Panoploscelis specularis (Orthoptera: Tettigoniidae: Pseudophyllinae): extraordinary female sound generator, male description, male protest and calling signals

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Abstract

Females of *Panoploscelis specularis* present a dramatic modification of their forewings for stridulation. The female generator is illustrated and its distinct form contrasted with that of males. The physical form of the signals that females might produce is inferred; male calling and protest signals are characterized. The male of *P. specularis* is described for the first time.

Key words

stridulation, katydid, Colombia, Ecuador, defense, acoustic

Introduction

Though male katydids are typically the sex that sings, tettigoniid females of many species also have tegminal stridulatory organs. Such structures may be universal among females of Phaneropterinae and Ephippigerinae (Hartley *et al.* 1974; Naskrecki 2000), where they function in pair formation as the sexes exchange calls. But the role of female generators in other katydid taxa is likely to be defensive not social, with sound given only under disturbance, *e.g.*, in females of the pseudophylline *Scopiorinus impressopunctatus* (Naskrecki 2000, p. 206).

The sound radiating wing speculae of female *Panopscelis scudderi* Beier (Eucocconotini) Beier 1950), are the basis of the species name. This sound generator is more elaborate than those of pseudophylline and phaneropterine females, being as complex as the respective male organs -- as is also the case in Ephippigerinae (Dumortier 1963, Fig. 163, p. 301). In females of Phaneropterinae, spines or pegs lie along veins on the upper surface in the anal field of the right tegmen (Leroy 1971). A sharpened, down curving margin on the ventral surface of the left tegmen overlaps and engages this irregular spine-field (Nickle & Carlysle 1975, Heller & von Helversen 1986). Among false-leaf katydids (Pseudophyllinae) other than *Panoploscelis*, female stridulatory structures, found in the tribes Polyancistrini and Pterophyllini (Naskrecki 2000), are again, relatively simple.

Last revised by Beier (1960), *Panoploscelis* Scudder (1869) contains 4 species found in rainforest understory in the higher drainage of the Amazon basin of Ecuador, Colombia and Peru. Beyond taxonomy little is published about these insects. They are mentioned in the context of defensive display (Nickle & Castner 1995), the ability of females to produce song (Castner 2000), and the evolution of calling song production and role-reversal in females (Gwynne 2001). The 4 *Panoploscelis* species are: *P. armata* Scudder, *P. scudderi* Beier, for which both sexes are described, *P. specularis* Beier and *P. angusticauda* Beier, the latter two known to date only by the female.

In the present paper we describe the previously unknown male of *P. specularis*, the generator morphology of its female and present a first analysis of the physical characteristics of male calling and protest sounds.

Methods

Field work and recordings.—Three adult specimens, studied while alive, were collected in Colombia and Ecuador: in Colombia (FM-Z), at Amacayacu National Natural Park (PNN) in the Depto de Amazonas (3°50' to 3°02' South, 69°54' to 70°20' West), between 24 April and 8 May 2000; in Ecuador (GKM), at Primavera, Prov. Napo, (0°25' South, 76°45' West) in late July of 1985. Amacayacu, 293.5 ha at an elevation of 100 m, receives an annual rainfall of 3000 mm and has a mean temperature of 27°C. Primavera is on the Rio Napo in the Oriente of Ecuador, 26.5 km east of Coca (Puerto Francisco de Orellana) at about 90 m above sea level.

Two adult males, 1 adult female and an immature of *P. specularis* were collected overall. These specimens were maintained in captivity on a diet of apples, carrots and small insects; the adult male from Ecuador was transported alive to Canada while the Colombian specimens were kept within Colombia. Two additional adult pinned specimens, a male and female, were also available for study (Royal Ontario Museum).

Some recordings, limited to the audio range (Sony Walkman Professional WM-D6C tape recorder, ECM 909 microphone) were made in the field at the PNN biological station in Colombia: *P. specularis* calling song was recorded from a single caged specimen. This male and a female were then transported to Palmira (Colombia, Depto del Valle del Cauca) where the male's calling, as well as protest sounds, were recorded using equipment incorporating both audio and ultrasonic ranges (flat response 100 Hz to 70 kHz): output of a 1/4" Bruel & Kjaer condenser microphone (4135) went to a B & K sound level meter (2204). Meter output was stored on a Racal instrumentation tape recorder at a speed of 30"/s. Sound levels with this meter were (re 20 µPa) maximum needle displacement on impulse setting. Recording of the Ecuadorean male was accomplished in Canada with the same ultrasonic-effective equipment. For analysis, slowed signals were digitized with a Tucker Davis Technologies PC board (TDT – System II) and examined with DADiSP software (DSP Development Corporation).

Scanning electron micrographs (SEMs) of specimens were made with a Hitachi S-2500 microscope (Department of Zoology, Uni-
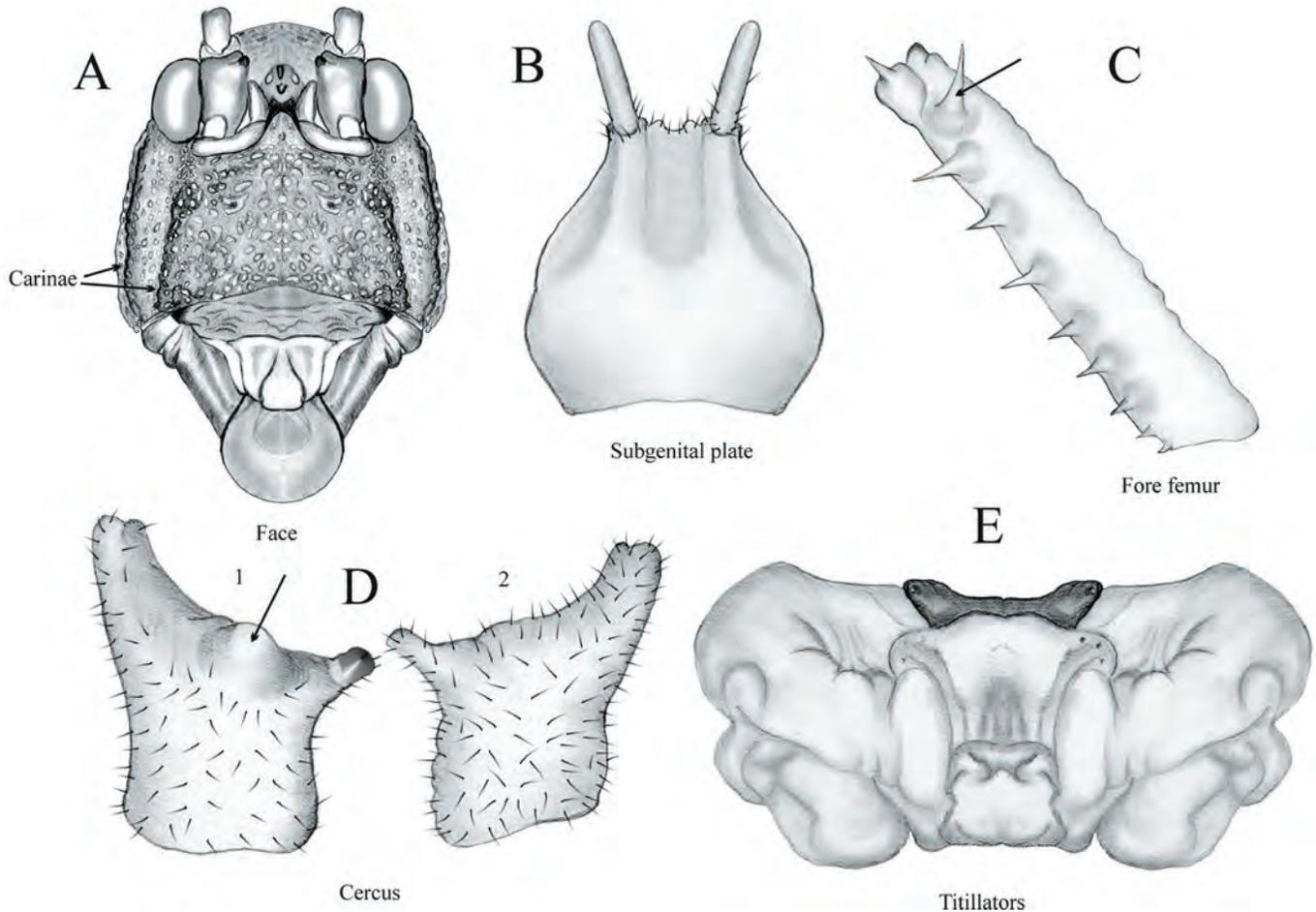
Fig. 1. *Panoploscelis specularis* male: A. Head in frontal view; B. Subgenital plate; C. Inner side of right fore femur (arrow indicates redirected species-diagnostic distal spine); D. Right cercus inner view (1), lateral view (2); E. Titillators, everted from alcohol-preserved specimen.

versity of Toronto). For males stridulatory file teeth measurements (inter-tooth distances and tooth angle) were calculated from SEMs using the dimension tools of Corel Draw. Inter-tooth distance was measured between tooth apices viewed side-on (Fig. 2B). The angle presented by each tooth to the advancing scraper (during closure) was measured at the base of the tooth face, as that between a base line established over (4 to 5) file teeth (an imaginary line joining the low points of gullets) and a line projected along the transverse apex of the tooth. This was accomplished with a series of SEM photos, using groups of teeth to minimize the error introduced by perspective (Fig. 2B).

Terminology (modified from Morris *et al.* 1989).

Call period: the time interval between the onset of 2 successive calls, incorporating the silent interval (down time) between calls.
Call duty cycle: proportion of the call period spent emitting song.
Rapid-decay pulse: a train of complex waves characterized by its transience, and showing rapid decay after only one or a few cycles at maximum amplitude. Such a pulse has a broad-band spectrum. This form of stridulatory sound production is known as nonresonant (Elsner & Popov 1978).
Sustained sinusoidal pulse: a wave train characterized by gradual onset of a sinusoidal waveform, sustained for several to many

cycles at or near, its highest amplitude. This kind of pulse has a narrow band spectrum and is referred to as pure-tone. Such sound production is termed resonant (Elsner & Popov 1978).
Quality factor (Q): tonal purity of an oscillator and a measure of the range of frequencies over which a system can be driven successfully (Prestwich *et al.* 2000); the resonant frequency of a system divided by the frequency bandwidth, usually at 3 dB below peak amplitude (Ewing 1989). The higher the Q value, the narrower the range of carrier frequencies and the more sharply tuned the system.
Tooth angle: the angle that each tooth face, measured at its base, makes to an imaginary line (base line) joining the low points of several spaces (gullets) between teeth.

Results

Description of the stridulatory apparatus.—**Female:** Females of *P. specularis*, and females of other species in the genus, possess a bilaterally asymmetrical tegmino-tegminal stridulatory apparatus (Fig. 2D, see also Gwynne 2001, Fig. 9.21). On both tegmina an ovoid 'mirror' (speculum) is traversed by subparallel weakly arcuate crossveins. The mirror of the right is slightly smaller than that of the left. Nearly equidistant on the left tegmen, the crossveins divide it into 4 subequal cells; on the right tegmen they are
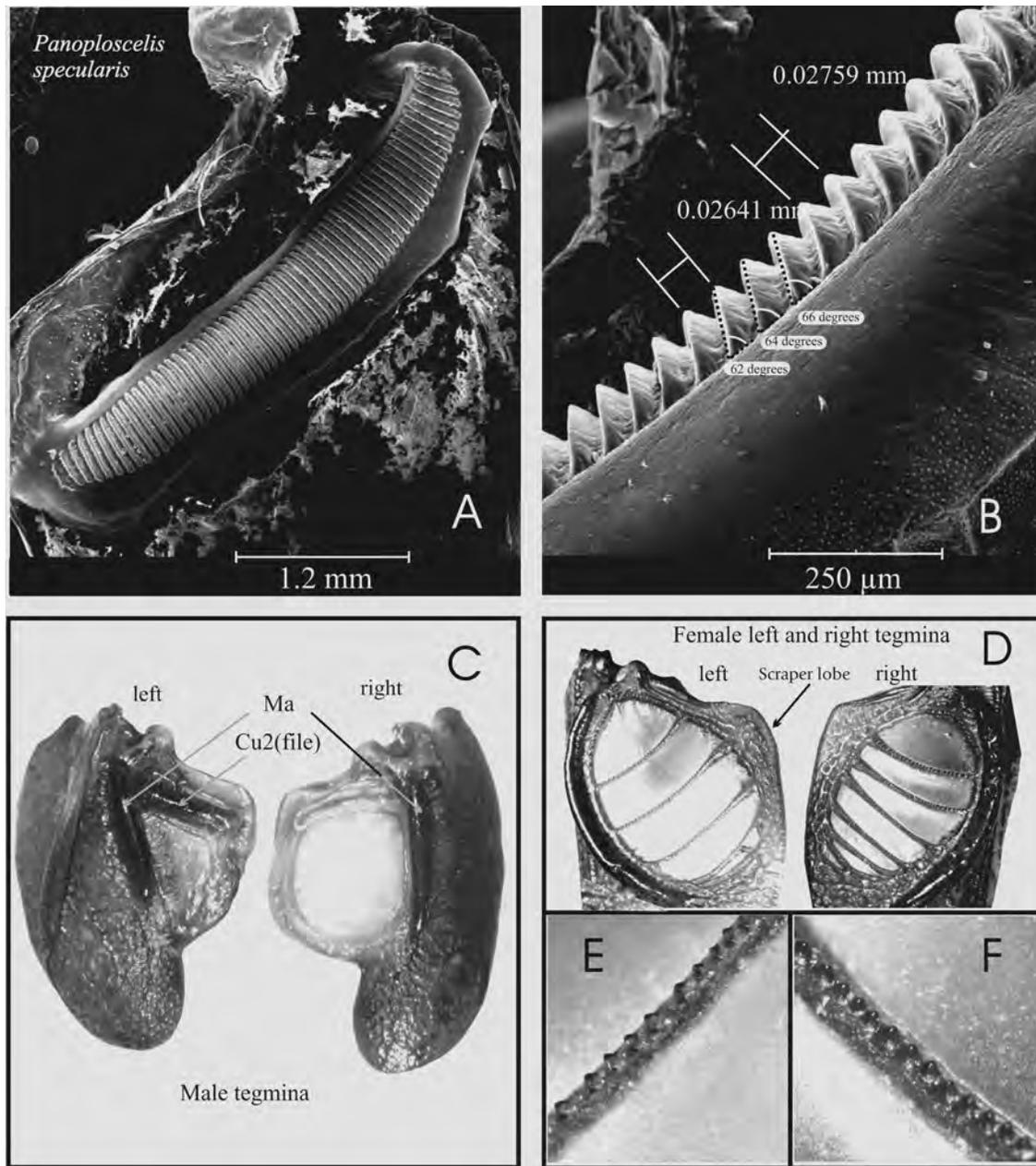
Fig. 2. Stridulatory structures. A. Stridulatory file of male; B. Lateral view of teeth in middle of male file; C. Left and right tegmen of male; D. Left and right tegmen of female; E. Tooth detail of crossvein of female left tegmen; F. Tooth detail of female right-tegmen crossvein.

slightly more robust. The crossveins run toward a curved, dorsally protruding, massive media (Fig. 2D). All these veins are topped equally by a series of small teeth (Fig. 2E,F). The crossvein teeth of the right tegmen are as well developed as those of the left; and similar teeth or denticles carpet the tegminal regions distal to the mirrors (Gwynne 2001).

In keeping with this wide distribution of dorsal-surface teeth, the apparent scraper is a very elongate downturned anal margin. It runs beside the speculae for their length and should be able to engage crossvein teeth on an underlying tegmen with either overlap. But the overlap observed in female specimens to date is always left over right, *i.e.*, as that of most tettigoniids (Masaki *et al.* 1987). Thus it seems that the female normally stridulates with the same overlap as her male. In keeping with this there is a tegminal asymmetry in the shape of the left tegmen scraper: just opposite the second crossvein from the wing base, the left forewing margin is drawn evenly out into a lobe (Fig. 2D). The downturned anal margin extends basad and distad from this lobe, so the lobe may not define the extent of the functional plectrum.

—**Male.** Ventrally the left wing possesses a stridulatory file with 55 to 62 rather broad teeth (Figs 2A). The file (Cu2) is strongly elevated on a swollen vein buttress. The male's right wing has a quadrangular mirror with a weakly corrugated surface. There are no other modified cells so only the mirror is involved in the radiation of sound.

The distribution of teeth on the file, their inter-tooth distance, is not very uniform (Fig. 5A), and tooth angle shows a substantial rather linear, increase proximad (*i.e.*, anteriorad on the file) (Fig.

5B). The distance between teeth is nearly constant in the middle portion of the file, but increases somewhat toward both extremities (Fig 5A).

Bioacoustics

Specimens were collected at night from understory foliage at about 1.5 m above the ground. The Colombian male was observed singing, just <5 m from a female and at about the same height; we did not detect any female acoustic response. The two Ecuadorean specimens were both males, one adult, one a penultimate instar. All specimens (except the immature) produced protest sounds repeatedly when collected: those of both sexes were loud and noisy.

Male calling song.—
The time-amplitude song element of this species, resolvable by the human ear, is a zip (a short noisy sound of <1s with perceptible infrastructure (Morris *et al.* 1989)). Zips are produced at the rate of about 1 per 3 s (25 to 26°C). Mean silent intervals of 3.2 s (n=9) occurred between songs.

(Values for various song parameters given below and accompanied by ranges, are means of 6 element repetitions for the single available male.) Each male calling song is 2 pulse trains, one higher in amplitude than the other (Fig. 3A, B). An average downtime of 132 ms occurred between these trains (Fig. 3B). Song duration was 0.160 s (range 0.15 to 0.17). The period of each song was 3.7 s (range 2.7 to 4.4). The higher amplitude pulse train, with 11 rapid-decay pulses (range 9 to 12) lasted 20 ms. The low-amplitude train with only 3 rapid-decay pulses (range 2 to 4) had a duration of 10 ms. Pulses of the high-amplitude train typically had two nearly equal amplitude maxima per pulse (Fig. 3C).

Spectra are almost identical for the two trains (Fig 3E, F), a band of carrier frequencies extending from mid-audio to well beyond 30 kHz in the ultrasonic. At 25 to 26°C, one song the time-sample basis of each spectrum, the mean of the maximally intense peak, was 11.3 kHz (range 11.0 to 13.4 kHz). Sound pressure level at 12 cm dorsal was ~103.3 dB (n = 5). No significant energy occured beyond 40 kHz.

Protest stridulation by the Colombian female, was heard in the field at the time of her capture. During monitoring of the calling male in the PNN field lab this female was nearby, but gave no acoustic response. The female during the indoor monitoring was very stressed and weak, which may have affected her behavior. Calling song by the Ecuadorean male was never observed.

*Male protest signal.—*As with the calling song, the shortest time-amplitude element of protest sounds resolvable by the human ear is a zip, recurring at a rate of once every 4 s at 23°C.

Protest sounds were recorded in Canada (1985, GKM), from the specimen collected in Ecuador, using full-range frequency equipment (100Hz-70kHz). The insect was stimulated to protest by spraying it with water or by blowing air on it. [Number of element repetitions contributing to means given below (followed by ranges) is 4.] Mean principal peak was at 11.2 kHz (23°C, range 9.2 to 15.5 kHz), very close to the mean principal peak of the calling song of the Colombian male. The sound pressure level, 12 cm dorsal, was ~100 dB. The protest spectrum also incorporated substantial ultrasonics: 20 to 35 kHz (Fig. 4C), but with no significant energy beyond 33 kHz.

Calling songs present common features with protest sounds. Both signals have almost identical low-Q, broadband spectra. But protest sound is apparently distinctive in its AM pattern: it consists of just 2 or 3 rather longer rapid-decay pulses (Fig. 4A) lasting about 8.3 ms (mean based on 4 sound repetitions, range 7.1-11.0) (Fig.4B).

Along with production of their protest sounds these insects assume a defensive 'deimatic' (see Maldonado 1970) posture. They face the source of stimulation, elevate the anterior of their body and lift their left and right foreleg femora well above their body, displacing their forelimbs to the side. Mandibles are repeatedly opened and closed, the labrum elevated and lowered. Released upon a bedspread in a hotel, the highly disturbed Ecuadorean male assumed this posture and repeatedly directed bites down to seize and lift the fabric. Given their size and black spiny appearance this display suggests the possibility of effective weaponry directed at an attacker.

Rearing displays by spiny species are reported in other tettigoniids, e.g., *Panacanthus* spp (Montealegre & Morris 2004), with "foreleg batting" (Nickle & Castner 1995) suggested as a "retaliatory defense" (= offense). It is probably relevant that these species, engaging in such behavior, are among the largest of tettigoniids. A particularly effective color illustration of a comparable display by the tettigoniid *Neobarrettia spinosa* is provided as a frontispiece by Cohn (1965).

Taxonomy

Panoploscelis specularis Beier

Distribution.— Western Amazon basin from Ecuador to the conjunction of Brazil, Colombia and Peru.

Description of the male.—
Head: fastigium frontis conical tubercular; a carina runs dorsad above anterior mandibular articulation, another more posteriorly crosses gena (Fig. 1A, arrows). **Thorax**: Pronotum minutely densely rugose, metazona lateroanteriorad with 2 smooth areas derived from the transverse sulcus. Transverse sulci deeply incised, the mesometazona sulcus deeper than the promesozona. Posterior margin of pronotum rounded, minutely notched mesad.
Legs: Anterior femora longer than mid femora, bearing strong spines on interior ventral margin; two distal spines more developed, oriented anteriorad with respect to other spines on this margin (Fig. 1C); without a dorsal spine series. Anterior and mid tibiae with dorsal and ventral spines, anterior tibia dorsal spines on both interior and exterior margins, mid tibia with only a row on internal margin.
Tegmina: reduced (Fig. 2C), reaching distal margin of second abdominal tergite. Sc and R converging at costal margin. Ma protruding, strong in both tegmina (Fig. 2C, arrow). Mirror area of left tegmen somewhat triangular. Stridulatory vein convex, bearing about 60 teeth, higher than broad and varying in intertooth distances (Figs 2B, 5A); tooth angle also variable (Figs 2B, 5B). Mirror of right tegmen subquadrate, plane of surface rather uneven with slight corrugations (Fig. 2C).
Abdomen: cercus short, stout, with 2 projections, one dorsal, one ventral; dorsal projection broader, apically broad, ventral projection narrower, incurved, apically sclerotized, subacuminate (Fig. 1D); a blunt tooth protrudes between both projections (Fig. 1D$_1$, arrow). Supraanal plate rounded, paraprocts triangular and conspicuously developed. Titillators mostly membranous except for sclerotized bicuspidate area in dorsal part (Fig. 1E). Subgenital plate broad at

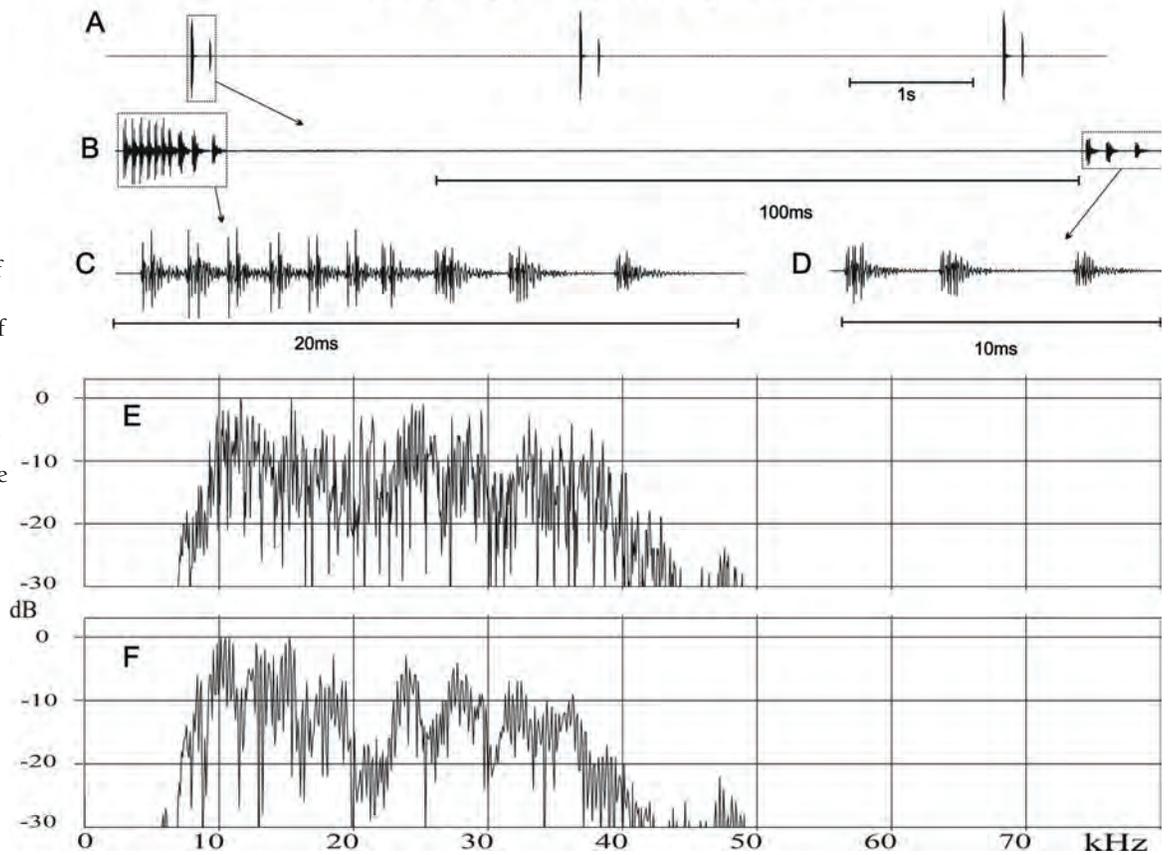Calling song of *Panoploscelis specularis*

Fig. 3. Calling song of *P. specularis* (Colombian) male.
A. Sequence of 3 consecutive songs;
B. Expanded view of the first song in A;
C. Expanded view of the first pulse in B;
D. Expanded view of the second pulse in B; E. Spectrum of C; F. Spectrum of the pulse train in D.
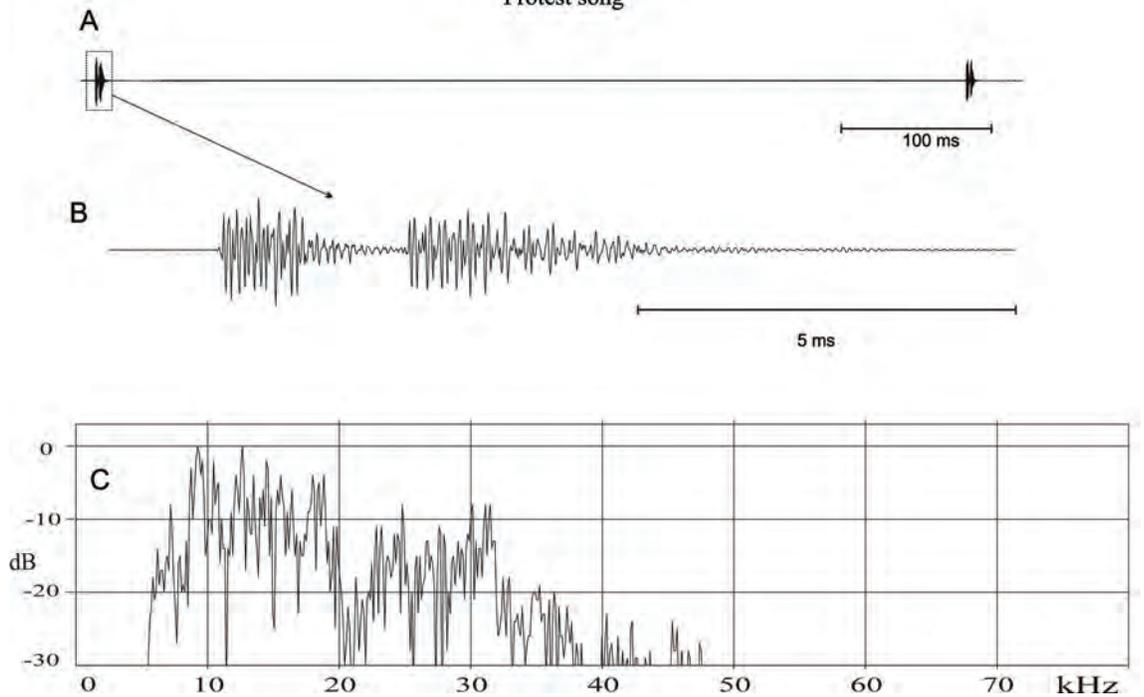
Panoploscelis specularis
Protest song

Fig. 4. Protest song of *P. specularis* (Ecuadorean) male.
A. Sequence of 2 songs;
B. Expanded view of the first song in A;
C. Spectrum of the pulse in B.

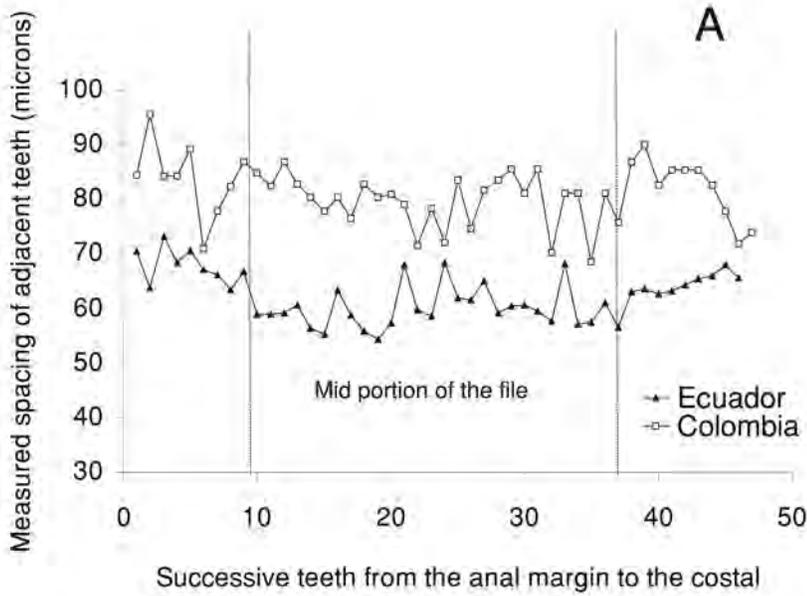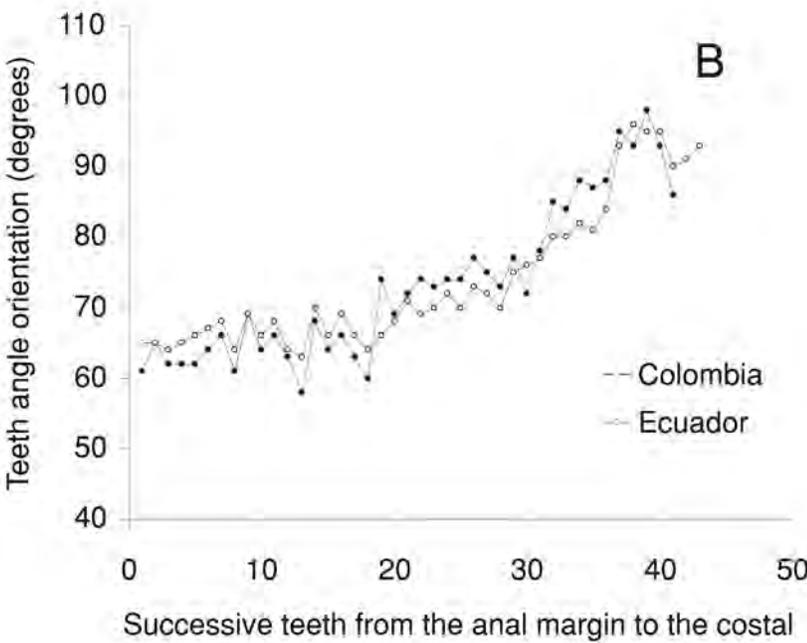**Fig.5**. Tooth arrangement on the file of *P. specularis*. A. Distance between successive teeth numbered from the anal margin;

B. Change in tooth angle along the male's file.

bases, tapering distally, distal margin medio-distally sinuate, with cylindrical and moderately elongate styles (Fig. 1B).

Color description.— (based on color slides of living specimens): Head, thorax and abdomen fuliginous. Legs and basal half of the ovipositor brunneus. Mandibles, dorsal part of the tarsi fulvescent. Cercus and ventral part of the tarsi helvus. Morphological measurements are given in Table 1.

Specimens examined.— COLOMBIA: Dpto del Amazonas: PNN Munchique: Quebrada Matamata: 1 adult male, 1 adult female,

Apr 30, 2000, Coll. F. Vargas & F. Montealegre-Z. (ICN). ECUA-DOR: Prov. Napo: Primavera: 1 adult male, 1 immature male; Jul 20, 1985, Coll. G.K. Morris (ANSP). Prov. Napo, Yasuni Natl Pk, 0°40'South, 76°20' West, Tiputini:1 adult male, Feb15-22, 1997, Coll. D.C. Darling (ROM). Prov. Napo, Yasuni Natl Pk, 0°40'South, 76°20' West, Tiputini: 1 adult female, Feb 14-19, 1998, Coll. D.C. Darling (ROM).

Remarks.— A diagnosis of this genus can be found in Beier (1950,1960). Other morphological traits and the habitus of *Panoploscelis* spp. are illustrated in the Catalog of Orthoptera (Naskrecki & Otte 1999). Characters presented in Table 2 will separate species.

Discussion

Female sound production.— The likely physical structure of the sounds made by female *Panoploscelis* can be inferred from the form of their generator. The tegminal membranes are excited into motion, not from a linear file of highly similar teeth, but from (at least) teeth distributed across 3 transverse veins. What are in effect multiple files cannot result in critically timed restimulation of the vibrating wing structures necessary for the working of a resonant generating mechanism. In such systems the rate of tooth contact must be phasic with the regular oscillation of a predominant resonator (Montealegre & Morris 1999). Along with this, and in conjunction with the bilateral asymmetry of the tegmina, *P. specularis* females have not one 'mirror' (resonator-radiator), but a series of tegminal cells (speculae) of varying size. The best frequency will be different for each because of differences in membrane area, thickness and mass. So the female mechanism is certain to be a nonresonant generator which through simultaneous occurrence of multiple carriers results in the production of a broadband, low-Q, spectrum.

Functions.—Tegmino-tegminal stridulatory structures among female Tettigoniidae are typically not homologous with male structures : Bradyporinae are an exception (Naskrecki 2000). In Ephippigerinae, Phaneropterinae and the pseudophylline tribe Polyancistrini, a region of toothed veins on the upper surface of the right tegmen acts as a 'diffuse file' and engages with an overhanging left-wing plectrum (scraper). Among Pterophyllini (Pseudophyllinae) there is a similar but differently located sound generator, again nonhomologous with the corresponding male generator: a diffuse file lies beneath the left tegmen and engages with a dorsal "edge" bearing dense teeth, on the underlying right tegmen (Naskrecki 2000).

The female generator of *Panoploscelis* is very like that of phanuropterines, except for its modified sound radiating wing cells which are lacking in phaneropterines. Naskrecki (2000) identifies two tegminal stridulatory features in his 'phaneropteroid type' of female generator: parallel toothed veins in the basal part of the

right tegmen, and a network of randomly distributed teeth distad on the marginal area of this tegmen. Both tooth arrangements are exhibited by *P. specularis*: the toothed crossveins and the more distad 'denticles'. Naskrecki suggests that the marginal teeth will produce broad-spectrum alarm/protest calls while the parallel-toothed vein arrangement will generate relatively pure-tone social calls. In the absence of any single predominant modified mirror and the operation of multiple teeth, this latter morphology is not consistent with pure tone generation.

Naskrecki concluded from his comparative study of tettigoniids that female stridulatory structures of a type involving parallel and toothed veins were primitive and then arose independently on another 3 occasions: in Ephippigerinae, in Phaneropterinae and in Polyancistrini. The structure of *P. specularis* indicates another instance of the independent appearance of this type of female structure, in the subfamily Pseudophyllinae.

Table 1. Measurements (mm) of *P. specularis*.

	Colombia ♂	Ecuador ♂85	♂97	Colombia ♀	Ecuador ♀98
Body	75.0	60.0	70.3	82.8	69.2
Pronotum	17.9	15.0	18.6	21.2	16.6
Tegmina	14.4	11.6	16.3	18.8	18.3
Fore femur	27.9	22.9	31.4	32.2	25.3
Fore tibia	29.9	27.3	34.5	35.9	30.0
Midfemur	23.9	19.8	26.7	28.0	22.6
Midtibia	28.4	23.7	32.0	33.9	26.3
Hind femur	42.6	35.1	48.1	50.0	40.5
Hind tibia	47.0	40.8	53.7	58.3	44.9
Cercus	4.7	4.5	4.7	-	-
Ovipositor	-	-	-	36.0	36.0
Subgenital plate	7.3	7.0	7.6	5.2	2.9

Table 2. Morphological features separating *Panosploscelis* spp. (mostly from Beier 1960).

Characters	Taxa: *P. scudderi*	*P. angusticauda*	*P. armata*	*P. specularis*
Both sexes				
fastigium frontis	spiniform acute	spiniform acute	spiniform acute	tubercular obtuse
antennal scape medioventrally	erect distal spine	erect distal spine	erect distal spine	small tubercle
pronotum hind margin	almost straight truncate	straight truncate, depressed in middle	evenly rounded	more strongly bent than other 3 spp.
forefemoral distal spine directed anteriorad	absent	absent	absent	present
fore & hind femora dorsally	armed	armed	armed	unarmed
Males				
cercus ventromedially	spine	male unknown	spine	blunt tooth
subgenital plate in middle	deeply incised	male unknown	very weakly emarginate	deeply rounded emarginate
Females				
ovipositor as long as broad	5X	~6.5X	5X	5X
crossveins of right tegmen	5 to 6	3 to 4	3 to 4	5 to 6
'mirror' cell development	moderate	moderate	moderate	extensive

A 'latching hypothesis' for the evolution of female stridulation, is advanced by Nickle & Carlysle (1975). They propose that these sound generation structures began as spines on the dorsal surface of the anal wing region of females, their original function being to latch the tegmina together. As the insect moved about, bent to groom terminalia, dodged the peck of a bird, or struggled in a predator's clutches, or as its perch vegetation was buffeted by weather, latching could have had selective value by avoiding mechanical damage or maintaining crypsis. And such latching spines do occur among females of many species in (apparently) the complete absence of sound generation, either social or protest e.g, *Orchelimum* (Fulton 1933). Possibly latching remains the current function of distad medial teeth in some phaneropterines.

Male song.—Each song of male *P. specularis* is 2 simple pulse trains, quickly repeated, each train comprised of a series of rapidly decaying pulses (Figs 3C, D). Such pulses are a common feature in tettigoniid songs (e.g., Heller 1988, Heller *et al.* 1997; Montealegre-Z. & Morris 1999) and their transience contributes to the breadth of the resulting spectrum. Loudest in the audio, but extending well into the ultrasonic, the band-like spectrum incorporates substantial energy over a width of 30 kHz and is produced by a non-resonant mechanism (Elsner & Popov 1978, Montealegre & Morris 1999). Both calling and protest signals, have this same spectrum.

A characteristic file morphology is associated with nonresonant, (low-Q) band-spectra. File teeth are compressed in the plane of the tooth series, making tooth elevation greater than the tooth's basal length (the length of the file axis occupied by the tooth base) (Montealegre & Morris 1999). By contrast, species engaging in resonant sound generation with narrow-peaked spectra (high-Q), exhibit file teeth that are scarcely compressed in the file axis, being low in relation to the tooth base. The file morphology of *P. specularis* males fits with that of katydid nonresonant broad-band producers (Figs 2A,B, 5A,B).

In species using resonant sustained songs (crickets, haglids and some katydids), inter-tooth distances increase gradually towards the basal portion of the file, *i.e.*, in the file region where the scraper is completing its closing stroke (Koch *et al.* 1988, Bennet-Clark 2003, Montealegre & Mason (in prep.)). In such species, over this file region, the speed of the scraper during the closing movement gradually increases. If the scraper were to contact all file teeth at uniform speed, all inter-tooth distances would have to be the same to result in a single output frequency. But in species using pure-tone calls teeth are not uniformly spaced: they gradually become more separated toward the base of the file. And scraper speed is not uniform: rather the insect maintains proper phase with its resonator by gradually increasing scraper speed, so as to always travel in the same time from one tooth to the next.

In *P. specularis*, file teeth are not distributed with incremental intertooth distances proximad; the inter-tooth spacing is more or less uniform in the middle region of the file (Fig. 5A) and shows no significant tendency to become wider toward the file base. Again this morphology is in keeping with nonresonant song generation.

The teeth of *P. specularis* males are asymmetrical in profile and the angle they present should be important by affecting the engagement of the scraper and therefore the frequency and loudness of the 'tick sounds' that this action produces during the releasing and engagement of the scraper (Bennet-Clark & Bailey 2002). In *P. specularis*, the tooth angle increases toward the proximal (anterior) part of the file (Fig. 5B); a feature of both males. Though the shape

of the file will be important, this observed tooth angle increase may also be supposed to compensate for the plane change of the tegmina as these shift (*e.g.*, during closure) from a more to a less acute apical angle during the run of the scraper along the file.

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Functions.—Many insects protest acoustically when disturbed, handled, or attacked (Masters 1980). Temporal and spectral characteristics of such sounds are somewhat convergent across species, even for quite unrelated groups (*e.g.*, Coleoptera and Hymenoptera)(Masters 1979,1980), raising the possibility of acoustic mimicry. Or the broadband nature of protest sounds may have evolved to permit sounds to be heard by a large range of predators whose optimal hearing ranges do not coincide (Masters 1980, Heller 1996). In addition, calling song may contain information (similar to protest song) that makes educated predators uninterested in catching them (Wiley & Richards 1978 and refs therein).

There is a general tendency to produce broadband protest songs among some singing Orthoptera (Naskrecki 2000). It might be that *P. specularis*, and some other nonresonant orthopterans living in rainforest understory (*e.g.*, *Choeroparnops* spp., Morris *et al.* 1994), evolved calling songs that also serve during defensive behavior. Montealegre-Z. & Morris (2004), show in a phylogenetic framework a correlation of body armature with the type of call used by males of *Panacanthus* spp. In general spiny individuals tend to generate nonresonant calls. Tuttle and Ryan (1981) reported species of bats that are able to differentiate the calling song of noxious frogs. Taking into account the exoskeletal morphology of *P. specularis* and other species producing broad-band songs living in the forest understory, it is reasonable to think that phonotactic predators can learn to identify unpalatable or difficult-to handle prey by the kind of songs they generate.

Acknowledgements

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