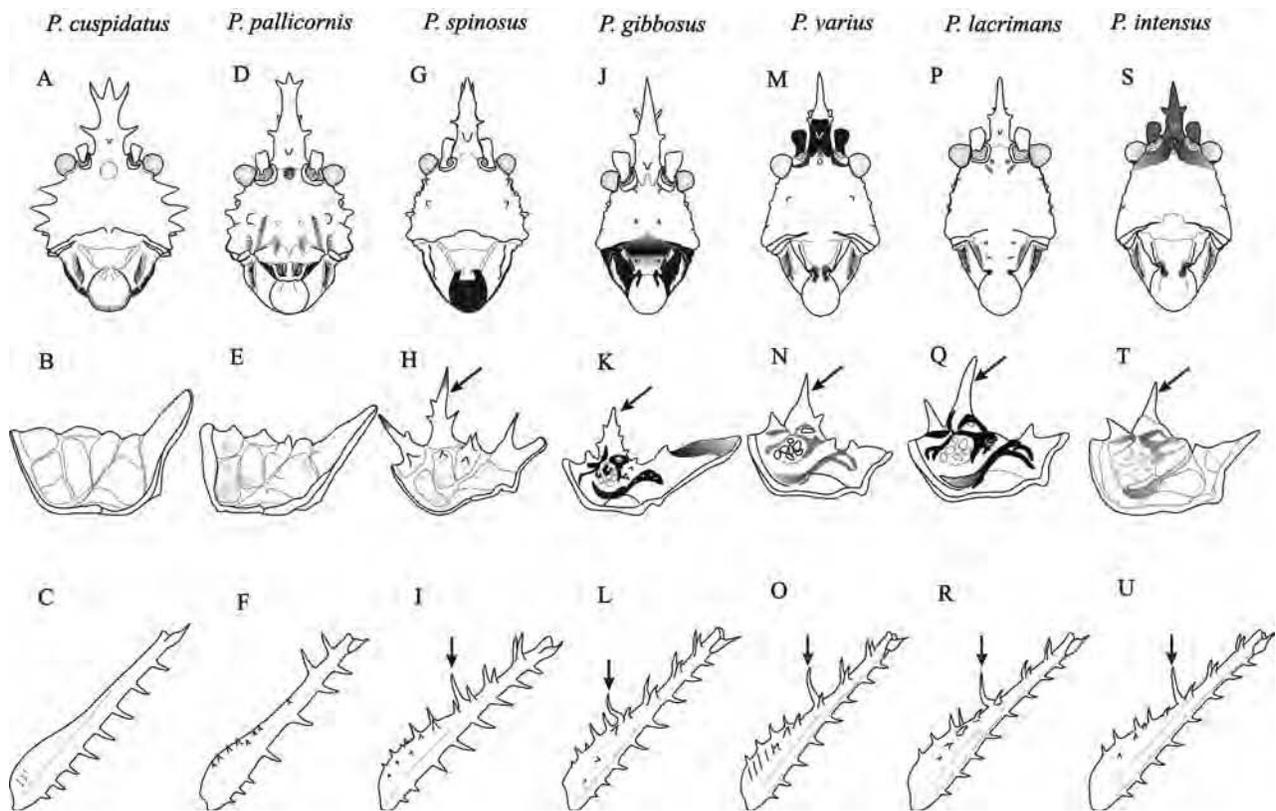
**Diagnosis.** Fastigium aduncate, with 2 dorsal elongate spines orientated cephalad; in frontal view appearing as a crown (Fig. 7A). Infra-ocular region with 3 triangular projections strongly developed. Frontal ocellus yellow, orbicular, large, almost same diameter as compound eye. Pronotum smooth, shining, with superficial elevations. Anal margin of tegmina straight, forming straight angle with costal.

**Redescription. Male.** Size large for genus (Table 1), form robust (Fig. 8A). **Head:** Fastigium long, declinate, its dorsal spines long, directed forward dorsally; dorsal teeth of basal row noticeably developed. Regions I, II and III of the genae strongly produced in triangular spines; regions IV and V similarly developed but shorter (Fig. 7). Frontal ocellus orbicular, flat, very conspicuous, about same diameter as eye. Frons flat, surface almost smooth, only inconspicuous wrinkles occur. **Thorax:** Pronotum surface smooth. Pro-

meso- and metazona clearly subdivided in smaller areas (Fig. 2A), without tubercles, granules or rugosities. Area 4 of metazona abruptly elevated distally. Pro- and mesosternum each armed with 2 conspicuous spines. **Legs:** Fore tibia dorsal spines aduncate, strongly developed. Posterior femur dorsally unarmed, its basal dorsal surface roughened (Fig. 7). **Wings:** Tegmen wholly formed, covering entire abdomen. Costal field wide, costal vein prominent, curved posteriorad and short (10 mm). Sc and R almost parallel, only diverging on distal third. Rs originates beyond midpoint of tegmina, forking on distal fifth, reaching posterior angle formed by anal and costal fields. Ma parallel to R and Sc a short distance to beyond its bifurcation; both branches reach anal margin. Cu1 fused to Mp. Stridulatory field broadly transverse, in dorsal view only extending to basal portion of tegmen. Stridulatory vein transverse, elongate (6.2 mm), straight, of 312 teeth, almost equally spaced. Anal margin of tegmina straight, forming right angle with distally rounded costal margin (Fig. 8A). **Abdomen:** Subgenital plate trapezoidal, with small divergent styli, medio-apically incised U-shaped



**Fig. 6.** Upper row, female subgenital plates; middle row, male subgenital plates; lower row, stridulatory area or mirror. '?' indicates that the character is unknown.



**Fig. 7.** Cephalic, pronotal and femoral differentiation of *Panacanthus* spp. Arrows show the main spine on either the pronotum or the femur.

(Fig. 6B). Cercus with 2 conspicuous spines, 1 short, originating on dorsal margin, curved inward, another, longer on ventral margin mostly black. Cercus ends apically in irregular downcurved lobe. Cercus in lateral aspect moderately upcurved (Fig. 5A).

Female. *Wings*: C, Sc and R as in male. Rs bifurcated in middle of its run. In most females Cu1 not fusing to Mp: only near, touches Mp slightly, then diverges a short distance, afterward disappearing. Cu2 and A1 run parallel transversely to anal margin; A2 bifurcates first branch somewhat curved anteriorad, more distant from A1 than A1 is from Cu2. Abdomen: Subgenital plate long, widely incised medio-apically, U-shaped, ending in 2 elongate acute projections (Fig. 6A). Ovipositor large, apically pointed, conspicuously curved dorsally in middle, making dorsal valve wider than ventral in lateral view.

*Colour*. General coloration oeruginous (bright green). Fastigium (distal half), eyes, clypeus, labrum and mandibles flavescent. Labrum flavotestaceous distad; mandibles atrous on inner margin. Spines on anterior tibia flavescent, apically atropurpureous. Tarsal segments aurantius (orange).

*Material examined*. ECUADOR: 2 ♀, Provincia Napo. Jaguar, Río Napo, 14 July 1989 (G. K. Morris); 1 ♀, same locality as preceding, 13 April 1989 (G. K. Morris); 1 ♀,

Misahualli, 18 February 1988 (G. K. Morris); 1 ♂, same locality as preceding, 14 July 1985 (G. K. Morris); 1 ♀ (nymph), Pastaza, Santa Cecilia 76°58'W, 0°2'N, on Río Aguarico, 24–27 July 1966 (C. R. Patrick) (MZUM).

*Distribution* (see Fig. 10). This species is apparently widespread in the upper basin of the Amazon River, in Ecuador, Peru and Brazil. In Ecuador it is abundant in the Oriente, along the Río Napo and well known to local human inhabitants as 'caballito'. In Peru it has been reported close to Iquitos; in Brazil the only known record is that of the type locality 'Espíritu Santo'. No record exists for Colombia, but it should also be present in the Amazonian region of that country abutting Ecuador. The stated type locality (Baeza, Ecuador) is in error, and probably represents the access route of the collector to the Amazon lowlands of Ecuador. No specimens of *P. cuspidatus* were detected at Baeza (by GKM), during many visits to that montane location. On the basis of their conspicuous audible song they could not remain undetected if present.

*Remarks*. Redtenbacher (1891) stated incorrectly in his key that the pronotum of *P. cuspidatus* is granular. He used 'tubercles' in referring to both *P. pallicornis* and *P. cuspidatus*. Tubercles (conical processes) are only present on the pronotum of *P. pallicornis*. In one of the examined females, the Rs vein is not forked; in another, Cu1 forks with one of

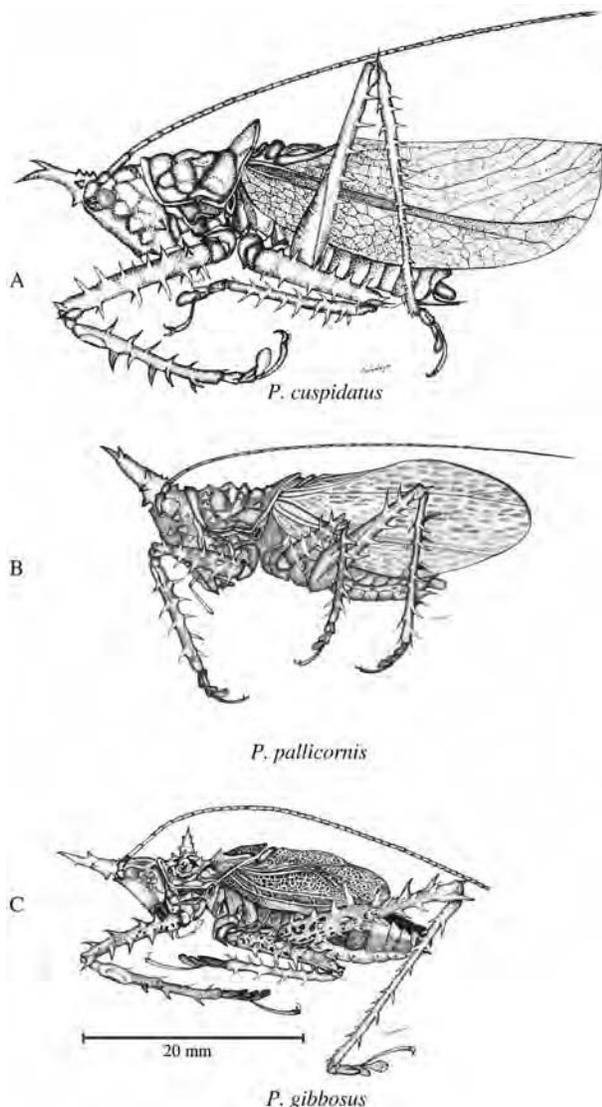


Fig. 8. Habitus of the male of some *Panacanthus* spp.

its branches then joining to Mp, the other following the normal direction of this vein as in other examined females.

**Song description.** The song structure given here is based on the analysis of a single male, collected in December 1985 at Misahualli, Ecuador, recorded later in Canada with ultrasonic-capable equipment. From another audio-limited field tape recording of a male (not shown), we obtained some additional measures (e.g. carrier frequency and call period). *Panacanthus cuspidatus* calls were very common in December 1985 in the early night, arising high in the forest canopy beside the Rio Napo.

To the human ear, each call is a pair of short whistle-like notes: musical, each note lasting <1 s and lacking any infra-structure. Notes commonly occurred paired in the field, two given about 0.1 s apart (note period ~0.1 s). Calls occur in

groups, two to five calls per group with a call period of about 1.5 s; there is a variable group interval of approximately one call each 17 s. Laboratory recordings at 20.7 °C show each note as a sustained 25 ms pulse with an extremely gradual amplitude increment from onset, becoming stable over the final third (Fig. 11A, B). This pulse at its maximum amplitude is composed of evenly sustained complex waves, each with a cusp or subcrest, a pattern indicative of two subequal harmonics (see below).

A slight but consistent upward frequency modulation occurred in this specimen: each pulse began just below 10 kHz and finished at about 12 kHz. The field male singing at 21.8 °C had its major peak between 10.2 and 10.3 kHz. Therefore, we consider this species' principal carrier as about 11 kHz (Fig. 12A). Harmonics, a very strong second with diminishing third and fourth, are readily apparent. The second harmonic, being within 10 dB of the fundamental, may prove of biological importance in reception.

Often tettigoniid specimens brought back alive from the tropics live for a remarkably long time in captivity: this male specimen lived more than 8 months beyond its first laboratory song recording date of 9 August.

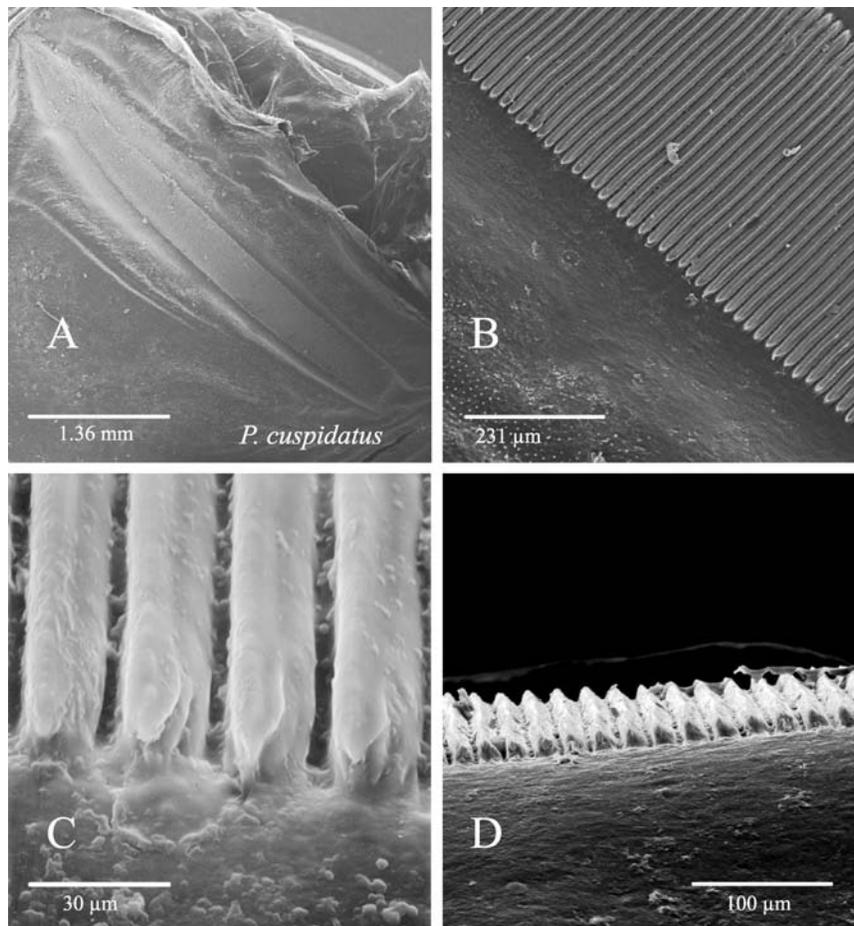
***Panacanthus pallicornis* (Walker) (Figs 2B, 5D–F, 6D–F, 7D–F, 8B, 13E, 14)**

*Storniza pallicornis* Walker, 1869: 334, holotype ♀ nymph), Colombia: Bogota (BNHM) (not seen).

*Panacanthus tuberculatus* Redtenbacher, 1891: 335; Kirby, 1906: 230; Karny, 1912: 9.

**Diagnosis.** Fastigium of vertex produced (Table 1, Fig. 7D). Eyes pink-red in life. Pronotum arrayed with tubercles (Fig. 2B). Hind femur bears 2 dorsal spines distally (Fig. 7F). Cercus apically globose, ventrally sulcate, long process arising distally near lateral margin, projecting mesad; a shorter acuminate process originates basally near internal margin and extends curving hindward (Fig. 5D, E).

**Redescription.** Male. Size moderate for genus, form rather robust. **Head:** Fastigium elongate (Table 1), moderately medially upcurved, apically moderately downcurved (Fig. 7D). Dorsal spines of fastigium short, directed anteriorly and near apex. Tubercles on regions I–V of genae conspicuous; tubercular development of 2 more regions (VI, VII) observed in this species. Regions II and V conspicuously developed as conic spines, the remaining armature only blunt tubercles (Fig. 7D). Mandibles massive, without any special characteristic. **Thorax:** Pronotum (Fig. 2B) with areas of pro-, meso-, metazona modified in tubercles or callosities. Prozona: area A of prozona with 2 tubercles, 1 dorsal, 1 ventral, the former larger; area B with 2 same-size tubercles, 1 dorsal, the other ventral. Mesozona: area A bears 1 tubercle; area B 3 protuberances, 2 tubercles dorsal and a callosity ventrad. Metazona: area A bears laterally an elongate tubercle similar to a callosity; area B with big rounded tubercle in dorsal part;



**Fig. 9.** *Panacanthus cuspidatus* file. A, The complete file; B, detail of the middle portion; C, a close view of the teeth; D, profile of the file looking basad.

area C bears a tubercle anteriorly, immediately followed by a longitudinal callosity; area D bears 1 tubercle on antero-lateral corner, rear part of this area extends far hindward, almost reaching the stridulatory vein, posterior margin rounded. *Wings*: Stridulatory file elongate (~6.6 mm), with approximately 248 teeth, noticeably curved posteriorly; teeth moderately bent on left side (Fig. 14C). Stridulatory field extensive, occupying middle portion of tegmen length. Costal margin conspicuously narrowing on distal half, costal field narrow, costal vein weak, inconspicuous. Sc and R parallel their entire course, both conspicuously swollen in basal half; Rs originates in distal third. M strong, Mp originates from last part of M as strong branch becoming weaker after fusing to Cu1. Cu1 curves towards anal margin, curves again towards costal margin suffusing with Mp. Hindwings small, atrophied, transparent. Texture of tegmina in life soft, not coriaceous. *Abdomen*: Tenth tergite ends in 2 rounded angles, mediolaterally widely roundly incised. Cercus (Fig. 5D, E) short, cylindrical, bearing 2 mesal processes, the more distad, fingerlike, ending bluntly, directed dorsad; the proximal strongly recurved basad, ending in 2 tiny black apical teeth. Subgenital plate simple, wide, almost square, with short styli, medio-apically narrowly roundly incised (Fig. 6).

*Female*. Metazona of pronotum shorter than in male; not produced hindward. *Wings*: Sc and R as described for male. Ma bifurcates on distal third; Mp originates in basal fifth, fuses with Cu1 at almost 3 mm from origin; both veins reach anal margin together in posterior fifth. Veins A1 and A2 diffuse, not very conspicuous. *Abdomen*: Ovipositor long (Fig. 13E, Table 1), stout, dorsally moderately convex, ventrally rather straight. Subgenital plate subtriangulate, ending in 2 divergent acute points; medio-apically incised rounded (Fig. 6D).

*Colour*. General coloration oeruginous (bright green). Eyes rubescent (becoming red). Clypeus and mandibles flavescens. Labrum fulvid. Inner margin and apex of mandibles atrous. Anal margin of tegmina rubescent; in males such colour confined to distal portion of stridulatory field. Tarsal segments aurantius (orange).

*Material examined*. COLOMBIA: 1 ♂, Antioquia, Alejandria, July 1979 (V. Ramírez) (MEUNM); 1 ♀, Antioquia, Guatapé, March 1993 (S. Arroyabe) (MEUNM); 1 ♂, Santander, Santander de Charalá, margins of Río Orbita, at 3.5 km from Cañaverales, 29 November 1979 (I. de Arevalo) (ICN); 4 ♂, 1 ♀, Valle del Cauca; Yotoco

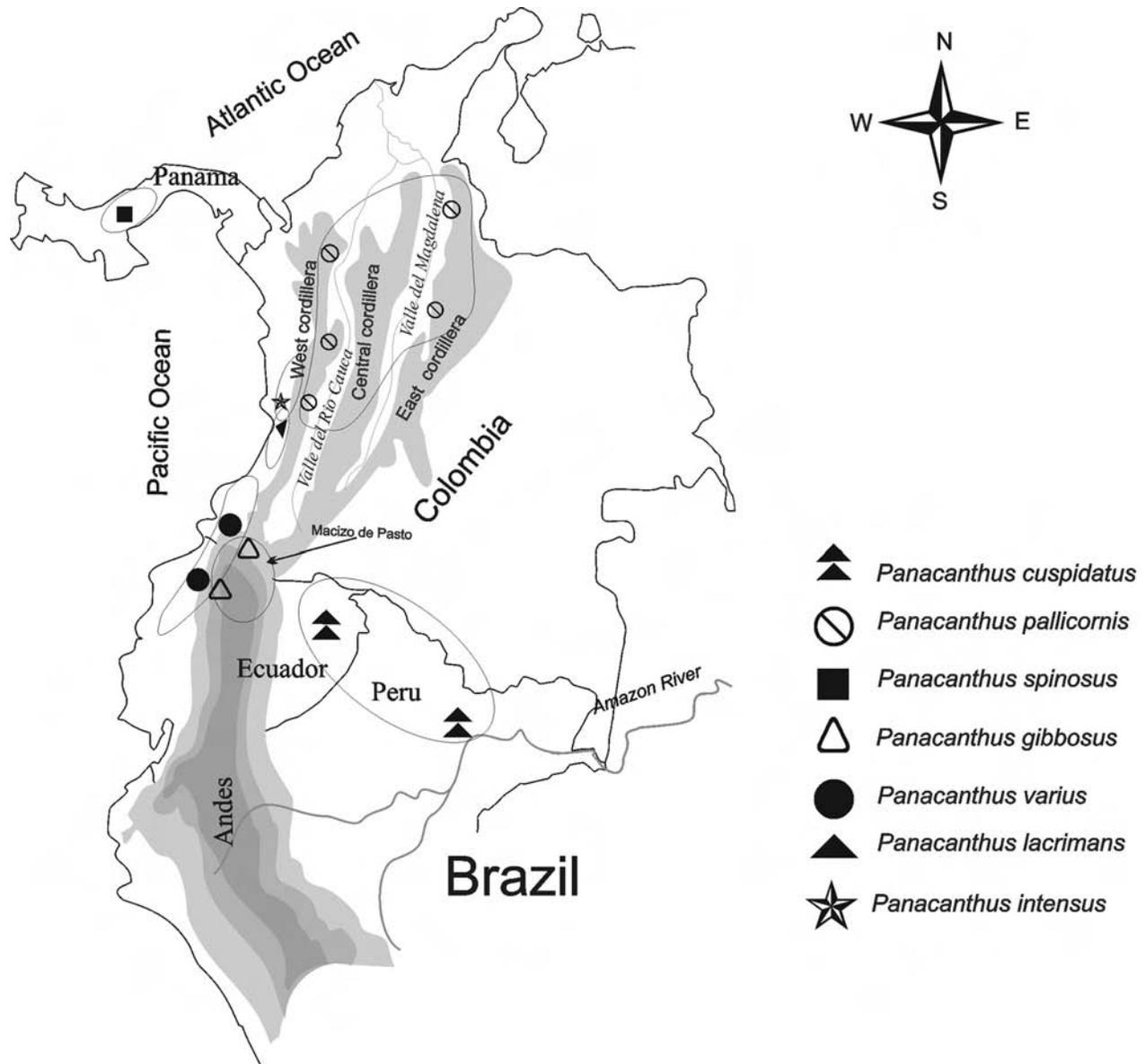


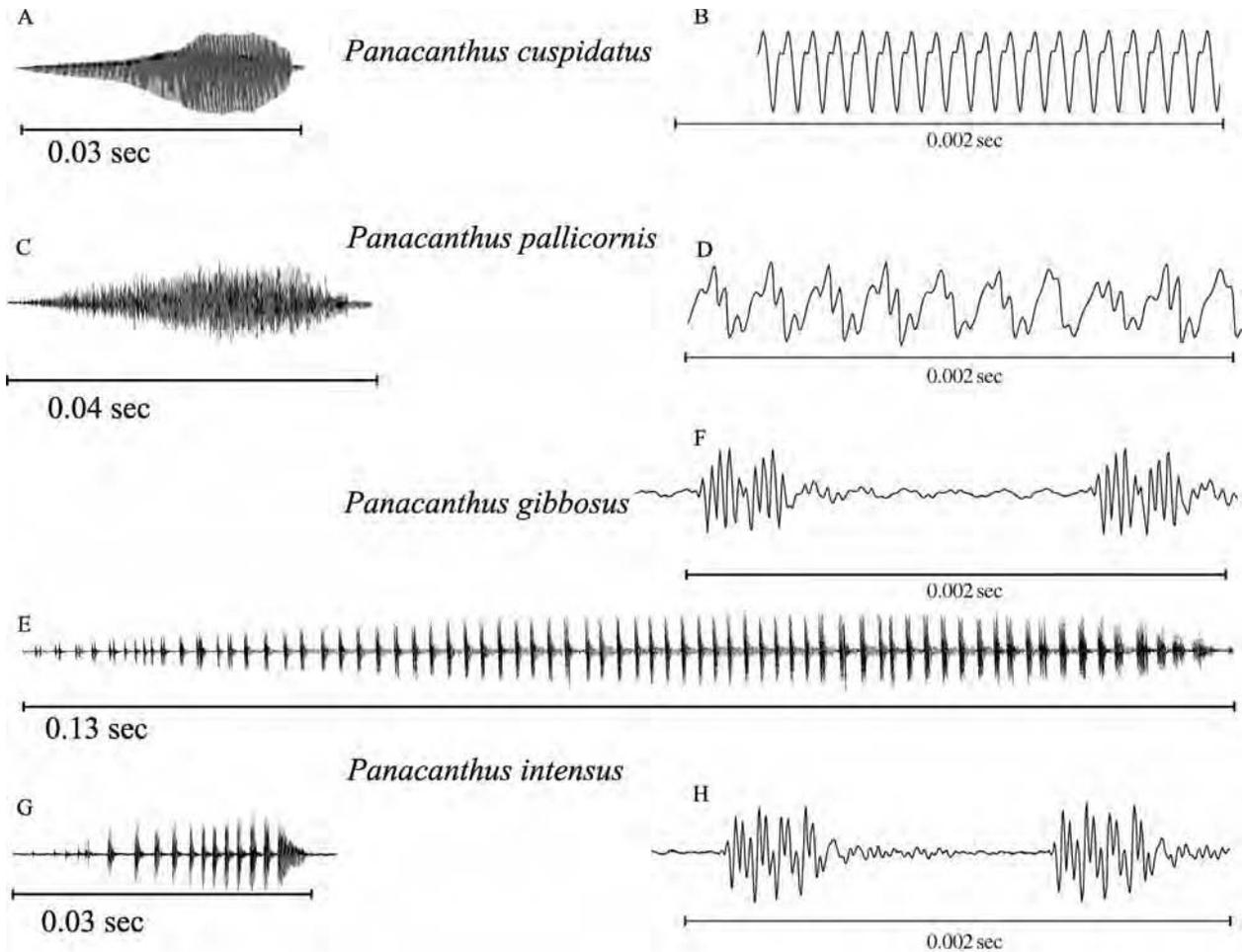
Fig. 10. Distribution of *Panacanthus* spp. in Central and South America.

(Reserva Natural de Yotoco), 1600 m, 10 April 1996 (Morris & Montealegre) (ICN, MEUV); 2 ♂, as preceding (MEUV); 1 ♀, as preceding, 13 April 1996 (F. Vargas) (MEUV); 1 ♂, as preceding, October 1996 (P. Chacón) (MEUV); 1 ♂, Valle del Cauca, Restrepo 1700 m, 29 October 1996 (MEUV). 1 ♂, 1 ♀ (no data) (MEUNP). 3 ♂, Chocó, Alto del Río San Juan, 4 September 1969 (Wolff) (USU); 1 ♀, Boyaca, Muzo, August 1915 (A. Maria) (ANSP).

**Distribution (Fig. 10).** This species is endemic to Colombia. In the Departamento del Valle del Cauca, it is reported from several locations on the east slope of the western cordillera, especially Bosque de Yotoco, in the neighbourhood of the

municipalities of Pavas and Bitaco. Because it is also reported for the Departamentos of Chocó and Antioquia on the same slope, its distribution must embrace the greater portion of the west cordillera (east slope). It has also been reported for some localities on the east cordillera: in the Departamento de Santander, for example, it is distributed along the Río Oibita.

**Remarks.** This species is widely distributed in Colombia. Walker (1869) described *Storniza pallicornis* after an immature female collected in or near Bogotá. We conclude that the species described by Redtenbacher as *P. tuberculatus* is the same species described some years before by Walker (1869), and synonymize them under *P. pallicornis*, which has priority.



**Fig. 11.** Song of *Panacanthus* spp. A, C, E, G, Phonatome; B, D, F, H, portion of the phonatome showing the waveform.

We did not access the holotype of *P. tuberculatus*, and have relied upon photographs in the Orthoptera database (Naskrecki & Otte, 1999). There is little variation between populations in male external genitalia, especially the cercus. The main variations noted are in size: individuals collected in Valle del Cauca ( $n = 16$ ) are all larger than those from Chocó ( $n = 4$ ).

**Song description.** The calling song of this species is remarkable for a very low audio principal carrier frequency (Fig. 12). Ten specimens were recorded in the field at 18 °C and their mean dominant peak, per single-note spectra, was 5.0 kHz (standard error = 0.6 kHz, range 4.6–6.1 kHz). High energy audio this low is unusual in tettigoniids (Heller, 1995) but is known for a few Neotropical species (i.e. *Choeroparnops*; Morris *et al.*, 1994). It puts the most intense peak of the insect's carrier near our best human sensitivity and so makes the species seem very loud to human listeners. At 24 °C, the call of ten males measured in the laboratory (10 cm dorsal, impulse) had a mean sound level of 97.6 dB (range 94–101 dB).

Eleven males were recorded successfully and analysed with full frequency range (ultrasonic effective) equipment

under laboratory conditions; the average values below are based on this sample. Their dominant frequency was 4.6 kHz. No significant energy was found beyond 25 kHz (Fig. 12B). Although the low and consistently prominent audio principal peak is rather narrow, the spectrum may still be best regarded as low-Q. There is a second broad band of energy from 15 to 25 kHz, peaking near 21 kHz ( $n = 11$ ). Each song lasted 54 ms, incorporating about 203 complex waves (Fig. 11C, D).

The shortest time–amplitude song element of this species resolvable by the human ear is a tick (short, noisy without perceptible infrastructure). Tegminal movement is readily observed and sound emission is seen to coincide with tegminal closure. Ticks are given in bouts of one to five with a bout period of 0.24 s. Between bouts there occur silences rather variable in duration of 2 s to tens of seconds. A succession of bouts incorporates increasingly more ticks to a maximum of five.

Tremulation calling was sometimes observed in this species, alternating with the airborne signal, but not all individuals did this. The simplest element of tremulation display was a succession of vertical body oscillations; a 'quiver'. Quivers were repeated at an irregular rate of five or so in a

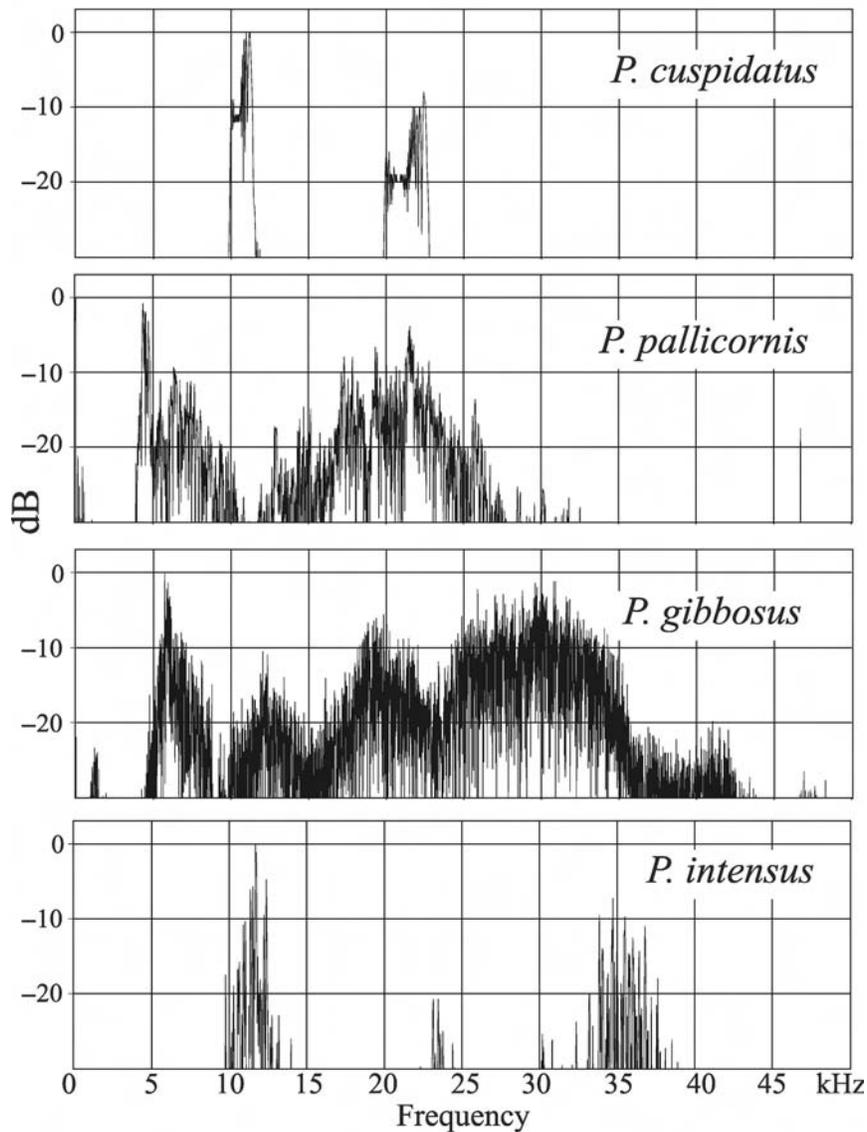


Fig. 12. Power spectra of *Panacanthus* spp.

bout. The time between these tremulation bouts was 5 s to several tens of seconds.

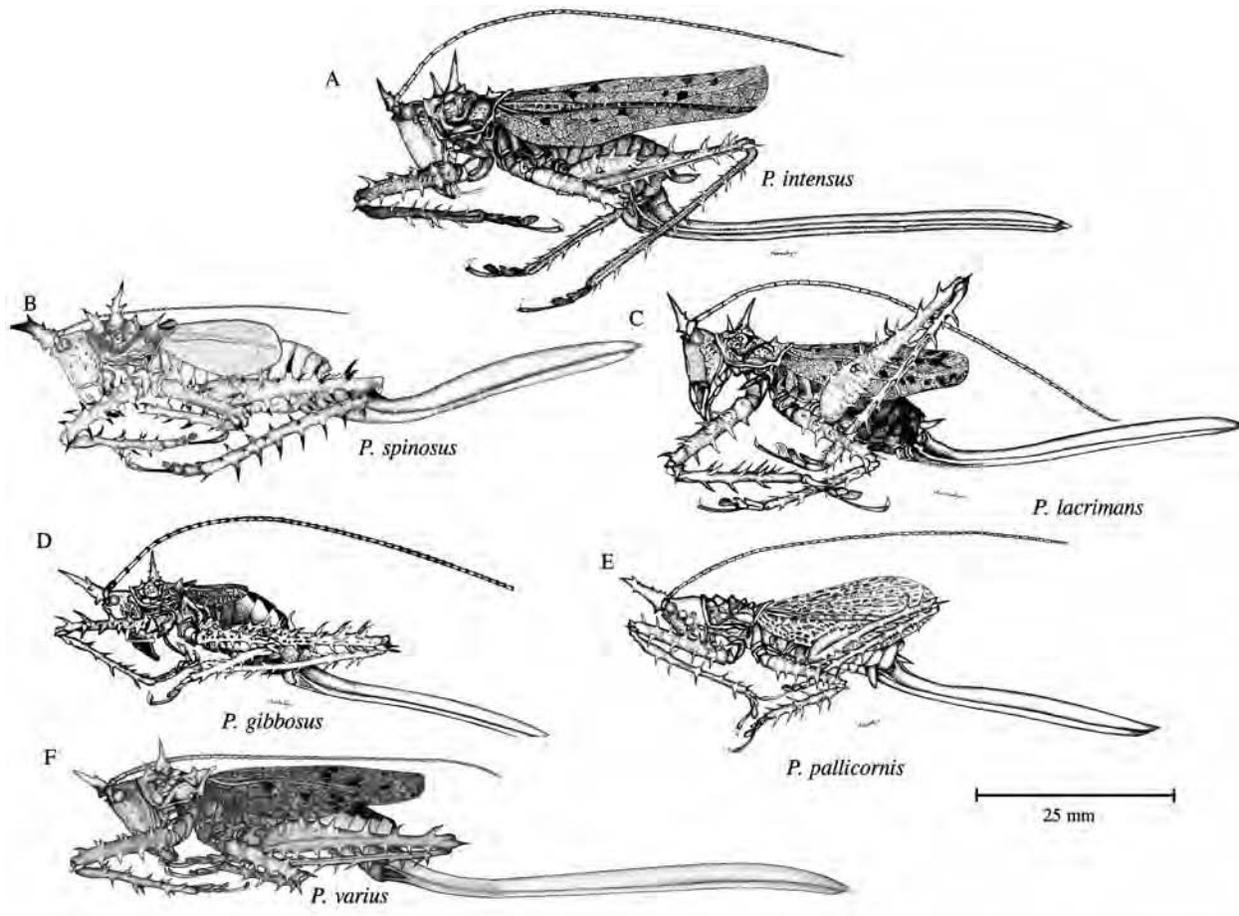
***Panacanthus spinosus* redtenbacher (Figs 2C, 5G–I, 6G–I, 7G–I, 13B)**

*Panacanthus spinosus* Redtenbacher, 1891: 335, holotype ♂, Panama (NMW) not seen); Kirby, 1906: 229; Karny, 1912: 9

**Diagnosis.** Distal part of fastigium, vertex, apex of pronotal and femoral spines fuscous. Area A of pro- and mesozona strongly developed into branched, laterally directed spines (Figs 2C, 7H). Area C of mesozona comprised of 3 small conical

spines. Female brachypterous, tegmina leaving exposed the 4 last abdominal terga; tegmen rubescent on anal edge.

**Redescription.** Male. **Head:** Fastigium elongate, thick, apically moderately declinate, major dorsal spines arise on distal third (Figs 7G, 13B); row of dorsal tubercles developed irregularly in size. Regions I–VII of gena developed as blunt tubercles; subregions Ia, IIa, IIIab, Vabc, and VIIab bear small tubercles (Fig. 7G). **Thorax:** Pronotum: prozona: area A with 2 spines, 1 dorsal, longer, the other ventral, smaller (Fig. 7H). Longest directed anterolaterally bearing 2 small blunt spines at midlength, orientated dorsally. Area B with small tubercle; area C moderately swollen, bearing a rudimentary tubercle. Mesozona: area A produced into 1 large branched spine projecting dorsolaterad and basally

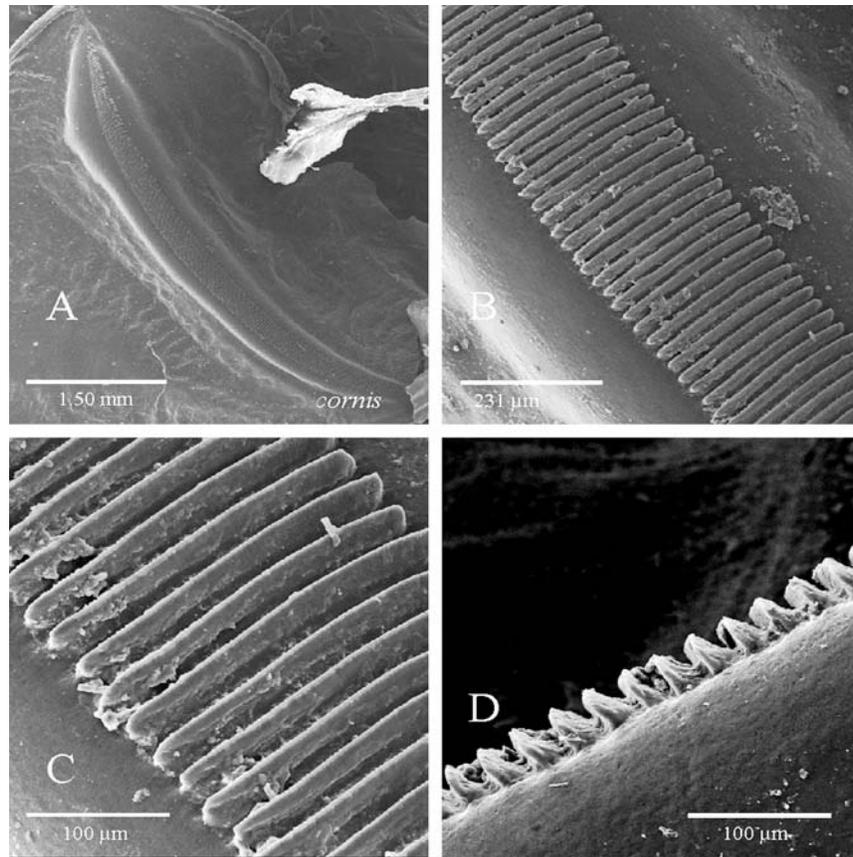


**Fig. 13.** Habitus of the female of some *Panacanthus* spp.

separated from its bilateral counterpart. Area B bears a small spine in dorsal part, rest of this area modified into small tubercles. Area C of mesozona with 3 conical tubercles. Metazona: area A inconspicuous, apparently fused to basal part of spine in area D. Area B with 2 callosities in dorsal part, the anterior-inferior corner of this area modified into small callosity. Area C also modified as callosity on upper edge. Area D produced in elongate spines on anterior corner. These spines conspicuously swollen basally, directed posterolaterad. Posterior margin of pronotal disk truncate. Prosternum bears 2 small tubercles. *Wings*: Brachypterous, tegmina just surpassing abdomen; thin pink-red band borders anal margin, reaching part of distal third of costal margin. Costal field narrow, costal vein not differentiated. Rs originates on distal third, branching into 3 small veins near midrun; R1 appears joined to 1 of those branches before reaching anal margin. Mp originates in midregion of M, branches into 3 veins, which reach anal margin. Cu1a curved laterad, fusing with Cu1. *Legs*: Dorsal part of hind femur bears conspicuous spine on mid-region, this spine larger than other dorsal spines, moderately curved, orientated posterolaterad (Fig. 7I). *Abdomen*:

Tenth tergite ends in 2 blunt projections, medially widely incised rounded. Cercus (Fig. 5G, H) short, cylindrical, bearing elongate, fingerlike, slightly upcurved projection ventro-distally; terminally with dorsal and ventral lobe; mesal aspect of lobes bearing short sclerotized tooth. Titillators with dentate part expanded (Fig. 5I). Subgenital plate with short styles directed laterally, medially broadly incised U-shaped (Fig. 6H).

Female (described for the first time). *Head*: Fastigium elongate, thick, apically moderately downcurved, major dorsal spines originating on distal third (Fig. 13B); row of dorsal tubercles developed irregularly. Regions I–VII of the gena developed as blunt tubercles, small tubercles in subregions Ia, IIa, IIIab, Vabc, and VIIab. *Thorax* (see Fig. 2C): Pronotum: prozona: area A with 2 spines, 1 branched, prominent, dorsad; the other smaller, unbranched, ventrad. Longer spine directed anterolaterally with 1 small blunt midrun spine. Area B with a small tubercle. Mesozona: area A has 1 large branched spine angled dorsolaterad, well separated basally from spine of other body side. Area B bears small spine in uppermost part, rest modified into small tubercles. Area C with 3 projections arranged laterad (Fig. 2C): 2 short spines on dorsum with small tubercle laterad. Metazona: area A inconspicuous, apparently



**Fig. 14.** *Panacanthus pallicornis* file. A, The complete file; B, detail of the middle portion; C, a close view of the teeth; D, profile of the file looking basad.

fused to basal part of spine in area D. Area B with 2 longitudinal tubercles in upper part, anterior–inferior corner of this area modified into small callosity. Area C with callosity on upper edge. Area D produced posterolaterad in elongate unbranched spine on dorso-anterior corner. The basal area of this spine conspicuously swollen. Posterior margin of pronotal disk transverse truncate. Prosternum with 2 small tubercles. *Wings:* Female brachypterous, tegmina covering first 6 abdominal segments; thin band of reddish pink borders anal margin reaching part of distal third of costal margin. Costal field narrow, costal vein not visible. Rs originates on distal third, branching into 3 small veins in distal half of its route; R1 appears joined to 1 of Rs branches before attaining anal margin. M straight on basal third, in this region parallel to Cu1; Mp originates in middle region of tegmina. Cu1 straight and fades in 2 branches on anal margin. A1 and A2 paralleled and short, but A1 closer to Cu2. *Legs:* Conspicuous spine developed in dorsal part of hind femur different to other dorsal spines in the appendage; orientated and moderately curved posterolaterad (Fig. 7I). *Abdomen:* Ovipositor long, comparable with that of *P. pallicornis* (Fig. 13B). Subgenital plate triangular, shallowly incised V-shaped (Fig. 6G).

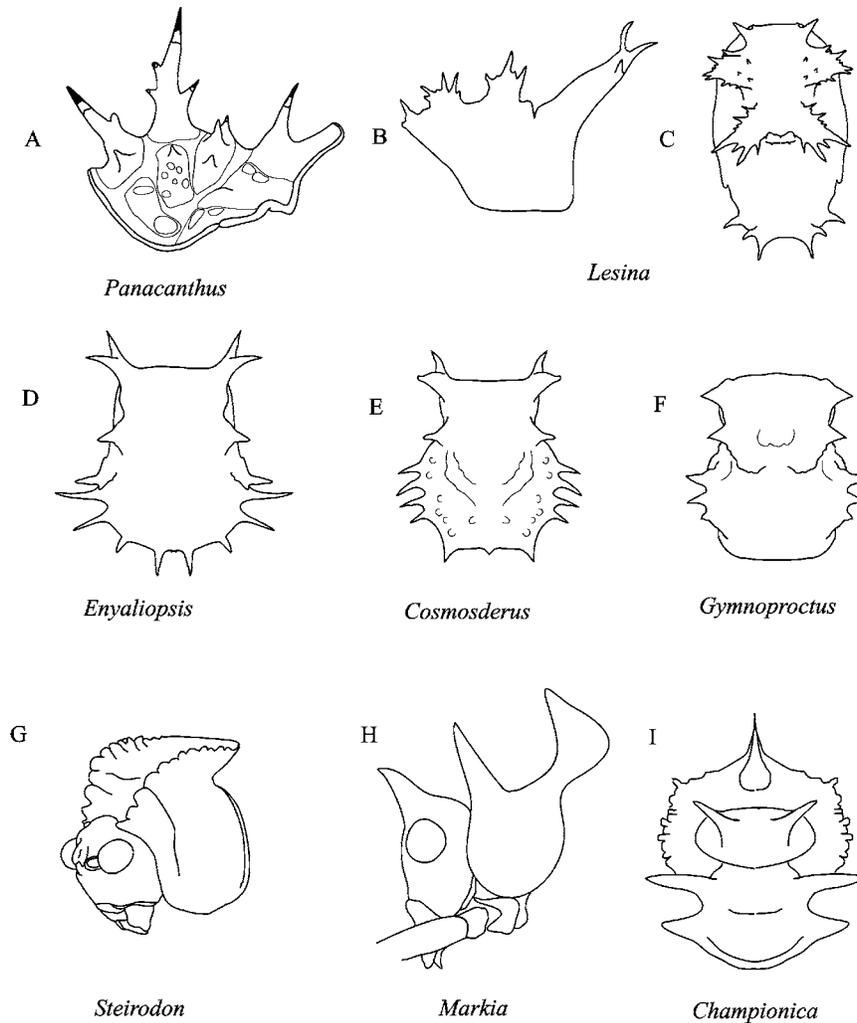
*Colour.* Oerugineous (bright green). Eyes rubescent (becoming red). Apical half of fastigium, apex of pronotal spines, distal

spines on the femora and spines of tibia fuscous. Pronotum dorsally vittate; infusate strip arising apically on fastigia, in metazona; band subdivided into 3 branches, 2 directed to posterolateral corners of pronotum, the other directed centrally; anal margin brunneus. Conspicuous rubescent band on anal margin reaches part of distal costal field.

*Material examined.* PANAMA: 1 ♀ (no data) (J. J. Belwood); 1 ♂, Provincia Cocle, El Copé (8°37'N, 80°35'W), 'Cloud forest', 9 January 1978 (P. Rosen M) (MZUM).

*Distribution* (Fig. 10). This species is known only from rain forests of the Cordillera Central of Panama.

*Remarks.* The spines in this species are displaced basally and directed dorsolaterally rather than being joined at the same bulb or protuberance. The pro- and mesozona are strongly swollen and the spines developed in their respective areas are directed dorsolaterally and separated basally. This separation and orientation may reasonably be attributed to the swollen shape of the pro- and mesozona, as in other species (e.g. *P. gibbosus*, *P. varius*, *P. intensus*), where these regions are less swollen, the spines on their respective areas A are closer, directed more vertically and joined basally in the same swelling. Similar changes may have occurred with the disappearance of



**Fig. 15.** Pronotal armature of *Panacanthus* compared with that of other Tettigoniidae. A, *P. spinosus*, lateral view; B, C, *Lesina ensifer* (lateral and dorsal views, respectively); D, *Enyaliopsis* sp. (dorsal aspect); E, *Cosmosderus* sp. (dorsal aspect); F, *Gymnoproctus* sp. (dorsal aspect); G, *Steirodon* sp. (dorsolateral view); H, *Markia histrix* (lateral view); I, *Championica pilata* (dorsal view). D–F after Glenn (1991), courtesy of the Academy of Natural Sciences, Philadelphia.

area A of the metazona: the protruding spines on area D are strongly developed and swollen basally which may have contributed to the reduction of area A in this zone.

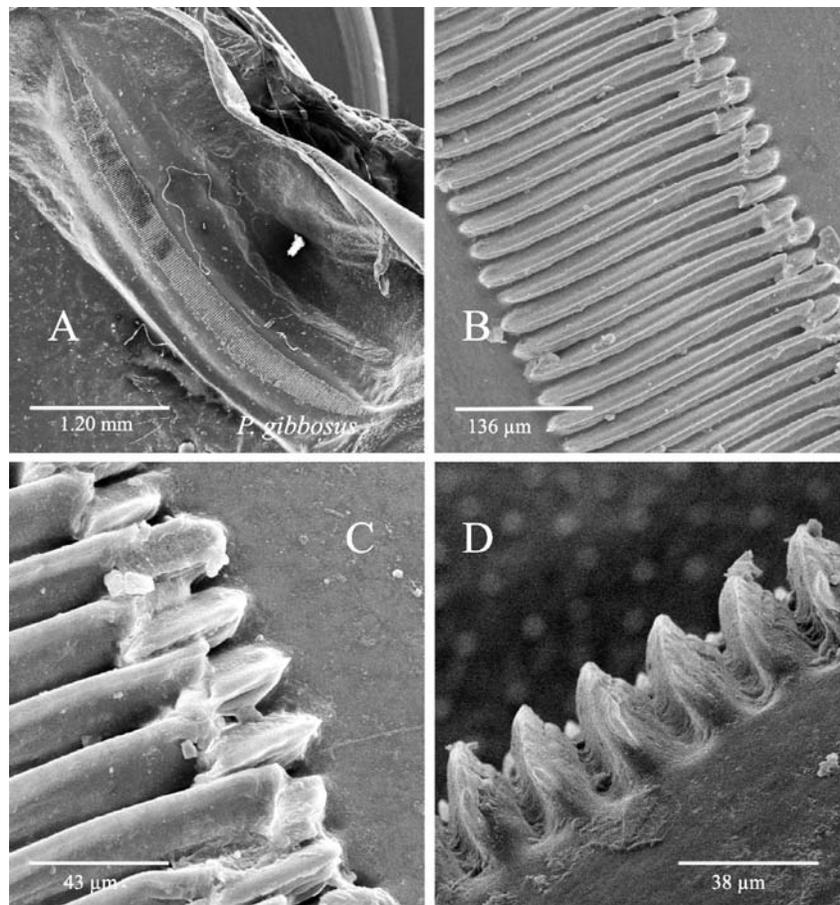
A remarkable change also occurs in the dorsal aspect of the hind femur of this species: a spine is normally larger and stronger than the other spines on the dorsal part of the femur. This spine is also conspicuously developed in other species of the genus, most of them described here for the first time. It is a synapomorphic trait for *P. spinosus*, *P. gibbosus*, *P. varius*, *P. lacrimans* and *P. intensus*.

***Panacanthus gibbosus*, sp. n. (Figs 5J–L, 6J–L, 7J–L, 8C, 13D, 16)**

*Etymology.* The epithet *gibbosus* refers to the ballooned tegmina of males.

*Diagnosis.* Face olivaceous, frons biguttate (Fig. 7J), area A of mesozona elevated into a branched spine (Fig. 7K), tegmen of males coriaceoreticulate, conspicuously addressed to abdomen, females brachypterous (Fig. 13D).

*Description.* Male. *Head:* Fastigium long, apex sharp, weakly upcurved, dorsal part with tubercle modified as spine in middle, ventrally with small tooth at beginning of distal third (Figs 8C, 13D). Genae with regions I–VII developed as small tubercles. Subregions Ia, IIa, and IIIab, Vabc and VIIab also developed as reduced tubercles; tubercle IIa at midpoint between tubercles V and VII. Subregions VIIab developed as longitudinal tubercles. Tubercle in Ia reduced to almost inconspicuous. *Thorax:* Anterior margin of pronotum almost truncate, with 3 small, almost inconspicuous tubercles (1 on midline, 1 to each side). *Prozona:* area A elevated in small blunt spine directed anterolaterodorsally; inferior part of area A



**Fig. 16.** *Panacanthus gibbosus* file. A, The complete file; B, detail of the middle portion; C, a close view of the teeth; D, profile of the file looking basad.

slightly inflated. Area B almost smooth, only inconspicuous wrinkles occur. Mesozona: area A elevated in 1 spine, branching into several small rudimentary spines (2 anterior, 2 posterior, 2 lateral (Fig. 7K). Small protuberance occurs on basal portion, bounded by smooth area. Area B with major tubercle or callosity in upper part, rest covered by small reticulated tubercles. Area C produced in 3 reduced tubercles, the superior 1 more conical than others. Metazona: area A flat, featureless. Area B bears 2 small tubercles above, anterior–inferior edge of this area modified as callosity. Area C slightly protruding, almost smooth. Area D of metazona with 1 spine on each anterior corner, directed forward laterodorsally. Prosternum armed with 2 small blunt spines. *Wings*: Tegmina adpressed to abdomen (Fig. 8C), costal field narrow, costal vein inconspicuous. Sc and R swollen, adjoined basally, then separate parallel, converging again from two thirds tegminal length, over last quarter in contact to tegminal margin. Rs forks on distal third and approaches Ma. M strong at beginning becoming narrower after giving rise to Mp, at tegmina midpoint; Mp immediately joins Cu1; Ma strongly curved towards costal field, disappearing apically. Cu1 curved laterad towards anal margin but turning back towards costal margin, fusing with Mp. Stridulatory field elongate, occupying great portion of

tegmina (Fig. 6L); file long (~5.7 mm,  $n = 20$ ) with about 240 teeth (Fig. 16A). Posterior wings reduced to small scales. *Abdomen*: Subgenital plate subquadrate, medially notched U-shaped, styli cylindrical, short (Fig. 6K). Tenth tergite medially widely incised rounded, ending in 2 small lateral spikes. Cercus of male distally noticeably curved inward, with long ventral digitate process, such that lateral aspect resembles boxing glove (Fig. 5M, N). Supra-anal plate triangular with medial black dot.

*Female*. *Wings*: Squamiform, tegmina scarcely reaching third tergite (Fig. 13D); hindwings very reduced, transparent. Sc, R similar to male. Ma nears but never touches Rs; Mp very short, fused to Cu1a short distance from origin. Cu1b arising before Mp fuses to Cu1a, shortly becoming inconspicuous. Ovipositor long (Table 1), green, slightly dorsally convex (Fig. 13D). Subgenital plate short, somewhat broad, terminally rounded emarginate, basally with rounded depression at each side (Fig. 6J).

*Colour*. Dorsal portion of clypeus and mandibles atrous, clypeus resinous, bearing dorsally melanic triangle. Fastigium resinous. Vertex bears conspicuous longitudinal infuscate band from dorsal spines of fastigium posteriorad; 2 paler rhomboid marks present each side of this band;

amber coloration present among infusate marks. Antennal scrobes and genae fumeus. Face olivaceous, black facial markings present, distributed as follows: 2 below each annulus of antennal scrobes, another 2 closer to each other placed near midtransverse line, 2, more separated, on dorsal part of clypeus. Dorsal part of clypeus and mandibles atrous; ventral part of clypeus and labrum resinous. Amber colour of fastigium extends to pronotum in prozona, incorporating both spines of mesozona (area A) and reaching spines of anterior corners of metazona. Metazona anteriorly and laterally atrous, with small atrous patch on distal half of posterior margin, rest fuscous. Ventral margin of lateral lobes (including area C of metazona) smaragdine (the brilliant crystalline green of the emerald). Some areas of pronotum marked atrovirens (Fig. 7K). Legs corticinus (barklike sculpture or texture), strongly irrorate (speckled; covered with minute spots) on basal half mostly, dorsal spines on femora vary from olivaceous to amber. Dorsobasal portion of hind femora torose (swelling in knobs, knots or protuberances). Abdominal terga with trapezoid fuscous mark (Figs 8C, 13D), olivaceous on dorsal half, ventral half infusate.

*Material examined.* Holotype: ♂, COLOMBIA, Nariño, RN La Planada, 2 May 1997 (F. Vargas, G. K. Morris & F. Montealegre) (ICN).

Paratypes: COLOMBIA 3 ♀, Nariño, RN La Planada, 2–3 March 1997 (F. Vargas, G. K. Morris & F. Montealegre) (MEUV, ICN); 1 ♂, same data, 2 April 1997 (ICN); 1 ♂, same data, 4 April 1997 (ICN); 1 ♂, same data, 30 April 1997, 2 ♂, same data, 2–4 May 1997; 1 ♂, same data, 9 May 1997 (MEUV); 9 ♂ alcohol, 3 ♂ pinned, 1 ♀ (F. Montealegre, A. Nastacuz, L. Moncayo), 30 May 2001. ECUADOR: 2 ♂, 1 ♀, Prov. Esmeraldas, El Placer, 675 m, 00°52'N, 78°33'W, 25 July–17 August 1987 (D. Wechsler) (ANSP).

*Distribution* (Fig. 10). This species occurs at several locations in the Colombian and Ecuadorean Andes, and is abundant in Macizo de los Pastos in Nariño, close to the point of convergence of the three main cordilleras in Colombia.

*Remarks.* In examined females, the ventral distal tooth of the fastigium is not as developed as in males. There is not enough evidence to suggest that this trait is a sexual character. The fastigium of one male paratype bears an additional ventral tooth immediately before the distal one. Although in most specimens the colour of the face is green, some have a light cream coloration. We have not established whether such a colour is related to age, but similar age-related pigment changes have been observed in other species (e.g. *Ancistrocercus* sp., Tanta Savin, University of Toronto, pers. comm.). There may be variation in facial maculae between populations. Two more marks are present in the only Ecuadorean specimen (female). The bent course of the vein Ma in the tegmina is a constant character in all of the males and is interpreted as autapomorphic for the species.

*Song description.* Calling by this species is known from the analysis of twelve males. One specimen was recorded

indoors at La Planada (Colombia Nariño) at 18.5°C, the others were also recorded under laboratory conditions at 23 ± 0.5°C. The shortest time–amplitude song element of this species, resolvable by the human ear, is a zip: brief, noisy and with perceptible infrastructure (Fig. 11E, F). Zips are typically produced in groups of two to eight and each is a pulse train of approximately fifty transient pulses; each pulse is a waveform involving three to four cycles, separated from the next pulse by 0.1–0.15 ms. A zip lasts on average 0.076 s ( $n = 5$ , range 0.060–0.087 s); each pulse lasts <0.5 ms. Tegminal movement is slow enough to determine, by inspection, that each zip coincides with a single tegminal closure.

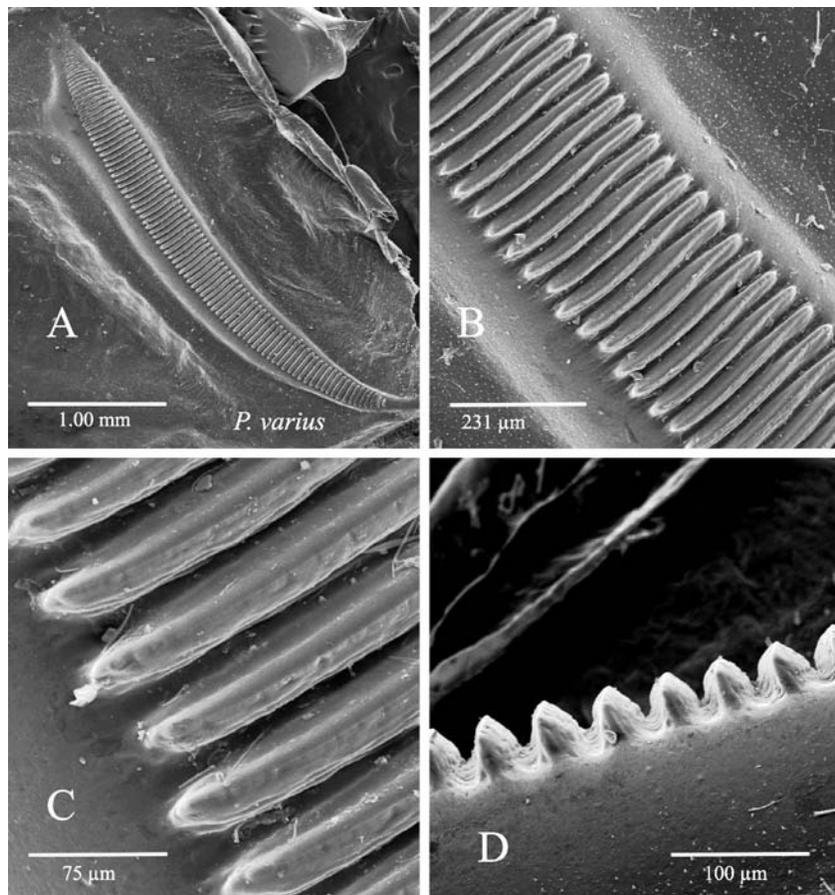
The spectrum of *P. gibbosus* is a noisy low-Q band. Measured 20 dB below its highest peak, it extends from 5 to 35 kHz. The most intense frequency varies: sometimes it is an audio peak at 6.4 kHz ( $n = 6$ ) and sometimes it is ultrasonic at 27.4 kHz ( $n = 4$ ). Less intense peaks occur consistently at 12.5 and 19.2 kHz ( $n = 9$ ). All these very broad peaks may be harmonically related with a fundamental near 6 kHz. Based upon single-note spectra, the most intense ultrasonic peak occurred at 30.2 kHz ( $n = 9$ , standard deviation = 1.6, range 26.6–31.9 kHz, Fig. 12C). The most intense audio peak averaged 5.9 kHz ( $n = 9$ , standard deviation = 0.1, range 5.7–6.0 kHz). The call is loud to human ears and, for one male, registered ~90–95 dB with the microphone 10 cm dorsal.

### ***Panacanthus varius walker* (Figs 1, 5M–O, 6M–O, 7M–O, 13F, 17)**

*Panacanthus varius* Walker, 1869: 333, holotype ♂, Ecuador, Quito (BNHM) (not seen)  
Karny, 1912: 9; Kirby, 1906: 229; Karny, 1912: 9.

*Diagnosis.* Dirty dark green or yellowish green, with slight brownish tinge. Face helvulus, ventral half of fastigium, antennal sclerites and scapus atrous.

*Description.* Male. *Head:* Fastigium straight, major dorsal spines short, arising in midregion of fastigial length. Row of dorsal tubercles present. Tubercles on regions I–VII of gena present. Tubercle in III elongate transversely, somewhat keeled. Tubercles in subregions Ia, IIIa and VIIab reduced. Tubercles in other subregions absent or poorly developed (Figs 1, 7M). *Thorax:* Pronotum: prozona: area A with 1 short well-shaped spine in upper part, this spine having rudiments of tubercles or spines on basal portion; additionally, inferior part has group of callosoid tubercles (Fig. 7N). Tubercles in areas B and C inconspicuous. Mesozona: area A produced into large, well-developed spine which arises on elevated lump; basally this spine with conspicuous blunt spine on posterior; additionally, some vestigial, almost inconspicuous, tubercles poorly developed on spine's laterobasal portion. Conical tubercle arising as independent area below area A. Area B with small, smooth, reticulated tubercles; tubercle absent on upper part; inferior part with elongate horizontal callosity. Area C produced in 3 flat,



**Fig. 17.** *Panacanthus varius* file. A, The complete file; B, detail of the middle portion; C, a close view of the teeth; D, profile of the file looking dorsobasad.

morphologically irregular tubercles, disposed almost vertically. Metazona: area A narrow, smooth; fused with area D. Area B smooth, shiny, with 2 poorly shaped tubercles above; inferior half softly roughened. Areas B and C fused, marked with small impressed punctures. Area D bears 1 conical spine on anterior corner. *Legs*: Hind femur conspicuously armed dorsally with paired spines. A major spine in this area is distinctively shaped (Fig. 7O). *Wings*: Tegmina elongate, narrowing along costal margin on distal half; anal margin straight, approximately forming straight angle with costal margin. Costal vein short, running diagonally on basal fifth of tegmina. Sc, R parallel, straight; Rs originates in distal fifth. Ma and Mp diverge at ~6mm from beginning of M. Cu1 joined to Mp. Stridulatory file with 90 teeth, compressed on one side, broadened on the other (Fig. 17). *Abdomen*: Tenth tergite widely incised, orbicular, pubescent. Supra-anal plate triangular, with 2 dorsal keels converging in midportion, reaching distal, acute margin as single keel or carina. Cerci bear digitate ventral projection on distal part, curving latero-interiorad to approach a ventrodistal lobular projection (Fig. 5M, N). Mesally each cercus with tooth projected posteriorad, originating from internal carina connecting both lobes, ending in blunt tooth or button-

shaped projection. Subgenital plate wide, medially circularly incised, with 2 styles curved laterad (Fig. 6N).

*Female* (described for the first time). *Wings*: Fore- and hindwings completely developed, covering last abdominal tergite. Anal margin almost straight on distal third, rounded apically, forming a straight angle with costal edge. Costal vein short, indistinguishable from archeductyon veins. Sc and R parallel, diverging slightly after Rs arises. M runs parallel to R; Mp arises distally on this vein, so never having contact with Cu1. *Abdomen*: Ovipositor narrow, conspicuously elongate, moderately curved dorsally in apical half (Fig. 13F, Table 1). Subgenital plate triangular, deeply incised U-shaped, noticeably depressed laterad (Fig. 6M).

*Colour*. Face tawny or dull reddish yellow; antennal sclerites, scapus and ventral half of fastigium atrous; rest of fastigium resinous. Vertex with light longitudinal infuscate band, originating on dorsal spines of fastigium ending at posterior margin of pronotum; 2 lighter rhomboid marks subtend this band. Amber coloration present among infuscate marks. Femoral spines hamate. Abdominal terga with trapezoidal atropurpureus stripe. Dorsal half of abdominal pleurites olivaceous, ventral half infuscate.

*Material examined.* ECUADOR: 1 ♀, Prov. Pichincha, Tinalandia, 16 July 1986 (G. K. Morris); 1 ♂ nymph) same data. COLOMBIA: 1 ♂ (preserved in alcohol), Nariño, Barbacoas, Cto. Altaquer, Reserva Natural de Nambi, 1370 m, 13 July 1995 (NN) (ICN).

*Distribution* (Fig. 10). This species was described originally from an unspecified locality in Ecuador. We found it in Tinalandia (Prov. Pichincha, Ecuador), but its distribution also reaches the southwest part of Colombia.

*Remarks.* Some parts of the pronotum seem to be developed as spines or conspicuous tubercles in the earliest nymphal stages. However, the same regions in the imago seem to be less developed. Such is the case for the spines in area A of the prozona and metazona, which presents rudiments of tubercles or spines and a tubercle on the superior half of area B of the metazona (well developed in nymphs).

#### ***Panacanthus lacrimans* sp. n. (Figs 6P, 7P–R, 13C)**

*Etymology.* The name of the species refers to the small facial subocular droplike marks.

*Diagnosis.* Face orange, somewhat rufescent with facial maculae only on upper part of frons and clypeus (Fig. 7P).

*Description.* Female. *Head:* Fastigium straight, rather short (5 mm) with basal ventral tooth (Fig. 7P); dorsal conical spines placed on midregion. Tubercles in regions I, II, III, IV, V, and VII of gena reduced in size. Tubercle III longitudinally elongate, keeled; tubercle IV not prominent but conspicuous; tubercle VI absent. Tubercles in subregions Ia, Vbc, VIIb absent, the rest conspicuous, although weakly defined. *Thorax:* Pronotum (Fig. 7Q): prozona: area A modified into single spine directed anterodorsolaterad; inferior part of this area divided into small region with poorly developed tubercle. Areas B, C roughened, poorly defined, separated from area B of mesozona. Mesozona: area A produced into large well-developed spine arising on elevated lump; this region also presents 2 vestigial tubercles on laterobasal portion. Area B completely covered with irregularly reticulated tubercles. Area C produced in 3 lobulations: superior, mid and inferior; inferior more prominent. Metazona: area A inconspicuous, apparently fused with area D. Area B with callosity in superior and anterior edge. Area C almost smooth, apparently fused to area B, both with small impressed punctures. Area D with a spine on anterior corner directed dorsoposterolaterad. Prosternum unarmed, only with 2 minute, poorly defined protuberances. *Wings:* Fore- and hindwings completely developed, tegmina scarcely extend beyond tenth tergite. Costal field basally narrow, becoming wider towards midlength. Distal part of tegmen abruptly constricted distad, so costal field abruptly narrowed (Fig. 13C). Costal vein inconspicuous. Sc and R parallel, diverging slightly in distal fifth of tegminal length; Rs arises in apical portion of R. Mp branches within 8 mm of M origin. Cu1 short (~13 mm), fused to Mp. Cu2, A1 and A2

running transverse but parallel. Tegmina have some dark shiny cells (Fig. 13C). *Abdomen:* Subgenital plate basally wide, mediodistally incised V-shaped, ending in 2 points directed inward. Ovipositor as described for *P. varius*.

Male unknown.

*Colour.* Occiput with dorsal fuliginous (sooty or smoky brown) band, starting on fastigial dorsal spines, ending at posterior pronotal margin; lateral maculae poorly defined. Face aurantius (orange) somewhat rufescent with facial markings only on upper part of frons and clypeus. Clypeus resinous, with 4 fulvescent (shining brown) spots; labrum presents same coloration. Mandibles aurantius with inner margins atrous.

*Material examined.* Holotype: ♀ (preserved in alcohol), COLOMBIA, Valle del Cauca, Buenaventura, San Cipriano, September 1996 (M. Reyes & D. Fajardo) (ICN).

Paratypes: COLOMBIA: 1 ♀, Valle del Cauca, Buenaventura, Alto Anchicayá, 680 m, 15 October 1993 (K. Encarnación) (MEUV); 1 ♀, Anchicayá, Río Danubio, 300 m, 15 October 1995 (F. Montealegre) (MEUV); 1 ♀, Valle del Cauca, Darien, Rio Azul, 500 m, April 1994 (R. C. Aldana) (MEUV).

*Distribution* (Fig. 10). Rain forests in the coastal plain of southern Colombia, between the eastern cordillera and the Pacific Ocean. This species does not occur at low elevations (<100 m) at the margin of coastal places or flooded forest. Its range of distribution is unknown; specimens have been collected from several locations belonging to rainforests of the municipality of Buenaventura in Valle del Cauca.

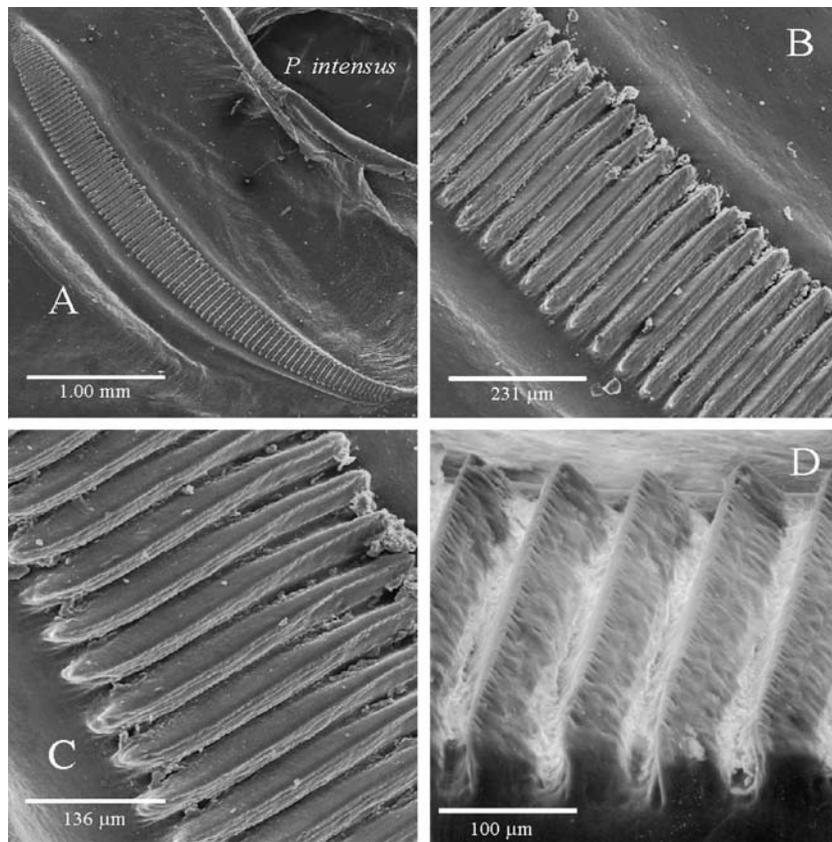
*Remarks.* Only females are known. This species is most closely related to *P. intensus* and their distribution ranges overlap in the Valle del Cauca.

#### ***Panacanthus intensus* sp. n. (Figs 5P–R, 6Q–S, 7S–U, 13A, 18)**

*Etymology.* The name of the species refers to the high intensity sound produced by males.

*Diagnosis.* Head large when compared with other congeners. Face fuscotestaceous without facial black marks. Fastigium short and moderately retroarcuate.

*Description.* Male. *Head:* Moderately larger than congeners. Fastigium short, moderately curved hindward; dorsal spines reduced, blunt, placed at midlength (Fig. 7S). Gena slightly roughened, mostly smooth (Fig. 7S). Tubercles in regions I, II, III conspicuous; latter poorly developed, somewhat elongate, keeled. Tubercle VII poorly developed, almost inconspicuous. Tubercles of subregion IIIa conspicuously developed. *Thorax:* Pronotum (Fig. 7T): anterior margin rounded. Prozona: area A with 2 spines projected anterodorsolaterad. Areas B and C with inconspicuous



**Fig. 18.** *Panacanthus intensus* file. A, The complete file; B, detail of the middle portion; C, a close view of the teeth; D, profile of the file from the left side.

tubercles, fused (in part) with area B of mesozona. Mesozona: area A elevated in single spine directed dorsally, moderately retroarcuate, its inferior part subdivided, elevated in a small conical tubercle. Area B with reticulated tubercles. Area C produced in 3 roughened regions poorly differentiated into tubercles, inferior 1 shaped as callosity. Metazona: area A inconspicuous. Area B almost smooth but subdivided above, where it bears vestigial longitudinal tuberculation. Areas C and B fused, marked with small impressed punctures. Area D with broad conical tubercle on anterior corner, directed laterodorsoposteriorly. Posterior margin of the pronotum truncate, not covering stridulatory sound field. Prosternum unarmed. *Wings*: Tegmina elongate, abruptly narrowing along costal margin distad, anal margin straight, forming a straight angle with costal margin, the latter moderately wider at midpoint. Costal vein short, indistinguishable from archidictyon. Sc, R parallel, straight, only diverging slightly distad; Rs arises in distal third of tegmen. Ma and Mp arise about 6 mm from beginning of M. Stridulatory vein elongate (5.1 mm,  $n=1$ ), curved anteriorad, arcuate dorsad, bearing 95 teeth compressed on one side, broader on other (Fig. 18). *Abdomen*: Tenth tergite widely roundly incised, densely pilose. Supra-anal plate triangular. Cerci with digitiform ventral projection on distal part, curving moderately upward to almost join at ventrodistal lobular projection of cercus. Cercus internodistal part with rib,

connecting both lobes and ends in blunt tooth or button (Fig. 5P, Q). Subgenital plate broad, medially circularly incised, with 2 styles moderately curved laterad (Fig. 6R).

*Female*. Differs from male chiefly in genital characters and size. *Wings*: Except for veins in anal field, main distribution of veins follows that of male. Cu1 appears joined to Mp; in some specimens both veins slightly converge at 2 points, then diverge again so that Cu1 separately touches anal margin. Culb fused to Cu1. *Abdomen*: Ovipositor distinctly elongate (Table 1). Subgenital plate medioapically circularly incised, ending in 2 acute points curved inward (Fig. 6Q).

*Colour*. Body generally brunneous. Face fuscotestaceous, hypographous (shaded; applied to a fascia that becomes gradually darker). This gradient starts at subantennal area and covers fastigium and antennal scrobes. Occiput fuscotestaceous with some lutescent reticulations, and 2 additional marks to each side, sketched by amber lines. Face, clypeus and labrum (to a lesser extent) fuscotestaceous; no facial marks. Scape, antennal scrobes and fastigium atrous. Pronotal spines of pro-, meso- and metazona (including areas A and B of prozona and area C of metazona), amber. Legs, thoracic pleura, tegmina (some cells of tegmina fulvescent), abdomen and base of ovipositor fulvid. Almost all spines and distal half of ovipositor aquamarine (in life).

*Material examined.* Holotype: ♂ (preserved in alcohol), COLOMBIA, Valle del Cauca, Bajo Anchicayá (Bellavista) (C. Saldarriaga) 15 June 1999 (ICN).

Paratypes: COLOMBIA: 1 ♀, Valle del Cauca, Buenaventura, 10 m, 4 December 1980 (C. E. Montilla), 1 ♀, same locality as preceding, 24 August 1986 (Martinez) (ICN); 1 ♀, Buenaventura, Alto Anchicayá, 680 m, 15 October 1993 (F. Montealegre) (MEUV); 1 ♀, Buenaventura, Bajo Anchicayá, 270 m 1981 (NN) (MEUV); 1 ♂ nymph, same locality as preceding, 20 October 1995 (F. Montealegre) (MEUV); 1 ♀, same locality as preceding 7 June 1999 (C. Saldarriaga) (ICN); 1 ♀, Villa Real, 30 September 1982 (Herrera) (MEUNP).

*Distribution* (Fig. 10). Coastal plain of southern Colombia, between the eastern cordillera and the Pacific Ocean; apparently not occurring at very low elevations (<100 m). The distribution range is unknown, limited so far to several locations (rainforests) in Buenaventura municipality, Valle del Cauca.

*Remarks.* Area A of the mesozona in some specimens bears tubercles instead of small spines at the base of the main spine. The processes on area D of the metazona vary from small and broad tubercles to conical and more elaborate spines. In the only nymph examined, the main spines on the mesozona are conspicuously bifurcate posteriorad. The same nymph has the dorsal spine on the posterior femur strongly developed when compared with that of adults (in a proportional scale). Coloration varies among specimens from dark brown to clear brown, reddish, with limb spination mostly green-bluish.

*Song description.* A single male was successfully transported to Canada, caged indoors and recorded at 22 °C with ultrasonic effective equipment. The shortest time domain element of this species, resolvable by the human ear, is a musical chirp (terminology, Morris *et al.*, 1989), lasting about 300 ms; the chirp has a suggestion of infrastructure. The chirp duty cycle is <1%, being effectively immeasurable: that is, a lone chirp occurred at very long, inconsistent intervals of many minutes to 1 h. Calling activity was typically noted after dark, but on one occasion a single call was noted during the day.

The chirp (song) is a train of eighteen pulses, increasing slightly in rate and duration (pulse rate overall 530 s<sup>-1</sup>). Each pulse is a complex wave train of approximately four to five major crests (Fig. 11G, H) bearing three or four smaller crests. The song is remarkable for its very high intensity: a call registered 112.9 dB (Impulse, hold) as recorded at 10 cm with the microphone directed at the dorsal field of the tegmina.

In the frequency domain, the mean dominant peak was 11.7 kHz (average of n = 7 calls, range 11.6–12.5 kHz; Fig. 12D); an apparent second harmonic, about 7 dB below the dominant, occurs near 23 kHz. At about 35 kHz (mean 34.8 kHz, n = 7), is a stronger third harmonic, only 3 dB below the dominant. The dominant peak is narrow

(11.7 kHz), so that, although the pulse waveform is more complex than that of *cuspidatus* or *pallicornis*, the song of this species may still be regarded as relatively high-Q, mainly for its transient nature (Fig. 12).

The high intensity of *P. intensus* implies that individuals singing in the field may be considerably spaced apart and indeed this species is not as abundant as cloud forest species. Being so loud is perhaps dangerous, in increasing exposure to acoustically orienting (eavesdropping) predators. *Panacanthus intensus* may trade-off loudness with a lower duty cycle. Because *P. varius* and *P. lacrimans* live in similar lowland habitat (lowlands), they may prove to have similar acoustical behaviour.

## Discussion

### Systematics

*Panacanthus* is more similar to the Neotropical genera *Copiphora* and *Lirometopum* than to any other genus of New or Old World katydid. *Lesina* Walker, 1869 (= *Eumegalongodon* Brongniart) was originally grouped with these genera, but should not be. Although closely related to *Panacanthus*, *Copiphora* and *Lirometopum* are not proposed as its sister group(s). *Panacanthus* is simply more closely related to them than to *Lesina*. The homology of the elaborate fastigium, protruding eyes, elongated optic lobes, mandibular and cercal morphology shared by the three genera is compelling. This affinity is also acknowledged by Naskrecki (2000b), who indicates that *Copiphora* and *Lirometopum* appear to share a common ancestor. However, a superficial survey of genital characters in species of *Panacanthus* shows some specialization, derived with respect to the inferred ancestral condition as seen in *P. cuspidatus*, *Copiphora* and *Lirometopum* (see below).

The monophyly of the genus *Panacanthus* is supported by synapomorphic states of characters 3, 12, 14, 15, 27 and 33. The sequential development of pronotal spines is synapomorphic for most internal branches, but this specialization is clearly derived from the ancestral condition presented by *P. cuspidatus* (Fig. 2). In a similar way, the development of the hooklike spine on the dorsum of the hind femur (character 28, Fig. 7) appears at node C and is a synapomorphy for this clade, but not for the entire genus. Among the generic synapomorphic characters, the bispinose fastigium, the upcurved lateral lobe of the pronotum and the hooklike spines of the hind femur are uniquely derived.

As stated, *Panacanthus* shares some synapomorphies with *Copiphora* and *Lirometopum* (see above), whose cerci and titillators strongly resemble those of *Panacanthus*. The cerci (character 32) of *P. cuspidatus* and *P. pallicornis* resemble those of *Copiphora* and *Lirometopum* spp.; but in the *Panacanthus* species distal to node C, these appendages undergo an abrupt transformation, the apex becoming forked and the cercus having only one internal process (Fig. 5G, H, J, P; see also Naskrecki (2000a) for details of the genitalia of *Copiphora* and *Lirometopum*). In this regard, *P. spinosus*

also links both groups of species by giving an idea of the evolutionary path taken by this trait (Fig. 5G, H). Excepting *P. cuspidatus*, titillators (character 33) in *Panacanthus* depart from those of *Copiphora* and *Lirometopum* in having the dorsal portion apically divergent and roughened (serrated), and they conserve the ancestral condition of this generic complex: a median slot reinforced by two layers of sclerotized cuticle (Fig. 5).

There is no significant difference between the trees constructed including or excluding behavioural data. Each separate analysis resulted in one most parsimonious tree with identical topology. With more acoustic data available it will be possible to show if these results are due to the limited number of behavioural traits used in the analysis.

We attribute the well-resolved phylogeny to the kinds of character used. They were assumed to be independent and thirty of them (77%) present a high *ci* (>0.7), showing low levels of homoplasy. This permits a high degree of reliance on the analysis. Certain characters, such as the morphology of the gena (characters 4–5), contribute little to the cladogram structure and mistakes in assigning character states do not produce important changes in the topology.

*An approach to the evolution of pronotal armature in Panacanthus.* The three pronotal zones of *Panacanthus*, the pro-, meso- and metazona, are clearly subdivided into smaller areas (A–D, Fig. 2A). These conspicuous areas are consistent in all *Panacanthus* as well as in other closely related Copiphorinae (e.g. *Vestria*, *Loboscelis*, *Monchecha* and some *Copiphora*). In species of these genera the prozona is divided into two main areas, the mesozona into three and the metazona into four (Fig. 2).

The main pronotal modifications of *Panacanthus* spp. are seen in area A of both the prozona and the mesozona, area C of the mesozona and areas A and D of the metazona. The pronotal surface of *P. cuspidatus* is wholly smooth and glassy. In *P. pallicornis* most areas are modified as short and blunt tubercles and callosities. Some of these tubercles are further modified into spines in other species (*P. spinosus*, *P. varius*, etc.).

The pronotum of *P. spinosus* provides a good model for understanding the possible evolutionary pathway of pronotal structures. The three tubercles of *P. pallicornis* (Fig. 2B, see arrows) within area C of the mesozona are recognizable in *P. spinosus* (Fig. 2C, see arrows) as small conical spines. The presence of conical spines in this area in *P. spinosus* suggests a link between both species (*pallicornis* and *spinosus*) and between both groups of species (*P. cuspidatus* and *P. pallicornis*/*P. spinosus* and the most basal species below this clade). It also supports the hypothesis that the character 'pronotal spines' has different states: smooth, tubercular and spinose. It is prudent to assume that the pronotal spination in area A of both the prozona and the mesozona, area C of the mesozona, and area D of the metazona is not an independent trait, as they appear simultaneously in the same developmental stage, although they do present different developmental conditions in each area. The evolution of pronotal defensive projections (Fig. 4B) using MACCLADE indicates that the most plesiomorphic state of the pronotal

structure is smooth (presented by *Copiphora*, *Lirometopum*) and that the pronotal spines in *Lesina* evolved independently.

Some species of *Panacanthus* show a reduction in pronotal structures. For example, area A of the metazona is distinct in *P. cuspidatus* and *P. pallicornis* but appears to have become fused with area D (Fig. 2C) in the species beyond node C. Other reductions involve: processes (spines or tubercles) on the gena, branched spines of the pronotum, area D in the metazona, tubercles or conical spines in area C of the mesozona, fastigium length, and even the reduction of prosternal spines (some of these characters were not included in the analysis). The gradual vanishing of several of these structures is in agreement with the tree topology obtained here. In some cases these processes are present in nymphal states and tend to disappear in adults. For example, nymphs of *P. intensus* have the main pronotal spines branched at one stage of their life.

Prosternal spines are conspicuous in *P. cuspidatus*, smaller in *P. pallicornis*, vestigial in *P. spinosus* and completely absent in all other *Panacanthus* spp. They show reduction distad on the tree between each species, as do other structures, such as area A of the metazona, fastigial spines and the tubercles of the gena. However, prosternal spines are a variable trait in Tettigoniidae and cannot be considered reliable as an argument in phylogenetic inference. Furthermore, the complete loss of a character state does not denote evolutionary direction or affinity, nor does it indicate whether the distribution among taxa is the outcome of parallel or convergent evolution (Hecht & Edwards, 1976).

*The pronotal processes of Panacanthus compared with other tettigoniids.* The pronotal processes of *Panacanthus* led us to make a broader search for these in other katydids. A complete analysis of pronotal spines for the genus *Eugaster* and their use in its systematics is presented by Grzeschik (1969). Pronotal spines are mentioned prominently in taxonomic descriptions of several other taxa (Redtenbacher, 1891; Karny, 1912; Beier, 1960, 1962; Grzeschik, 1969; Emsley, 1970; Glenn, 1991). Genera having species that present pronotal modifications (spines, tubercles or papillae) are shown in Table 2.

In conocephaloid katydids, if pronotal processes occur they are directed either dorsally or laterally. Among these katydids, the longest dorsally projecting processes occur on the mesozona in species of *Panacanthus*. The most prominent laterally projecting pronotal processes occur in species of the genus *Lesina* (Fig. 15B, C); they are produced as strong dentate projections on both the pro- and mesozona (De Jong, 1942). The pronotal processes of *Lesina* correspond topographically to some extent with those of *Panacanthus*, but are intrinsically dissimilar (Fig. 15). This leads us to code the feature (pronotal armature, character 15) using a different state for *Lesina* (a racklike state 4) and to conclude that in those genera, pronotal processes have evolved separately. This is confirmed in the phylogenetic analysis presented here. Although defined by a transformation series of three states (smooth, tuberculose and spinose), pronotal armature is presented as synapomorphic for

**Table 2.** Some genera of Tettigoniidae with defensive processes on the pronotum.

Taxa	Subfamily	Process type	Modified region	Type of sound	Reference
<i>Acanthodiphrus</i>	Pseudophyllinae	Blunt spines	Metazona	Unknown	Beier, 1962; Naskrecki & Otte, 1999
<i>Acanthorhinischia</i>	Pseudophyllinae	Blunt spines	Metazona	Unknown	Beier, 1962; Naskrecki & Otte, 1999
<i>Aedeus</i>	Pseudophyllinae	Blunt spines	Disk	Unknown	Beier, 1960; Naskrecki & Otte, 1999
<i>Aspidonotus</i>	Pseudophyllinae	Blunt spines	All margins	Unknown	Beier, 1960; Naskrecki & Otte, 1999
<i>Batodromerus</i>	Pseudophyllinae	Blunt spines	Metazona	Unknown	Beier, 1962; Naskrecki & Otte, 1999
<i>Champeonica</i>	Pseudophyllinae	Tubercles/spines	Lateral carines	Broad band/pure tone	Beier, 1962; Naskrecki & Otte, 1999
<i>Choeroparnops</i> spp.	Pseudophyllinae	Conical tubercles	All over	Broad band	Beier, 1960; Morris <i>et al.</i> , 1994
<i>Cymatomera</i>	Pseudophyllinae	Blunt tubercles	Metazona	Unknown	Beier, 1960; Naskrecki & Otte, 1999
<i>Haemodiasma</i>	Pseudophyllinae	Blunt tubercles	Disk	Unknown	Beier, 1962; Naskrecki & Otte, 1999
<i>Orpacanthophora</i>	Pseudophyllinae	Blunt tubercles	All over	Unknown	Beier, 1960; Naskrecki & Otte, 1999
<i>Pantecphylus</i>	Pseudophyllinae	Sharp crests	Lateral carines	Broad band	Beier, 1962; Naskrecki & Otte, 1999
<i>Paradeclus</i>	Pseudophyllinae	Blunt spines	Metazona	Unknown	Beier, 1960; Heller, 1996
<i>Parasimodera</i>	Pseudophyllinae	Rows of blunt tubercles	Lateral carines	Unknown	Beier, 1960; Naskrecki & Otte, 1999
<i>Pemba</i>	Pseudophyllinae	Blunt spines	Posterior margin	Unknown	Morris <i>et al.</i> , 1994
<i>Poliacystroides</i>	Pseudophyllinae	Tubercles/spines	Disk/fore/hind margin	Unknown	Beier, 1960
<i>Polyancistrus</i>	Pseudophyllinae	Tubercles/spines	Disk/fore/hind margin	Unknown	Montealegre-Z. & Morris, 1999
<i>Pristonotus</i>	Pseudophyllinae	Rows of blunt tubercles	Disk/fore/hind margin	Unknown	Belwood & Morris, 1987; Beier, 1962
<i>Pseudophyllus</i>	Pseudophyllinae	Small spines	Disk	Likely pure tone	Naskrecki & Otte, 1999
<i>Sagephorus</i>	Pseudophyllinae	Blunt spines	All over	Unknown	Naskrecki & Otte, 1999
<i>Simodera</i>	Pseudophyllinae	Rows of blunt tubercles	Fore/hind margins	Unknown	Beier, 1960
<i>Spelaeala</i>	Pseudophyllinae	Blunt spines	Lateral carines	Unknown	Naskrecki & Otte, 1999
<i>Lexinas</i> spp.	Conocephalinae	Sharp crests	Fore/hind margins	Unknown	Naskrecki & Otte, 1999
<i>Panacanthus</i> spp.	Conocephalinae	Tubercles/spines	Lateral carines	Broad band	De Jong, 1942; Heller, 1983
<i>Loboscelis</i>	Conocephalinae	Tubercles/sharp crests	Disk/lateral lobes	Broad band	Naskrecki & Otte, 1999
<i>Rhyncoceros</i>	Conocephalinae	Sharp tubercles	Disk/lateral margins	Broad band	Redtenbacher, 1891; Nickle & Naskrecki, 1999
<i>Etyalopsis</i>	Hetrodinae	Sharp spines/crests	Disk	Unknown	Naskrecki & Otte, 1999
<i>Eugaster</i>	Hetrodinae	Sharp spines/crests	Lateral carines	Unknown	Glenn, 1991
<i>Cosmoderus</i>	Hetrodinae	Sharp spines/crests	Lateral carines	Broad band	Grzeschik, 1969
<i>Gymnoproctus</i>	Hetrodinae	Sharp spines/crests	Lateral carines	Unknown	Naskrecki & Otte, 1999
<i>Markia</i>	Phaneropterinae	Sharp spines	Lateral carines	Unknown	Glenn, 1991
<i>Steirodon</i>	Phaneropterinae	Blunt and sharp crests	Anterior margin	Broad band	Naskrecki & Otte, 1999
<i>Stilpnochlora</i>	Phaneropterinae	Blunt and sharp crests	Lateral carines	Broad band	Emsley, 1970
			Lateral carines	Unknown	Emsley, 1970

*Panacanthus*. A character analysis may show that an observed deviate condition is homoplastic and consequently to be rejected as a synapomorphy for all taxa sharing it. However, this character (pronotal armature character 15) is proposed as synapomorphic for less inclusive groups, i.e. for each of the groups in which it is hypothesized as independently present (De Pinna, 1991). Pronotal armature in the genus *Lesina* is more akin to what Glenn (1991) called the 'rack' for species of the genus *Enyalipsis* and its congeners, *Cosmoderus* and *Gymnoproctus* (see Fig. 15D–F).

Pronotal processes in Pseudophyllinae are either apically rounded (blunt) and about the same diameter throughout their length or strongly acute. In most species, blunt projections are arranged in longitudinal rows, as in *Pristonotus*, *Simodera*, *Parasimodera* and in the genus *Tabaria* (see illustrations in the Orthoptera database; Naskrecki & Otte, 1999). All of these processes within a given species have about the same length. In species with acute projections on the pronotum (e.g. *Championica*, *Pantecphyllus*, Fig. 15I) the tips of these processes are acutely sharpened and, if they occur in the metazona, are placed around the hind margin in a crown or rack shape. In some species of Pseudophyllinae having pronotal armature, an erected spine is developed in the midline of the anterior margin of the disk (Table 2, Fig. 15I). In *Choeroparnops*, a nearly continuous field of short conical tubercles occupies regions of the disk and lateral lobes.

Several Phaneropterinae present a pronotal and/or cephalic armature. In various genera of the tribe Steirodontini are species in which the lateral carina of the pronotum is serrate (*Steiroidon* spp. for example, Fig. 15G). In most of these, no armature occurs upon the disk and the armatures, commonly called crests, are orientated laterodorsally (Table 2, Fig. 15). Other species of the same subfamily (*Markia* spp., *Aegimia* spp., and *Paraphidnia* spp.) have pronotal and cephalic projections, used apparently as defensive mechanisms. In *Markia* spp., for example, spines occur on the fastigium, the anterior and posterior margin of the pronotum, and all spines project towards the head (Fig. 15H).

Unrelated lineages have adapted independently to similar habitats by assuming similar armature. The differences in body armature are mainly in number, shape and topography. Some species, distantly related to *Panacanthus* but which co-occur (Table 3), have elaborate defensive spines on the dorsal part of the pronotum as well as on the hind femora. These spines are postulated to have originated independently due to similar selection pressures. The morphological design options for spination in these organisms is somehow limited, which constrains unrelated individuals, resulting in the repeated development of similar morphological structures in several parts of a lineage (Wake, 1991).

#### *Spination (adaptive consequences)*

*Spines on the limbs.* Spines used offensively should mostly be located on limbs so that an insect can deploy them against its prey: spines on the body proper will usually be defensive. Predatory limb spines should also be mostly on the ventral limb surfaces. Among tettigoniids, a clear example of offensive limb spines occurs in Listrosclinae (Rentz, 1995). These spines are articulated and so comparatively flexible and relatively blunt: apparently not designed for penetration. They occur along the ventral aspect of all tibia, in a regularly spaced row of relatively uniform length. Apparently they are used to confine prey within a temporary 'cage' while the insect renders it immobile from above with its mouthparts.

Defensive spines on tettigoniid limbs, on both the tibiae and the femora, can occur both dorsally and ventrally and are usually sharp and nonarticulated (Table 4). They are strong, tapered, rigid extensions of the integument. These spines achieve penetration by the movement of the limb or function as passive mechanical defence when a katydid's own predator tries to manipulate it.

We compared the topography and possible origins of pronotal and femoral spines of selected genera (Tables 2, 4)

**Table 3.** Locations and shared congeneric species with strong body armature in Colombia and Ecuador.

Upland regions	
East slope of west cordillera, Colombia	Macizo de los Pastos, Colombia
<i>Panacanthus pallicornis</i>	<i>Panacanthus gibbosus</i>
<i>Tabaria</i> sp. 1	<i>Tabaria</i> sp. 2
Pleminiini nov. gen. sp. 1	Pleminiini nov. gen. sp. 2
Lowland regions	
Lowlands in Valle del Cauca, Colombia	Lowlands in Pichincha, Ecuador
<i>Pristonotus colombiae</i>	<i>Pristonotus</i> sp.
<i>Championica bicuspadata</i>	<i>Championica echinus</i>
<i>Championica</i> sp.	<i>Championica walkeri</i>
<i>Panacanthus intensus</i> / <i>P. lacrimans</i>	<i>Panacanthus varius</i>

**Table 4.** Some genera of Tettigoniidae with defensive/offensive processes in the limbs.

Taxa	Subfamily	Place where spines occur	Type of spination	Reference
<i>Arrhenotettix</i> spp.	Pseudophyllinae	Ventral on hind femur	Rigid, nonarticulated	Beier, 1960
<i>Myopophyllum speciosum</i>	Pseudophyllinae	Ventral on hind femur	Rigid, nonarticulated	Morris <i>et al.</i> , 1994
<i>Mystron</i> spp.	Pseudophyllinae	Ventral on hind femur	Rigid, nonarticulated	Montealegre-Z. & Morris, 1999
<i>Choeroparnops</i> spp.	Pseudophyllinae	Dorsal on hind femur	Rigid, nonarticulated	Beier, 1960
<i>Diacanthodis</i> spp.	Pseudophyllinae	Dorsal on hind femur	Rigid, nonarticulated	Beier, 1960
<i>Panoploscelis specularis</i>	Pseudophyllinae	Latero-internal on fore femur	Rigid, nonarticulated	Castner, 2000
<i>Lesina</i> spp.	Conocephalinae	Dorsal on hind femur	Rigid, nonarticulated	De Jong, 1942
<i>Panacanthus</i> spp.	Conocephalinae	Dorsal on hind femur	Rigid, nonarticulated	Naskrecki & Otte, 1999
<i>Terpandrus</i> sp.	Listrosclidinae	Ventral on fore tibia	Flexible, articulated	Rentz, 1995
<i>Hexacentrus</i> sp.	Listrosclidinae	Ventral on fore tibia	Flexible, articulated	Rentz, 1995
<i>Chlorobalius leucoviridis</i>	Listrosclidinae	Ventral on fore tibia	Flexible, articulated	Rentz, 1995

with the situation in *Panacanthus*. Defensive spines on the limbs and the pronotum are distributed variably, indicating that defensive spines have evolved more than once in this family. Topographical equivalence is only a parameter for supposing a hypothesis of homology (De Pinna, 1991). De Pinna recognized this as primary homology and stated that its assertion is hypothetical, based on similarity, and reflects the expectation that there is a correspondence of parts that can be detected by an observed match of similarities. In other words, we did not find this primary homology in the pronotal structure nor in the femoral surfaces between *Panacanthus* and other spiny genera. The spines of *Panacanthus* differ morphologically and topographically in a number of ways (Fig. 15). They do not represent homoplasy, but a unique pronotal design in *Panacanthus*.

In *Panacanthus*, a positive correlation exists between the armature of the pronotum and the hind femora. Hind femur dorsal spines are absent in *P. cuspidatus*, which has no pronotal spines. In *P. pallicornis*, rudimentary femoral spines appear distally and to a lesser extent basally, whereas the dorsal pronotum has only small formations of tubercles and callosities. In species of clade C, spines are prominently distributed upon the dorsal surface of the femora and all species in this group also have the pronotum strongly armed. We consider the strong development of one of these spines (character 28) in the middle region of the femur to be a synapomorphy for species arising at node C (Fig. 7, arrows).

**Cephalic armature.** Another important correlative relationship involving armature in *Panacanthus* is an inverse relationship between cephalic armature and the dorsal aspect of the limbs: most pronounced facial spines occur in conjunction with the pronotum and the hind femora, which are minimally armed dorsally. In *P. cuspidatus*, the genae and the frontal fastigium form a dramatic facial ring of spines, whereas the pronotum and the dorsal aspect of the femora completely lack spines (Fig. 7A, B). Facial spines are reduced in *P. pallicornis*, although still contributing notably to the character of the face; the pronotum has some small tubercles and the hind femora are moderately armed on their dorsolateral face. Facial armature has

become minimal in species beyond node C, and at the same time the pronotum is maximally spinose, with several major spines, for example *P. spinosus* (Fig. 7H). At the same time the dorsolateral surface of the hind femur is strongly armed (Fig. 7I, L, O, R, U). What might account for this relationship?

Predators typically attack an animal's head because injury to the brain quickly disables a prey (Alcock, 1989). Diurnal predators recognize a head visually and quite independent of its position on the body (Robinson, 1969a). Vertebrate predators (e.g. birds, bats, mice, monkeys) on capturing a katydid first remove the head (Belwood, 1990). Fastigial and genal spines may well have been selected as deterrents of such predatory behaviour.

Alternatively, one might propose that cephalic ornamentation plays a role in intraspecific aggression when males compete for female access. However, this hypothesis is inconsistent with the observation that *Panacanthus* armature shows no sexual dimorphism. In *Panacanthus*, both females and males invest equally in cephalic spines and it is generally not the case that Orthoptera, engaging in aggressive behaviour, exhibit any cephalic armature (e.g. Gryllus, Alexander, 1961; *Cyphoderris montrosa*, Mason, 1996; *Orchelimum gladiator* Morris, 1971; *Ligurotettix* Greenfield & Minckley, 1993).

**Spines and eavesdropping predators.** Heller (1995) indicated aspects of katydid behaviour that may be adaptive in reducing costs arising from phonotactically orienting predators. These are: (1) an increased reliance on substrate-transmitted reproductive signals such as tremulation, (2) a reduction in the calling song duty cycle and (3) the use of a more limited set of carrier frequencies, i.e. shifting to frequencies to which the eavesdropping predator is less sensitive. Tremulation signalling occurs in *P. pallicornis* as an integral part of the calling display; it is an open question whether substrate signalling takes place in congeners. The song duty cycles of *P. intensus* and *P. cuspidatus* are indeed reduced: the former, a broad-band species, is found in coastal lowland of Colombia, whereas the latter, a pure-tone species, inhabits Amazonian lowlands (of the two species the duty cycle of *P. cuspidatus* is

somewhat higher). There is no clear association of reduced duty cycle and restricted carrier frequencies. Most species have actually shifted away from an ancestral pure-tone song towards a broader band of carrier frequency, possibly increasing their exposure to a phonotactically orienting predator.

Morris *et al.* (1994) found sexual dimorphism in spines on the ventral surface of the hind femora in the Neotropical katydid *Myopophyllum speciosum* and speculated that in this species such spines are more developed in males because this sex is more exposed, by their singing, to eavesdropping predators. However, qualitative sexual dimorphism in armature is uncommon in katydids. Topographically and morphologically there is no qualitative sexual dimorphism in the facial, femoral and pronotal armature of *Panacanthus*. The same is true for other species, unrelated to *Panacanthus* but sharing *Panacanthus* habitat (see Table 3). Two possible interpretations arise: (1) there is no predator-related cost to singing for *Panacanthus* males and the spines function only against daytime predators, (2) there is a predator-related cost to singing, but it is genetically expensive to produce two different phenotypes for males and females in the same species. Therefore, females are selected similarly as males.

*What are the spines for?* According to Söffert (1932), three lines of evidence must be evaluated in order to accept the adaptive advantage of traits as useful in antipredator defence: (1) evidence of convergence of similar characters with distinct morphological origins in different species or species groups. Here we find evidence that pronotal armature has evolved several times in Tettigoniidae. (2) Evidence that the traits are correlated in their taxonomic distribution with appropriate behaviour patterns necessary for them to be effective. The defensive deimatic display shown by all *Panacanthus* is such a behaviour pattern. (3) Evidence of character function. Unfortunately we have no evidence of character function for *Panacanthus* spp.

Spines can also function in crypsis (Robinson, 1969a,b; Edmunds, 1974). *Panacanthus* species are active nocturnally but must (like most tettigoniids) hide themselves motionless in plant refugia through the day. *Panacanthus* spp. spines might conceivably afford protective resemblance by matching the appearance of a spiny plant. In one species (*P. spinosus*), the uniform green of the long tapering spines is interrupted by abruptly dark tips (Figs 7H, 15A): perhaps this improves the resemblance to the insect's refugium where plant spines are actually absent. Crypsis need not conflict with the defensive function of the spine, as the insect mimics a structure, which also serves in mechanical defence. Furthermore, spines might be aposematic, while retaining their effectiveness during actual attack: a predator could come to recognize the characteristic spine-studded *Panacanthus* silhouette, associating it with previous negative experiences with such prey.

Cryptic coloration patterns (Cott, 1957) in the species distal to node C, and observation of some of these species, suggest that *P. lacrimans* and *P. intensus* hide near the

ground. One should not need elaborate spines if the day is spent near the forest floor, camouflaged by coloration. Thus, these species have less elaborate fastigia, and the spines on their limbs are green against a dark background, protected against attack by a diurnal predator. However, they do exhibit the deimatic defence and flight presumably constitutes a secondary escaping strategy.

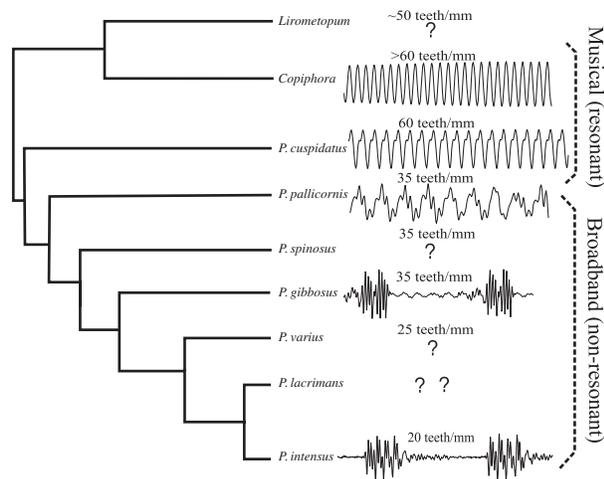
*Possible predators.* *Panacanthus cuspidatus*, *P. pallicornis*, *P. spinosus* and *P. gibbosus* have loud songs with (relative to other *Panacanthus*) high duty cycles. They sing extremely loudly, from elevated perches ranging from understory plants to tree canopy. The high duty cycle, the increased intensity and the openness of the surrounding forest above ground level (Paul & Walker, 1979) all contribute to better range for the calling song and the attraction of more females. But such callers may also more readily attract eavesdropping predators.

Bats can hear over a wide range of frequencies (Simmons & Young, 1999) and may be attracted to calling katydids (Belwood & Morris, 1987; Belwood, 1988). Some bats may be able to detect the spines of katydids by echolocation (Belwood, 1990), although this has not been tested. Bats are capable of sophisticated learning (Tuttle & Ryan, 1981; Barclay, 1982). Thus, eavesdropping bat predators might be able to associate spines with difficult prey insects. Spiny katydids may possibly benefit from such learning (Annamarie Surlykke, Odense University, pers. comm.). Alternatively, bats may be unimportant as predators of large katydids like *Panacanthus* (Otto von Helversen, University Erlangen-Nürnberg, pers. comm.).

The coloration of some species (*P. cuspidatus*, *P. pallicornis*, and *P. spinosus*), and the use of the deimatic display must discourage visually hunting colour-sensitive predators, such as birds. Unlike other katydids (some Pseudophyllinae, for example), which use cavities in branches or curled leaves as refugia during the daytime (Nickle & Castner, 1995; Louton *et al.*, 1996), *Panacanthus* spp. (and some Copiphorinae katydids) usually rest under living tree leaves (Nickle & Castner, 1995). Due to their size and shape, it is difficult for them to enter into a narrow space with the axis of their body parallel to the long axis of folded leaves or bark crevices, as a great number of Pseudophyllinae do (Belwood, 1990), increasing their accessibility to diurnal predators.

#### Bioacoustics

Our cladistic analysis indicates that in *Panacanthus*, non-resonant sound generation has evolved from resonant sound generation. Above node C, the known songs of *Panacanthus* species comprise increasingly shorter pulses and broadened spectra. Below node C, the *P. cuspidatus* phonatome is a sustained sinusoidal wave train (a sustained pulse) of gradually changing amplitude (i.e. it has a smoothly changing amplitude envelope). This has evolved in *P. pallicornis* into a more complex wave train, similar in duration but much



**Fig. 19.** Evolution of the song of *Panacanthus* spp. Showing portions of the song (not at the same scale). The density of teeth is indicated above each oscillogram. '?' indicates that the song is unknown.

more variable in amplitude (Figs 11, 19). Beyond node C, in *P. gibbosus* and *P. intensus*, the phonatome wave train is broken into a number of separated amplitude elements of still greater wave complexity. The spectra of these species reflect this shift from narrow to broader peaks.

These acoustic changes, from resonant to nonresonant, are accompanied by a dramatic reduction in tooth density and in the total number of file teeth (Table 5, Fig. 19). There is an increased intertooth distance and a change in the tooth height/width ratio, i.e. teeth become proportionately higher and narrower (Table 5). For the two species which generate sustained pulses, the teeth locate closer together based on the file and overall there may be less variation in intertooth distance (Montealegre-Z. & Mason, unpublished). These two species making sustained pulses have files less convex and straighter in a transverse direction (Table 5, Figs 9, 14, 16–19) so that the teeth are more nearly coplanar. Some of these same file features correlate with the production of pure-tone songs in Neotropical Pseudophyllinae (Montealegre-Z. & Morris, 1999): teeth in these species are many times broader than high, occur at a relatively high density and their files are elevated on a

'projecting bar separated from the overlying tegmen which may serve to give the scraper a straighter file passage'. The linearity of scraper travel should promote the maintenance of proper phase between tooth and resonator.

The mirror area of *Panacanthus* spp. producing nonresonant song has also undergone changes (Fig. 6C, F, I, L, O, S) which may be consistent with a shift to nonresonant stridulation. The modified tegminal membranes of nonresonant singers are increasingly glassy and thin, and so perhaps more capable of vibrating in intrinsic modes as a result of successive transient tooth impacts. The mirrors of the resonant singers *P. cuspidatus* and *P. pallicornis*, are less transparent and thicker, as expected in a mechanism where membranes are driven by tooth contact rates. The mirror associated vein  $Cu1_b$  is broadened (Fig. 6C, F, I, L, O, S, arrow) in the nonresonant species, a feature shared by all species distal to node C (Fig. 3, Appendix 1, character 23). Demarcating the mirror more sharply with this vein may relate to intrinsic rather than driven vibration.

The polarity of evolving stridulation among exoskeletal animals should always be from broad band towards pure tone, i.e. the ritualization of sound signals must always begin as a nonresonant mechanism. When unspecialized body regions make contact with each other for the very first time, they should produce an unspecialized, broadband, complex waveform. Resonance may then arise subsequently as an apomorphic characteristic in which the file scraper morphology achieves a carefully controlled phase between tooth and radiator movement. To make a sustained pulse there must be many identical teeth, of uniform spacing and higher density. Such a resonant system may still be used on occasion by the insect to make nonresonant output (e.g. cricket aggressive song); but the reverse is not true: a stridulatory structure that is not shaped to achieve proper phase can only produce nonresonant output.

Although all resonant mechanisms must have nonresonance in their history, it does not follow that the emergence of nonresonance from ancestral resonance is a rare event. Desutter-Grandcolas (1997) showed that the evolution of the stridulatory apparatus in phalangopsine crickets (Phalangopsidae) is very plastic. Her work indicates the readiness with which evolution shifts back and forth among several generator states (up to seven). So, it is not in the least surprising that in *Panacanthus*, evolution follows

**Table 5.** Distinctive morphological features of the forewings (tegmina) of *Panacanthus* spp. which might coincide with song differences.

Taxa	Tooth density	Tooth profile symmetry	Tooth number	Tooth dimensions
<i>Copiphora</i> sp.	58–98 teeth $mm^{-1}$ (high density)	Symmetrical	150–275	Broader than high
<i>P. cuspidatus</i>	60 teeth $mm^{-1}$ (widely spaced)	Symmetrical	312	Broader than high
<i>P. pallicornis</i>	38 teeth $mm^{-1}$ (widely spaced)	Asymmetrical	248	Diagonal, narrow
<i>P. spinosus</i>	40 teeth $mm^{-1}$ (widely spaced)	Asymmetrical	210	Diagonal, narrow
<i>P. gibbosus</i>	42 teeth $mm^{-1}$ (widely spaced)	Asymmetrical	240	Diagonal, narrow
<i>P. varius</i>	25 teeth $mm^{-1}$ (widely spaced)	Asymmetrical	130	Diagonal, narrow
<i>P. maculifrons</i>	25 teeth $mm^{-1}$ (widely spaced)	Asymmetrical	130	Diagonal, narrow
<i>P. intensus</i>	19 teeth $mm^{-1}$	Asymmetrical	95	Diagonal, narrow

a reversal of the larger trend towards resonance from non-resonance mechanisms.

Naskrecki (2000b) showed that female stridulatory structures are plesiomorphic in older tettigoniid lineages such as Ehippigerinae and Bradyporinae. In his view, females used these structures to respond to male calls, and in defence (as protest sounds directed at predators). These primitive female acoustic signals are supposed to have been resonant in nature (Naskrecki, 2000b), i.e. pure tones were the most plesiomorphic condition among singing female tettigoniids. This conclusion is based not upon published spectral analyses of female tettigoniid sounds, but on the argument that female generators are comparable in structural sophistication to those of their males.

This inference of pure-tone stridulation by ancestral female tettigoniids is unjustified. The essence of resonant stridulation is phasing between the teeth of a pars stridens and the oscillation of a uniformly composed, typically single, tegminal resonator. Tooth contacts must be timed to the ongoing harmonic movement of the radiating tegminal membrane to keep it moving smoothly at a particular frequency. The pars stridens of Ehippigerine females involves a single transverse file which Naskrecki takes as the basis of social signal generation, as well as some additional toothed veins nearby, which he considers likely to serve only in defensive stridulation. However, there is no evidence that all of these are not used concurrently, and many of the other female stridulatory systems, including the independently evolved Phaneropterine type, involve multiple-toothed pars stridens, better characterized as tooth fields than files. Such a structure cannot contribute proper phasic inputs to a resonating wing cell if several teeth engage at the same time. In *Ehippiger bitterensis* (Finot) (Dumortier, 1963, fig. 163), males with a similar but more robust file produce a markedly nonresonant spectrum. There is little morphological basis for expecting the females of this species to be any different and thus we expect that in these ancestral lineages, nonresonant female stridulation is the more probable ancestral condition (Robinson, 1990), and not the production of pure tones.

What selective pressures might effect a shift from resonant to nonresonant stridulation in katydids? One possibility is competition between males in the acoustic stimulation of prospective mates. If a male's calling causes firing by a higher proportion of sensory audioreceptors of listening females than a rival's, that male should fare better in competing for her attention. In general, the ear-tuning curves of katydids are quite broad (Nocke, 1975; Kalmring *et al.*, 1985; Oldfield, 1985; Römer, 1985), perhaps as a result of the importance of bat detection. So it is not unreasonable that there might be ample room to increase a call's stimulatory effectiveness by shifting towards a band rather than a tuned spectrum.

Broad-band songs might also evolve as an adaptation for distance ranging by differential degradation of higher vs lower carrier frequencies in dense vegetation (Michelsen, 1985). Keuper *et al.* (1986) measured changes in the power spectra of the calls of species living close to the ground. They confirmed that calls having a lower dominant frequency

propagated over longer distances. Generating a song with a broad-band spectrum would increase the probability that spectra code for the intervening distance between a signalling male and an approaching female. Broad-band signals are also less vulnerable to the masking effect of noise than high-Q signals.

We noted within *Panacanthus* a possible correlation between the production of low-Q spectra and the possession of spines (a similar conjecture was made recently by Nickle & Naskrecki, 1999). However, there might be a high probability of observing this association by chance in our study, given the small number of species in the clade. Many other aspects of the natural history of these interesting insects await study.

## Acknowledgements

This study was supported by Natural Sciences and Engineering Research Council of Canada operating grant (4946) to GKM and by a grant from the Orthopterists' Society to FM-Z. We acknowledge the valuable comments of Douglas Currie, Robert Murphy and Andrew Bennet of the University of Toronto and the Royal Ontario Museum, Canada. Thanks also to the following people from Colombian institutions for providing help while FM-Z worked on each collection: Dr Nora Cristina Mesa and Ing. Reinel Garcia (MEUNP), Professor Oscar E. Ortega (MEUNM), Dr German Amat, Dr Eduardo Florez and biologists Fredy Gomez and Andres Varon (ICN), Dr Ranulfo Gonzalez, Dr Nancy Carrejo and Dr Patricia Chacon (MEUV). Piotr Naskrecki provided material from his collection and made helpful comments on the manuscript. Special thanks to Carlos A. Saldarriaga 'Capullo' for his company and hard work in the rainforest locations of the Pacific Coast of Colombia. Harol Berrio, Paul DeLuca, Dita Klimas and Adrienne Rigler participated in field collection in 1996. The biologists Milton Reyes 'cacorrín' and David Fajardo 'pulgoso' provided some material from their work at Escalerete. Dr Janse Bittner, Pedro Moreno and Maria Fernanda Moreno provided permits and accommodation enabling work at the reserva La Planada, Abelardo Nastacuaz and L. Moncayo helped during fieldwork at this location. All photographs in the field were taken by F. Vargas. S. Taran Grant from the American Museum gave guidance and ideas at the beginning of this project. Fanny and Maria C. Montealegre took care of the insects in captivity. We also thank Anne Gerber for providing her unpublished information and Dr Otto von Helversen and the people of his laboratory for all their useful feedback. Thanks to Liliana Castaño for helping with the edition of the manuscript and for taking care of the specimens in the laboratory and to Ariadne Angulo for allowing us to use the MACCLADE software.

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Accepted 26 February 2003

**Appendix 1.** Matrix with thirty-nine characters, all unordered. No weightings were applied.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	
<i>Lesina</i>	2	2	0	0	0	0	0	0	0	0	0	0	0	0	4	0	1	0	0	0	0	?	0	2	1	0	0	0	?	?	0	4	3	2	0	?	?	?	?	
<i>Copiphora</i>	0&1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2
<i>Lirometopum</i>	0	1	1	1	0	0	1	1	1	2	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
<i>P. cuspidatus</i>	1	0	2	2	0	0	1	1	1	2	1	2	1	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	2	0	0	1	1	2	0	0	0	1	1	
<i>P. pallicornis</i>	1	0	2	2	1	0	1	2	1	2	1	2	0	1	1	0	0	1	1	1	1	0	0	1	0	1	1	0	2	1	0	0	2	3	0	1	0	0	1	
<i>P. spinosus</i>	1	0	2	2	1	0	1	2	1	2	1	2	0	1	2	1	0	1	1	2	1	0	1	1	1	2	1	1	2	1	0	2	2	4	1	1	1	0	1	
<i>P. gibbosus</i>	1	1	2	1	1	1	1	1	1	2	1	2	0	1	2	1	2	0	1	2	1	0	1	2	1	2	1	1	2	1	1	3	2	4	1	1	1	2	1	
<i>P. varius</i>	1	1	2	1	1	0	1	1	1	2	1	2	0	1	3	2	2	0	2	2	1	1	0	2	1	2	1	1	2	1	1	2	2	5	2	1	1	2	1	
<i>P. lacrymans</i>	1	1	2	1	0	1	1	1	1	2	1	2	0	1	3	2	2	0	2	?	?	?	0	2	1	2	1	1	2	1	1	?	?	5	2	?	?	?	1	
<i>P. intensus</i>	1	2	2	1	0	0	1	1	1	2	1	2	0	1	3	2	2	0	2	2	1	1	0	2	1	2	1	1	2	1	1	2	2	5	2	1	1	2	1	

**Appendix 2. Character description**

- Form of the vertexial fastigium*: (0) short, acute, toothed; (1) elongate, acute, toothed; (2) semi-elongate, not toothed. ci = 1.0.
- Structure of the vertexial fastigium*: (0) curved ventrally on the apex; (1) straight; (2) curved dorsally on the apex. ci = 0.5.
- Dorsum of vertexial fastigium*: (0) smooth; (1) granulate; (2) spinose. ci = 1.0.
- Gena I (external surface)*: (0) smooth; (1) moderately tuberculate; (2) strongly spinose. ci = 0.67.
- Gena II (tubercle on region III)*: (0) absent; (1) present. ci = 0.5.
- Marks on the clypeus*: (0) absent; (1) present. ci = 0.33.
- Eyes*: (0) normal; (1) protruding from the head capsule. ci = 1.0.
- Eye colour in life*: (0) other; (1) yellow-cream; (2) red-pink. ci = 0.67.
- Ocular lobe of the brain*: (0) normal; (1) strongly elongate. ci = 1.0.
- Basal tooth of the lacinia*: (0) ventrally broad and carinate; (1) ventrally narrow and serrate; (2) ventrally narrow and carinate. ci = 1.0.
- Mandible I (molar lobe)*: (0) small, far from the mandible apex; (1) conspicuously developed, close the mandible apex. ci = 1.0.
- Mandible II (incisor)*: (0) absent; (1) present but poorly developed; (2) present and conspicuously developed. ci = 1.0.
- Frontal ocellus*: (0) small, oval; (1) big, orbicular. ci = 1.0.
- Pronotum I (ventroposterior margin)*: (0) straight; (1) upturned. ci = 1.0.

15. *Pronotum III (defensive processes)*: (0) absent; (1) present as tubercles; (2) present as branched spines; (3) present as smooth spines; (4) racklike. ci = 1.0.
16. *Pronotum IV (dorsal medial strip on the disk)*: (0) absent; (1) straight; (2) bifurcate on the occiput. ci = 1.0.
17. *Pronotum V (dark marks on the lateral lobe)*: (0) absent; (1) present as type 1; (2) present as type 2. ci = 1.0.
18. *Anal margin of the tegmina*: (0) colourless; (1) reddish. ci = 0.5.
19. *Costal margin of the tegmina*: (0) straight; (1) marginally curved; (2) abruptly constricted on the distal half. ci = 1.0.
20. *Bifurcation Cu2 and 2A (mirror veins)*: (0) slender; (1) moderately broad basally; (2) broad basally. ci = 1.0.
21. *Stridulatory area in both tegmina*: (0) symmetrical; (1) asymmetrical; ci = 1.0.
22. *Teeth of the stridulatory file*: (0) straight; (1) bent and curved in one side. ci = 1.0.
23. *Females wings*: (0) macropterous; (1) brachypterous. ci = 0.5.
24. *Fore limbs*: (0) shorter than the midlimbs; (1) longer than the midlimbs; (2) about equal to the midlimbs. ci = 0.67.
25. *Hind femur compared with the fore femur*: (0) shorter; (1) longer. ci = 0.5.
26. *Hind femur armature*: (0) absent; (1) distally present; (2) covering the whole surface; ci = 1.0.
27. *Fore tibia armature*: (0) dorsally smooth; (1) dorsally strongly armed. ci = 1.0.
28. *Dorsal hook on the hind femur*: (0) absent; (1) present. ci = 1.0.
29. *Proventriculus I (barbate lobe)*: (0) type 1; (1) type 2; (2) type 3. ci = 1.0.
30. *Proventriculus II (texture of the sclerotized appendage)*: (0) strongly harsh; (1) moderately harsh. ci = 1.0.
31. *Abdominal terga coloration*: (0) colourless; (1) with dark trapezoidal marks. ci = 1.0.
32. *Cercus of the male*: (0) apically blunt with one internal process; (1) apically semiforked with one internal process; (2) apically forked with one internal process; (3) apically folded and semiforked with one internal process; (4) different. ci = 0.5.
33. *Titillators*: (0) apically smooth; (1) apically hooked and smooth; (2) apically minutely dentate; (3) other. ci = 1.0.
34. *Female subgenital plate I*: (0) type 1; (1) type 2; (2) type 3; (3) type 4; (4) type 5. ci = 1.0.
35. *Female subgenital plate II (lateral surface)*: (0) smooth; (1) moderately depressed; (2) conspicuously depressed. ci = 1.0.
36. *Type of sound mechanism used*: (0) resonant; (1) non-resonant. ci = 1.0.
37. *Infrastructure of the sound envelope*: (0) absent; (1) present. ci = 1.0.
38. *Duty cycle*: (0) high; (1) medium; (2) low. ci = 1.0.
39. *Deimatic defence*: (0) absent; (1) present as type I; (2) present as type II. ci = 1.0.