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Stridulation songs of some Tettigoniidae (Ensifera, Orthoptera) from Papua New Guinea

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Abstract

Frequency-domain power spectra and time-domain wave amplitude patterns of stridulation signals, are presented for 20 tettigonioid taxa from Papua New Guinea (PNG). Songs of 13 extant species accompany those of 7 species new to science. Extant are *Acauloplacella immunis* (Phyllomimini), *Eumecopoda cyrtoscelis*, *Segestidea novaeguineae* (Mecopodinae), *Salomona ustulata*, *Philmontoides wau*, *Parahabetia pictifrons*, *Glennagraecia curvata*, *Trichophallus capillatus*, *Morocera nigrifrons*, *Pseudorhynchus cornutus*, *Conocephalus semivittatus semivittatus* (Conocephalinae), *Hexacentrus mundus* (Hexacentrinae) and *Phyllophora lanceolata* (Phyllophorinae). New taxa being described include the species *Paraphyllomimus pipiens* **sp. nov.**, the subspecies *Paraphyllomimus buergersi wauensis*, (Phyllomimini), also the subspecies *Charisoma karschi* 'goggle eye', *Eumecopoda pumila*, *Rentziella* **gen. nov.**, *Rentziella rufa*, *Rentziella* 'big blue'(Mecopodinae) and *Salomona* 'darth' (Conocephalinae).

The term '*strigin*' is suggested as an effective way to refer to the organ of ensiferan sound generation. From waveforms of the sounds and from strigin morphology at least three kinds of stridulation can be inferred: transient, resonant and elastic uncoupled. The resonant-stridulating species *Acauloplacella immunis* presents an exceedingly high-Q_{10} value of 45 for its lone 8.8 kHz spectral peak. The 2 species of *Eumecopoda* frequency modulate (FM) sinusoids in the audio frequency range. The strigins of many species of Mecopodinae incorporate a modified anal vein, the overmirror fold (OF), that cantilevers out above the mirror (speculum) and partially occludes its dorsal aspect: the form of this OF and possible acoustic function are discussed. Old World Phyllomimini contrast a dorsoventral leaf mimicry with a laterally compressed sagittal leaf mimicry seen in New World Pterochrozini and species of both tribes seem to favour very high-Q audio carriers. Defensive sternocoxal stridulation by a phyllophorine katydid has a broad band 'noisy' spectrum.

Key words: katydid, transient, resonant, elastic uncoupled, bioacoustics, leaf mimicry, frequency modulation, broad band, Q, protest, mirror, harp, specula, strigin

Introduction

The cuticle of insects is a remarkable fibrous composite material "praeternaturally multifunctional", having "all the functions of a skin and skeleton" (Vincent & Wegst 2004). For ensiferan Orthoptera one of those multifunctions is stridulation, the act of making a sound in air by shearing of exoskeletal integument. The articulating joints and sclerites of an insect's exoskeleton predispose it to the evolution of sound generating surfaces almost anywhere on its body, wherever one protruding chitinous part moves close upon another.

To stridulate most tettigoniids keep their forewings flexed, tilted above the back, while drawing them to and fro with co-opted thoracic flight muscles. A projecting edge (scraper) of the right tegmen engages the underside of the transversely running cubitus (Cu2) vein of the left tegmen; this vein bears a series of teeth called a file. As the canted forewings retreat from and approach the plane of the insect's back, successive tooth-scraper events excite oscillation in extremely thin cuticular 'shells' (speculas) of adjacent vein-delimited wing cells—primarily two called the 'mirror' and 'harp'.

Larynx and syrinx are convenient terms for the sound generating organs of mammals and birds respectively, but an equivalent term for the sound making organs of acoustic Orthoptera seems to be lacking. We suggest *strigin*, a contraction of 'stridulation' and 'gin', the latter referring to a mechanical device as in 'engine' (Hinton 1946). Strigin as a term should be understood to include body parts beyond the file and scraper; extending rather to thoracic muscles powering the forewings, to costal baffles (Morris *et al.* 2016, Jonsson *et al.* 2017) and to partially demarcated chambers: the metazona of the pronotum produced above the tegminal speculas, the speculas themselves deployed above the insect's back. The air masses partly contained may be considered as loading the specular diaphragms. A strigin generator can even share its acoustic function with other nearby organs: e.g., as the larynx shares function with the tongue in human speech so the katydid strigin shares in the function of flight.

Stridulation primer

Tegminal movements of the scraper upon the file are mostly too fast for the unaided human eye. But for each of the 20 species we try here to infer from the waveform and spectrum which of three sorts of stridulation behaviour is likely to be involved: 1) transient, 2) resonant coupled, 3) resonant uncoupled. As an aid to understand the sound signal descriptions that make up our results, here follows a brief primer on the 3 commonest ways of stridulating by tettigoniids.

Resonant stridulation is indicated by the presence of single-frequency (simple) harmonic sinusoids in the time domain and a narrow peak of high central tendency in the frequency domain. Resonant uncoupled stridulation is made apparent by the presence of strong high-Q, usually ultrasonic peaks. Transient stridulation is indicated by broad-band spectra in the frequency domain and a distinct time-separated train of complex wave rapid-decay impulses in the time domain.

Fletcher (1992, p. 241) poses stridulation as "a stick-slip process" involving a file and a pick. The two wings converge in shear and the pick (scraper) lodges behind a file tooth; the moving wing's inertia builds an elastic deformation force into the wing region behind the scraper which manifests as a shape change, letting the pick slip free to advance and catch on the next tooth. If the slip rate is "very much lower than the natural resonance frequency ω_0 of the driven structure, then each slip event will simply generate in the structure a pulse of resonant vibration that will substantially die out before the next slip event. Such a characteristic time record will be clear in the sound waveform" (Ibid.). Thus, scraper interaction with each file tooth evokes a transient complex waveform which is the result of combining the instantaneous amplitudes of two or more simple (pure tone) sine waves (sinusoids). In this way low slip rates can produce a long train of such transient impulses. Examples in the present paper of single-tooth transient stridulatory acoustic output are the calling songs of *Trichophallus capillatus* (Fig. 69), *Morocera nigrifrons* (Fig. 72) and *Conocephalus semivittatus* (Fig. 76).

For all transient signals "the shorter their duration the broader their spectra" (Haughton 2002). The ultrasonics often seen in tettigoniid calls have been supposed to owe their presence in part to this general phenomenon (Dumortier 1963, p. 356): "…as the analysis in the Fourier's series shows" [transience] "gives rise to a whole group of frequencies, wider as the phenomenon becomes shorter". Low slip rates, broad-band low-Q spectra and partially time separated short impulses associated with each scraper-tooth event (i.e., the amplitude modulation pattern shows the number of tooth-scraper events): these are the hallmarks of transient stridulation.

At higher slip frequencies a katydid singer may match a resonator's natural frequency, ω_0 (resonance frequency), applying scraper force events at each tooth, phased to seamlessly join successive oscillations into a sustained wave train, i.e., a sustained sinusoid with only very slowly shifting amplitude envelopes. At an optimum angle "the pick itself will have a component of vibration in a direction parallel to the file" which tends to pull the phasing of tooth events into reinforcement "producing a nearly steady and coherent vibration" (Fletcher 1992). A building or 'flat amplitude' sinusoid wavetrain is an indicator of stridulation at the resonant frequency of the system. At the same time the spectrum will show an increased central tendency (high Q value), i.e., very narrow spectral peak or peaks (harmonics). Strong examples of resonant stridulation in the present work are provided by *A. immunis* (Figs 3, 4), *P. buergersi wauensis* **ssp nov.** (Fig. l4) *P. pipiens* **sp. nov.** (Fig. 15).

Several tettigoniid species improve on slip frequency and scraper velocity by drawing upon the elasticity of scraper cuticle (Patek 2011). They uncouple the pick's movements from the closing movement of its tegmen. They make a train of short sinusoid ultrasonic pulses by lodging the scraper at intervals along the file, arriving at a 'one-tooth, one-wave' ultrasonic carrier. This mechanism was first proposed to explain the 35 kHz ultrasonic generation of the Canadian spruce-bog tettigoniine *Sphagniana sphagnorum* (Morris & Pipher 1972). It has since been shown to be the basis of the extreme ultrasonic songs of *Myopophyllum speciosum* (Montealegre-Z *et al.* 2006) and species of *Supersonus* (Fabio 2014).

At each lodgement while the forewings maintain their closing inertia, the now coupled scraper region is bent; this stores elastic energy as deformation of the wing region immediately behind the lodged scraper. Changing its angle within the intertooth space, the scraper slips free and uncoupled, its stored energy returns its resting shape which drives it rapidly along the next several file teeth at a much enhanced velocity. As the stored deformation energy is exhausted, the scraper region regains its original shape. This, and perhaps also the ventrally concave shape of the file, causes the scraper to lodge once again behind a file tooth; this process repeats along the file.

When a song's spectral peak is relatively high-Q ultrasonic, when its time-domain shows as a brief series of short sinusoid wave trains, these wave trains (= pulses) cleanly down-time separated with a regular period (Montealegre-Z 2006)—then elastic uncoupled stridulation may be inferred. Given that these pulses are short and therefore more affected by side bands, the spectral peak will have a somewhat lowered Q. For examples of probable elastic uncoupled stridulation in the present work see *Philmontoides wau* (Fig. 58) and *Glennagraecia curvata* (Fig. 67).

If the slip rate is "only a few times less than the resonance frequency, then slip from one tooth of the file may take place before the vibration from the previous slip event has died away. …The slip impulses will then all tend to occur near the same phase of the vibrations cycle and thus to reinforce each other, producing a nearly steady and coherent vibration" (Fletcher 1992).

Again, complex waveforms may result, but now manifesting as a series of periodic transient complex wave trains scarcely separated by intervals of silence. A small subset of adjacent file teeth may be involved in creating a waveform that is more sinusoid in having several uniformly high amplitude waves before the pattern must repeat. Some examples in the present paper of reinforced transient stridulatory acoustic output are the songs of *Charisoma karschi* 'green goggle' (Fig. 19) and *Philmontoides wau* (Fig. 58),

Materials and methods

Collection

Dita Klimas, Glenn Morris and James Fullard travelled from Canada via Hawaii to Papua New Guinea (PNG) in the summer of 1981, staying for the month of August in a cottage on the grounds of the Wau Ecology Institute (WEI, Gressit & Nadkarni 1978) (lat 7º 24'S, long 146º 44'E). Prof. Fullard trapped bats and recorded their echolocation calls as part of his studies on moth defensive stridulation; Klimas and Morris hunted katydids on Mts Kaindi and Nissim and in the nearby Bulolo Gorge.

Searching pathside vegetation at night with headlamps, we were guided sometimes by the insect's song aided by a heterodyne 'bat detector' (Ultrasound Advice). Capture was by hand or involved hand-herding the specimen to effect a leap down into the opening of a large insect net. Sometimes we climbed short trees. A small remnant of mature forest fringing a broad trail leading from the Wau Ecological Instutute down to the Wau Country Club was productive. A species of *Acauloplacella*, and of *Hexacentrus* were common singers on the Institute grounds, for the rest we hiked several times up Mt. Kaindi, walking a narrow path near the top through relatively undisturbed forest. We also collected in the nearby Bulolo Gorge in McAdam National Park.

The stridulation calls of 20 species of Tettigoniidae from Papua New Guinea (PNG) were recorded, their spectra and time-domain modulations analysed subsequently.

Recording

The insects were kept in individual cylindrical metal screen cages and fed small pieces of apple. Recording occurred at night in a small room of the WEI cottage; their songs were gathered onto an instrumentation tape recorder (Racal Store 4D). For the recordings 3 microphones were employed: 1) a Bruel & Kjaer ¼" condenser microphone 4135 mounted on a 2204 B&K sound level meter set to linear response, 2) a mylar capacitance microphone and amplifier made by QMC Instruments SM1 for bat studies, 3) a 2203 B&K sound level meter with a half inch condenser microphone (4165), ultrasonic sensitivity limited to below 40kHz. The microphones were directed at the sound-radiating specular (anal) tegminal region of the singer from 5–15 cm distance. The Racal received and amplified (Direct not FM board) the microphone outputs, recording the signal onto 6.25 mm magnetic tape travelling at 30"/s. This recording system was flat to 70 kHz where it began to 'roll off'. Sound levels were measured (unless otherwise specified) using the Bruel & Kjaer 2204 sound level meter set on 'linear impulse hold'. Some recording of insects was carried out back in Canada on specimens transported alive as hand luggage.

Analysis

The analog tape recordings were digitized for analysis: played back from the Racal at 3 ¾"/s, a slowing factor of 8, into a PC computer running the app Cool Edit Pro (Syntrillium Software Corporation, Phoenix, Arizona) at 48000 samples/s. To avoid aliasing, the analog output signal of the tape recorder was double low passed at 20 kHz using a Krohn-Hite 3202 filter. Analysis was of exported wave files using the mathematical spreadsheet DADisp (ver 6.5); figures were assembled in Corel Draw. Rather than Q_3 as a quality factor we used Q_{10}, calculated as the resonance frequency (centre of frequency peak) divided by peak width at 10 dB down.

Preservation

We employed a specimen preservation technique using no. 5 jeweller's forceps attributed to Carlos Carbonell. The cervical membrane behind the head is pierced with the closed forceps and a powder mixture of equal parts boric acid and talcum applied. The insect's innards are removed and the body cavity swabbed again using the forceps pinched on a bit of cotton. The powder is finally 'shovelled' into the body opening and blown. Excess surface powder is removed from the insect with a fine brush; this treatment does much to preserve the original colouration.

Acoustic thin plates

Tettigoniid tympana and specula present as low-mass sheets of extremely thin cuticle, functioning respectively to extract pressures from sound waves (as eardrums) or introduce pressure waves into the air (strigins). The thickness of a sound-radiating tegminal speculum is only a few microns: in the tettigoniid *Xiphelimum amplipennis* the mirror speculum is just 2.35 microns (Morris *et al.* 2016). In SEM figures of specula, where exposure of both sides of the mounted specimen leads in effect to a double coating, an area of electron charging is seen, a useful indicator cueing the extent and shape of the thinnest region, hence presumably a region of significant oscillation (Figs 22, 23, 28, 29).

Overmirror fold

In the right tegmen of Mecopodinae (e.g., *Eumecapoda cyrtoscelis*, *Rentziella rufa*) there is an interesting structure cantilevered above the mirror speculum, the "overmirror fold" (Gorochov 2020). We speculate here on its possible acoustic function. Description of tegmen morphology assumes the wing's extension as in flight. Thus, the overmirror fold is located in males upon the posterior rim of the specular mirror of his right tegmen; the harp wing cell shares much of the anterior mirror rim (Fig.17B, Fig. 37C).

Naturalis Biodiversity Center, Leiden (NBCL) is the depository for all the specimens collected by Morris & Klimas in PNG during 1981. Of the 20 taxa whose songs are analysed here seven (sp./ssp.) are apparently new to science.

Results

Pseudophyllinae Burmeister, 1838

Phyllomimini Bruner v. W., 1895

Acauloplacella Karny, 1931

Acauloplacella (*Papuaprium*) Beier, 1954

Type species of genus: *Morsimus serraticollis* I. Bolivar, 1890 (by original designation).

Acauloplacella (*Papuaprium*) *immunis* (Brunner v. Wattenwyl, 1895)

(Figs 1–4)

Specimens studied. PNG, nr Wau, W.E.I., 4 & 10 &12 & 17 viii 1981; coll. G.K. Morris (5 males, 1 female); two specimens recorded (81-1, 81-2) (Depository NBC Leiden).

Description. This material agrees with the redescriptions in Beier (1954, 1962), except for the white median spot on the posterior margin of the male pronotum (Fig. 1) which extends a little both frontally and laterally, making it widely cross-shaped, rather than triangular. Male stridulatory organ not previously described, elongate, about 5.5 mm long and 2.0 mm wide, distally transversely truncate, inflated part of file of left elytron in dorsal view about 2 mm long, its base bulging; membrane of distal cells of stridulatory area dark brown in their centre with numerous superimposed tiny black points, similar to spots upon remainder of elytra; stridulatory file of left elytron in ventral view (Fig. 2A) of usual shape, shortest distance between most proximal and distal tooth 2.3–2.5 mm, basad very narrow and strongly curved with 13–15 teeth, the main part wider, only slightly curved in ventral view and faintly concave in profile, with 150–180 transverse teeth, parallel to each other and closely set (Fig. 2C,D). Fifteen to 18 teeth per 0.25 mm, distally increasing to 22–26 teeth per 0.25 mm; transverse, shallow, leaning basad, strong midtooth deflections (Fig. 2C, D).

Distribution. From scarce records (Beier 1963) and the limited additional material before us, the range of this insect reaches at least from extreme northeast West Irian through northeast New Guinea to southeastern Papua. By lack of acoustic data and particulars of the male stridulatory apparatus, it is an open question whether *A. regularis* (Jong 1938), from extreme northwestern West Irian, is conspecific with *immunis* as considered previously (Jong 1950, Beier 1962).

FIGURE 1. *Acauloplacella* (*Papuaprium*) *immunis*, habitus of adult male, dorsal aspect, on vertical glass in daytime cryptic posture.

Crypsis and resonance. *A. immunis* was seen to adopt a cryptic daytime posture, flattening itself upon a supporting broad tree leaf (see Fig. 1 in Robinson 1973, Fig. 1 here). The insect extends its forelegs directly forward, the prothoracic femora resting against its genae and apposes its antennae between; femorotibial joints of the other limbs hide under the broadly ovoid tegmina which are pressed flat to the leaf surface. Body and tegmina colors match the colour of the perch. All of this adds up to a diurnal refuge for the katydid. Hiding the angular femorotibial

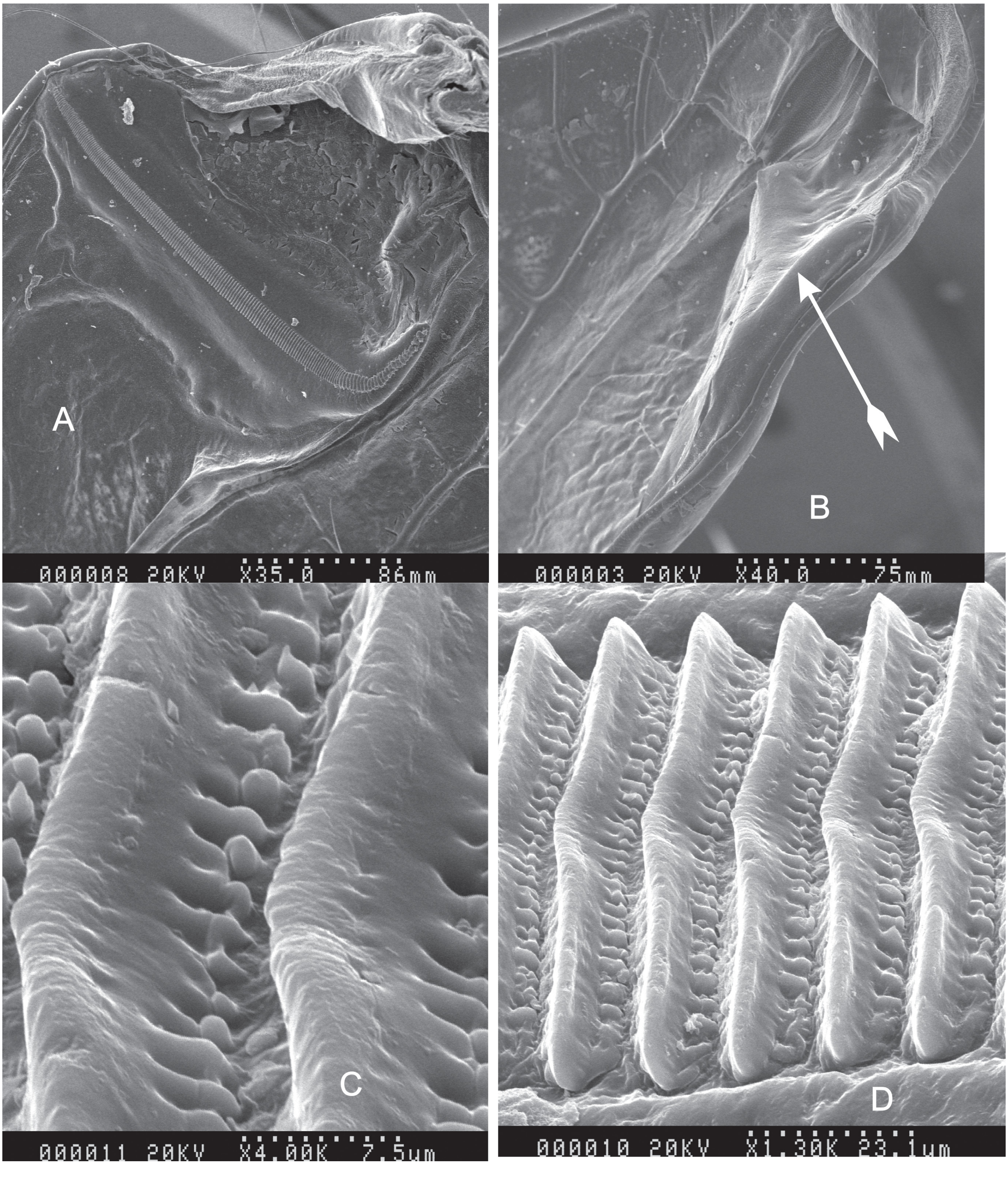


FIGURE 2. Scanning electron micrographs (SEMs) of *A. immunis* strigin parts: A) Left tegmen ventral aspect, straight file of broad teeth; B) Oblique foreshortened view of wide transverse vein backing scraper (arrow) on underside of right tegmen; C, D) File teeth close-ups show mid-breadth inflections and gullet nodules.

joints may remove a detection cue used by predators (Robinson 1973). The dorsoventral compression seen in other members of the tribe Phyllomimini to which *A. immunis* belongs suggests daytime concealment in this fashion may be a common strategy for avoiding predators.

Though many tettigoniids mimic the foliage on which they perch, this crypsis seems particularly marked in Phyllomimini of the African and Asian tropics and also in the Pterochrozini of the American tropics. But there is an interesting difference in the leaf mimicry exhibited by these two tribes: among Phyllomimini this camouflage involves dorsoventral compression, a flattening of the body, while in new world Pterochrozini the body is laterally compressed, extending the animal in the sagittal plane. Puzzlingly, both taxa associate these cryptic features with high-Q resonance stridulation.

A. immunis has a relatively straight file (Fig. 2A) with broad teeth, each tooth bisected midbreadth by a shallow bend (Fig. 2CD). The collective effect is an unbroken series of midtooth features, running the middle of the length of the file. Some Malaysian Phyllomimini, *Tympanophyllum arcufolium* and *Onomarchus uninotatus,* tribal relatives of *A. immunis*, also show a mid-breadth angle change in their broad file teeth, causing them to seem "fused in the middle" (Heller 1995). A similar tooth form also occurs in three species of the pterochrozine Ecuadorean South American genus *Typophyllum*: *T. mortuifolium, T. bolivari* and *T.* nr. *trapeziforme* (Morris *et al.* 1989).

Perhaps these bisected teeth enhance the insect's sinusoid (high-Q) resonant stridulation by serving as a scraper-shaping 'guide', functioning to mesh the teeth more intimately to the shape of the scraper. Such a guide function does not seem a requirement for making a high Q signal but those several species in which it occurs do make an extremely high Q. The function of songs with a dominant narrow frequency peak may have something to do with mate localization in a manner similar to the mechanism employed by some crickets.

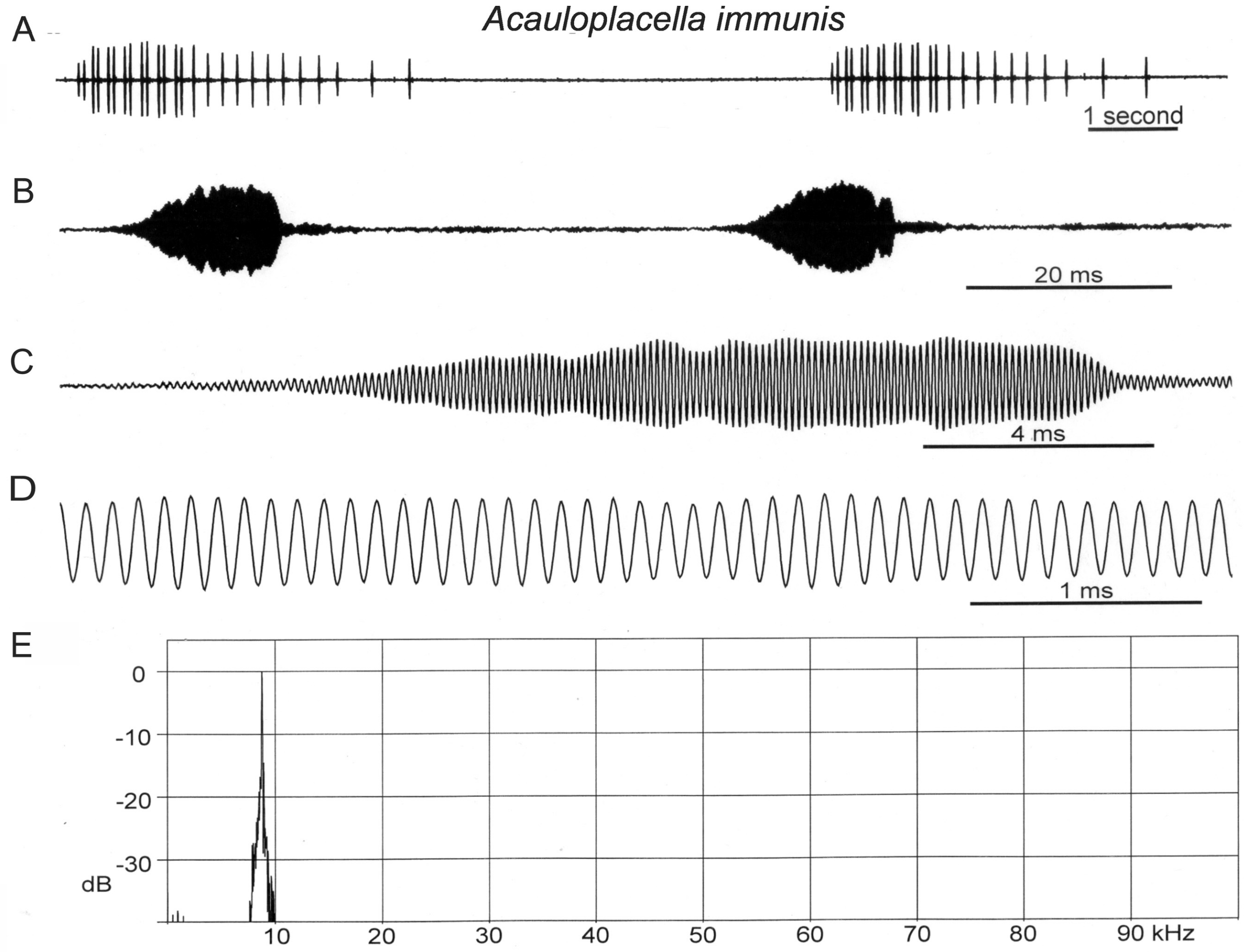


FIGURE 3. *A. immunis* acoustic analysis: A) Two songs, trains of sinusoidal pulses, first several pulses paired in time; B) Pulse pair at higher resolution; C) Single pulse at still higher resolution; D) Portion of pulse time-resolved, strongly sinusoid wave train; E) Fourier transform spectrum, single extraordinarily high-Q spectral peak near 8 kHz.

Stridulation. *A. immunis* is a definitive example of resonance stridulation. Its call was a common nocturnal sound on the grounds of the Wau Ecology Institute, issuing from lower tree foliage and the higher parts of shrubs. Only a few males were perched low enough for their capture to be attempted from the ground. *A. immunis* calls were also a strong part of the night chorus in the Bulolo Gorge.

A. immunis' frequency carrier lies in the low audio range where humans hear well. There is a single very high-Q peak ($Q_{10} = 45$). in the vicinity of 8 kHz (Fig. 3E, Fig. 4). The marked tonality of this phyllomimine rivals the characteristically high-Q songs of new-world Pterochrozini such as *Typophyllum mortuifolium* (Morris *et al.* 1989). Phyllomimini also share remarkably accomplished leaf mimicry with Pterochrozini. But high-Q songs are not confined to these two exceptionally camouflaged tribes: the copiphorine *Artiotonus artius* (Montealegre-Z *et al.* 2011) has a comparably high Q of 42.6 in the ultrasonic at about 40 kHz.

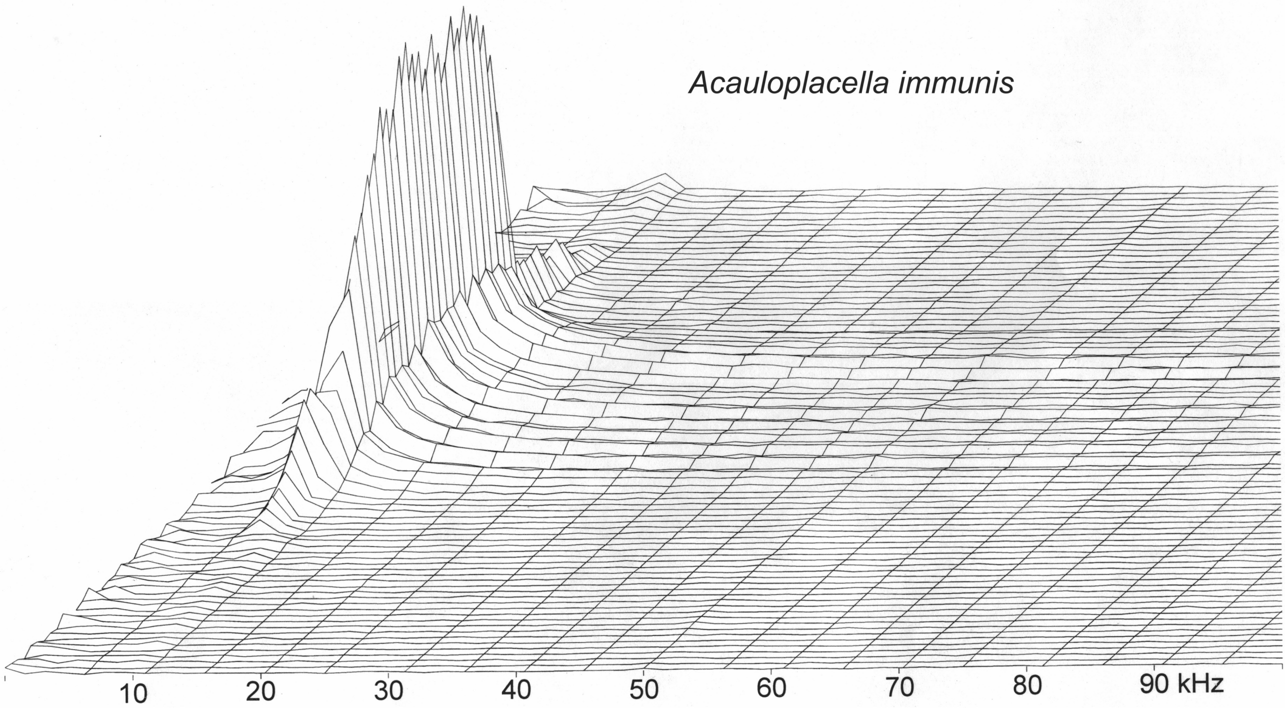


FIGURE 4. *A. immunis* frequency-domain waterfall display of pulse; time advances into page.

The songs of two males recorded at 17 and 21 °C, are the basis of the time-domain values given below. The dominant carrier is a single very high-Q peak at 8.6 kHz, lacking any significant harmonics (Fig. 3E, 4). There is also no indication of frequency modulation (FM) and no sign of a vestigial file on the underside of the right tegmen (Fig 2B). To make just one high-Q carrier frequency would seem to require vibration of just a single speculum, which suggests the absence of the harp as a functional speculum.

A. immunis' call is a train of 17–26 sinusoid pulses (Fig. 3), the train lasting 3 to 6 s. At typical field temperatures these pulses arrive at a just countable rate. At 17°C a caged singer (specimen 1) produced three 7-s trains; each song separated from the next by 6 to 7 s of silence. The mean song duration for 10 songs of this same individual was 6.0 s.

Two songs are shown in Fig. 3A. Over the first third of the train the pulses are grouped temporally in pairs, while over the last two thirds they are given singly. But the repetition rate of both pairs and single pulses is about the same: 5–6/s at 21°C. Both measured specimens had this stereotyped arrangement of double pulses followed by singles. For each song the amplitude of the first double pulse was always substantially lower than those following. The amplitudes of the single pulses fall away toward the end of the call and the pulse period lengthens (Fig. 3A). An individual showed some variation in the number of double pulses (5 to 9) and single (9 to 18) between songs.

A pulse was sampled from each of 10 different songs made by specimen 1 singing at 17°C, giving a mean pulse duration of 18.2 ms. The mean carrier frequency, calculated over the entire pulse was 8.57 kHz (Fig. 3E), specimen 2. There is no frequency modulation during the pulses. A third harmonic, very weak, was detected at 26.1 kHz, more than 39 dB below the carrier, so likely of no biological consequence.

In comparison to other Tettigonioidea, the sound level is rather low: 85.5 dB (impulse, hold) dorsal 10 cm, for the earlier double-pulses, dropping by about 3 dB for the later single pulses.

Paraphyllomimus Beier, 1954

Paraphyllomimus buergersi buergersi Beier, 1954

(Figs 9A, 10ACE.)

Specimens studied. Holotype male: "D.N. Guinea Schraderberg 2100 m 22.–31.V.13 Kais. Augustafl. Exp. Burgers S.G.", "no. 344", "*Paraphyllomimus buergersi* n. sp. det. Beier male Type !" (Zool. Mus. Berlin).

Redescription of holotype. General appearance as in Fig. 9A. Cercus slightly upcurved, tip smooth, somewhat flattened and recurved; posterior margin of last abdominal tergite very broadly wedge-like excised, lateral margins of the thin supra-anal plate shriveled and curled, creating a biconcave profile in dorsal view; styli about as long (1 mm) as stalk of subgenital plate (Fig. 10 ACE). Foremost part of median carina of pronotum depressed and pale yellow, bordered laterally with dark brown stripe on either side. Number and size of dark dots in elytron cells limited by R, origin of Rs and part of M and adjacent cell between M and Cu remarkably larger than the single dots in other cells. Stridulatory area of left male elytron 5.5 mm long, 2.6 mm wide, rectangular distally, file dorsally inflated over 2.5 mm; file in ventral view of usual shape, shortest distance between most proximal and distal tooth 2.5 mm, greatest width of teeth 0.125 mm, total number of teeth >200, almost regularly spaced, in mid part about 27 teeth per 0.25 mm.

Distribution. Known only from the male holotype of Mt. Schrader, 2100 m, extreme SE Eastern Sepik District.

Comments. Type species of the genus *Paraphyllomimus* is *P. apterus* Beier, 1954 by original designation. This genus was known from three species, all from NE New Guinea (Beier 1954). It was a surprise to find, high on Mt. Kaindi, morphologically similar specimens from the same region of undisturbed forest producing two different songs. As well, from differences of the male stridulatory file it became clear we deal with two distinct species. One of our species from Wau comes near *P. buergersi*. The latter is known only from the male holotype. By lack of sufficient data in the original description it became necessary to compare the holotype with our specimens. Opportunity is taken here to give some additional notes on this specimen.

Stridulation. Song unknown.

Paraphyllomimus buergersi wauensis ssp. nov.

(Figs 5–8, 9B, 10BDF, 11B, 12B, 13B, 14)

Specimens studied. Holotype (male): "30.VIII.81, Mt. Kaindi 81-2 squeaker confirmed", "nr. Wau PNG 2-2 coll. G.K. Morris" (depository, NBC Leiden)

Paratypes: PNG, Mt, Kaindi, 30 viii 1981, G.K. Morris (3 males) & idem, contour trail 19 viii 1981 (2 males) (all NBC).

Description. Male.—General appearance (Fig. 9B), size and coloration as in nominate subspecies but differing as follows: posterior margin of last abdominal tergite slightly sinuately excised, cercus strongly upcurved, tip not recurved, styli slightly longer (1.3–1.4 mm) than stalk of subgenital plate (0.74–0.85 mm) (Fig. 10BDF). Elytron as in nominate form but stridulatory area of left elytron slightly larger, length 6 mm, width 3 mm; file in dorsal aspect inflated over a shorter distance (2.1–2.4 mm); file in ventral view slightly longer, shortest distance between most proximal and distal tooth 2.9–3.0 mm, teeth wider, maximum width 0.175 mm, total number and spacing about similar as in nominate form, in mid part about 24 per 0.25 mm.

Female.—The female *Paraphyllomimus* in one of our photographs (Fig. 8) bears a spermatophore and may be either of *P. buergersi wauensis* or *P. pipiens*).

Distribution behaviour and habitat. Known only from Mt. Kaindi near Wau, Morobe District, NE New Guinea. The species was found at higher elevations of the mountain. Like *A. immunis* it adopts a flattened cryptic posture by means of which its ovoid tegmina completely cover and conceal the knee angles of its partially flexed limbs. When kept caged it will adopt this same pose.

Measurements. (Length in mm) (male n = 6): body 14.1–16.4; pronotum 3.6–3.9; elytron 19.1–21.2 (greatest width 7.8–8.1); hind wing 14.3–15.0; hind femur 8.0–8.2.

Etymology. Named after the area of occurrence.

Comments. The most obvious differences between nominate *P. buergersi* and *P. b. wauensis* are the strongly recurved male cerci and relatively longer styli in the latter. Whether the slight differences of the stridulatory apparatus are important is an open question, mainly as variability and song of the nominate form are unknown. For the time being we propose to give the new taxon subspecies status.

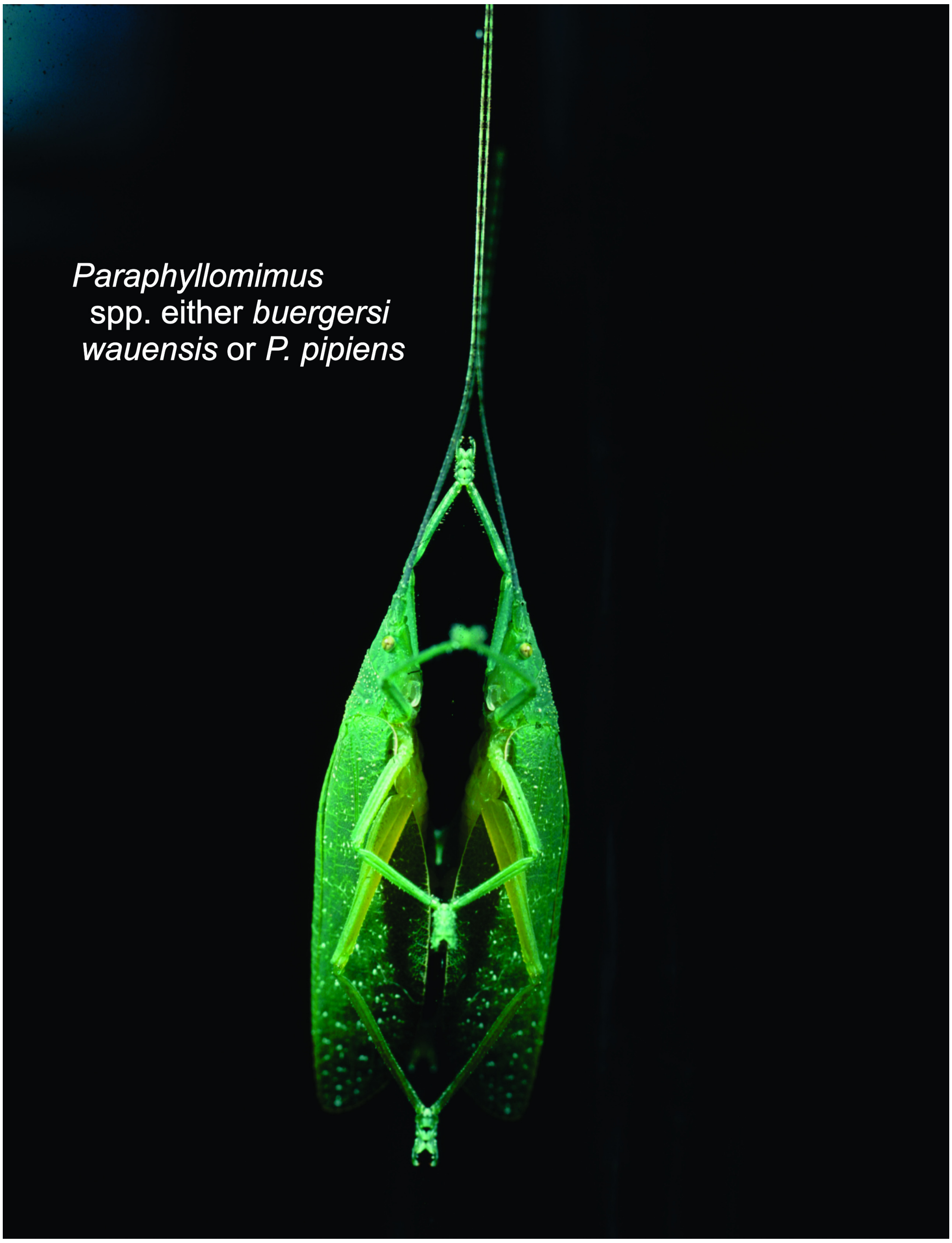


FIGURE 5. *Paraphyllomimus* male habitus, lateral view reflection on vertical glass; either *P. buergersi wauensis* or *P. pipiens*, the two being indistinguishable at this resolution.

Stridulation. Call period during steady singing near 20°C is ~0.4s (Fig. 14A), slightly more than 2 calls per sec. Slowed by a factor of 16, the call is heard as a fast repetition of highly tonal pulses: three shorter sinusoids lengthen and intensify into a concluding most intense wave train lasting ‘almost 20 ms’ (Fig. 14B). The strongly sinusoidal nature of the pulses is apparent in a time sample from this last and longest pulse (Fig. 14D). An FFT spectrum of one complete song shows a dominant frequency peak at ~11 kHz (Fig. 14C) with a Q_{10} of 5.7.

Spectra calculated early and late during the ‘almost 20-ms’ prolonged pulse of Fig. 14B show an upward frequency modulation (FM) of ~1000 Hz. Two arrows (Fig. 14B) mark the start of each of these 512-point time samples. The two resulting FFT spectra are overlain in Fig. 14E: from 10.9 kHz the carrier peak shifts to 11.9kHz. The Q_{10} value of 5.7 determined on the whole call is misleadingly low. The peak of one of the spectra in Fig. 14E has a Q_{10} of about 20. The insect is engaged in resonant stridulation and contacts teeth at an increasing scraper speed.

Frequency modulation is rare in tettigoniid stridulations, but is known for several species (e.g., Morris *et al.* 2016 and see *Eumecopoda cyrtoscelis* and *pumila* in the present paper).

FIGURE 6. *Paraphyllomimus* spp., male habitus, dorsal view, clings to vertical glass.

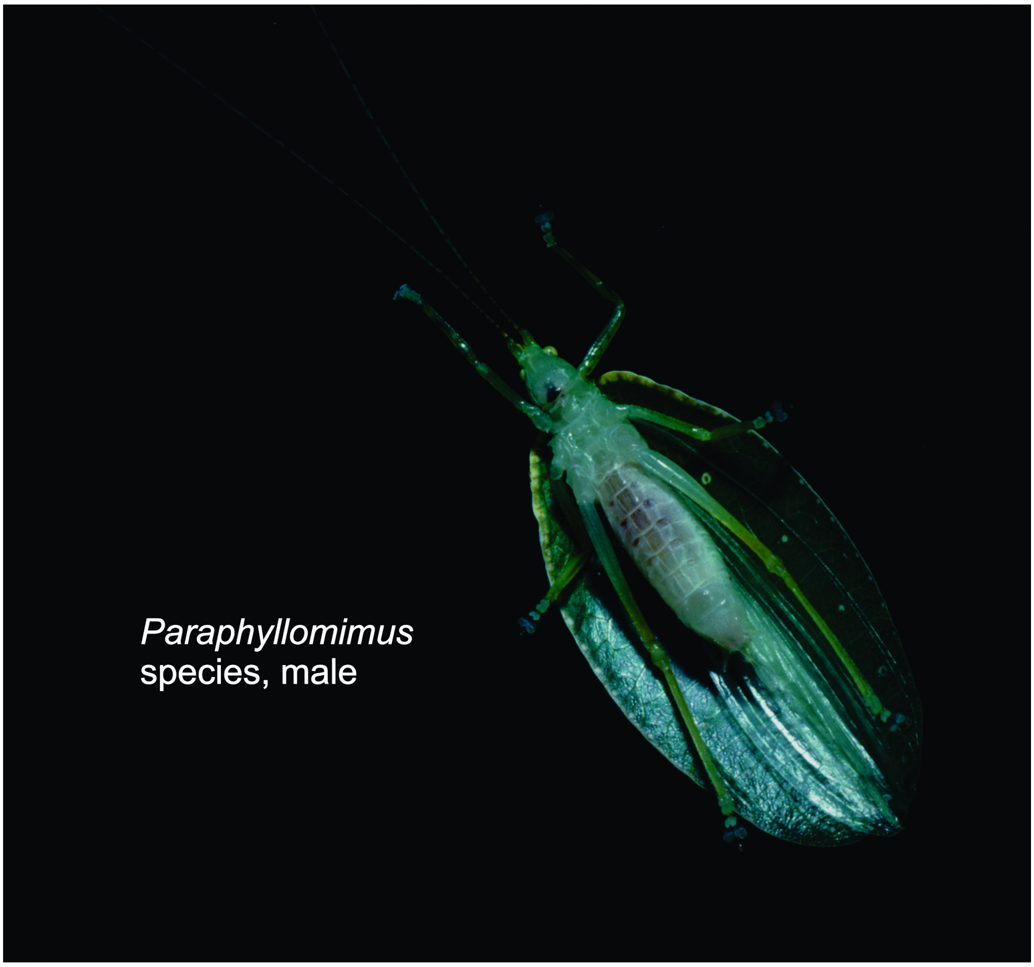


FIGURE 7. *Paraphyllomimus* spp., male habitus, ventral view, clings to vertical glass.

FIGURE 8. *Paraphyllomimus*, female habitus, ventral view, on vertical glass with attached spermatophore.

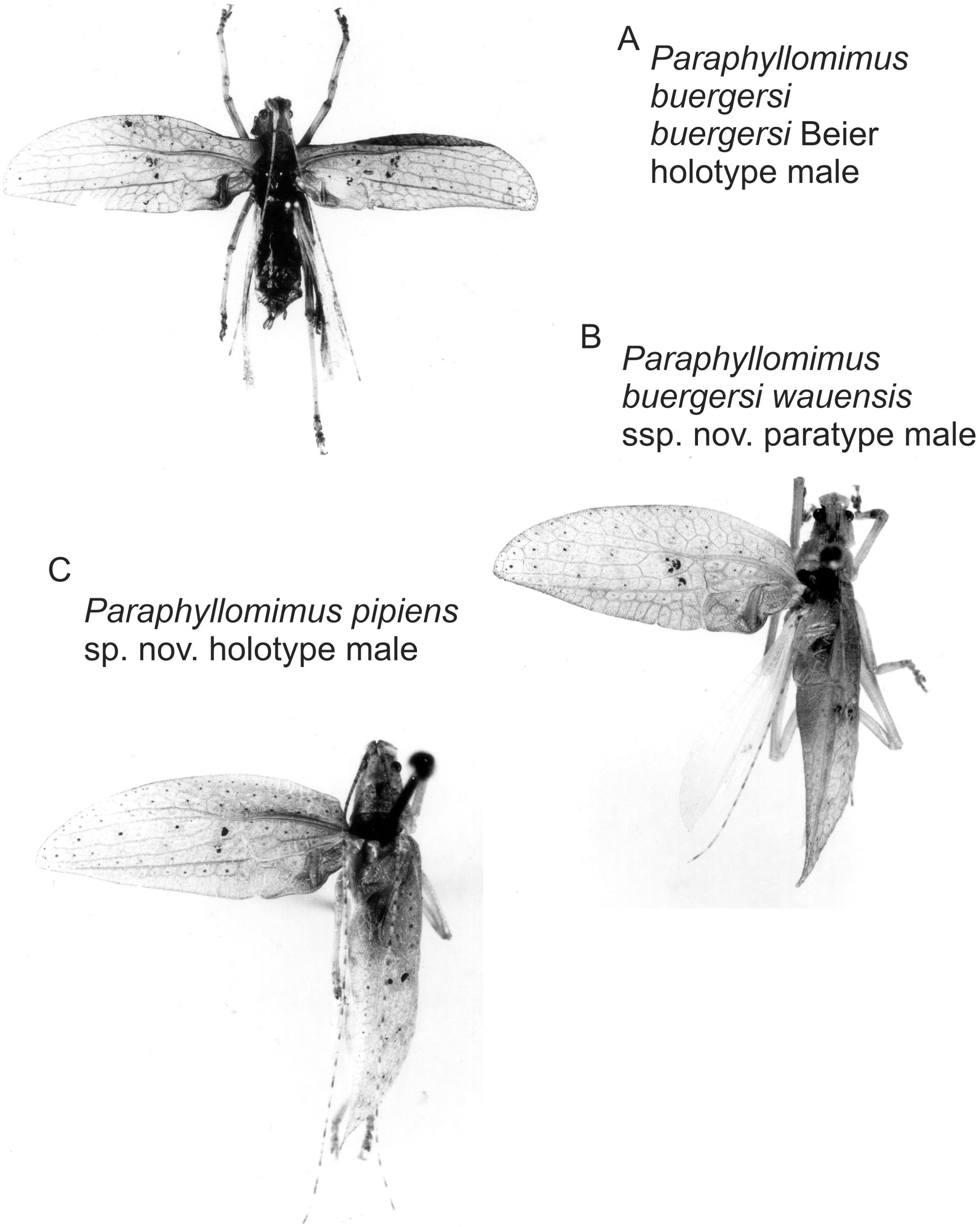


FIGURE 9. Habitus of types: A) *Paraphyllomimus buergersi buergersi* Beier (holotype male); B) *P. buergersi wauensis* **ssp. nov.** F. Willemse (paratype male); C) *P. pipiens* **sp. nov.** F. Willemse (holotype male).

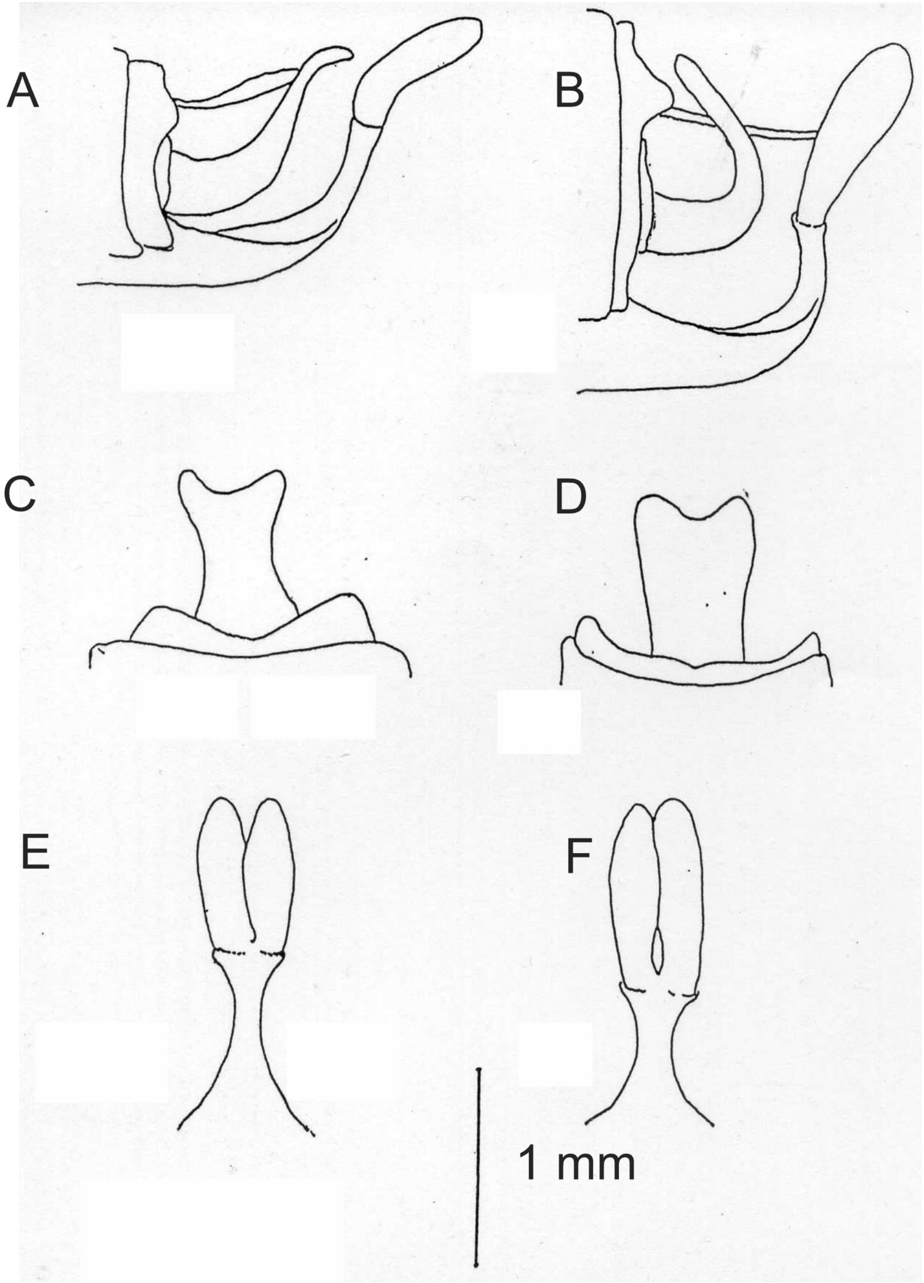


FIGURE 10. *Paraphyllomimus* terminalia: A,C,E) *P. buergersi buergersi* Beier (holotype); B,D,F) *P. buergersi wauensis* (paratype); A,B) lateral aspect terminalia; C,D) dorsal view supra-anal plate; E,F) subgenital plate styli ventral view (scale 1 mm).

***Paraphyllomimus pipiens* sp. nov.**

(Figs 5–8, 9C, 11A, 12A, 13A, 15)

Specimens studied. Holotype male: "19.viii.81 Mt. Kaindi PNG Acaulo. small zipper 81-1" &"nr. Wau PNG 3-1 coll. G.K. Morris (Depository NBC Leiden).

Paratypes: 2 males PNG, near Wau, Mt Kaindi, 30.viii.1981, G.K. Morris (Depository NBC Leiden).

Description. Male.—General appearance (Fig. 9C) close to *P. buergersi wauensis* described above but size slightly smaller. Elytron shorter, anterior margin less bowed, more strongly tapering apically but venation as in *P. buergersi* (s.l.), i.e., M ending into apex, Cu just behind, Rs just in front of it. Stridulatory area of left elytron 5.1–5.4 mm long, 2.2–2.4 mm wide, file in dorsal aspect inflated over 1.6–1.9 mm; file in ventral view of usual shape, shortest distance between most proximal and distal tooth 2.1 mm, number of teeth about 100, spacing widest in mid part, about 10–11 teeth per 0.25 mm. Abdominal terminalia with supra-anal plate narrow, elongate, flat, posterior margin roundly excised; cercus strongly upcurved; subgenital plate narrowing distally into a strongly upcurved, short and undivided stalk bearing elongate styli which are about one third longer than length of stalk.

Coloration as in *P. buergersi wauensis* except for the general pale green which is mixed with rufous brown and the elytra spots which are apparently less conspicuous. Female unknown. The female insect in Fig. 8 is either *P. pipiens* or *P. b. wauensis*.

Measurements. (Length in mm) (male n = 3): body 12.9–13.3; pronotum 3.5–3.7; elytron 15.0–16.5 (greatest width 6.5–6.6); hind wing 10–11; fore femur 3.5–3.9; hind femur 6.4–7.1; stem of subgenital plate 0.5–0.8; stylus 0.8–1.0.

Etymology. Derived from the Latin verb *pipiare* = whistle.

Diagnosis. This new species can easily be distinguished from nominate *P. buergers*i and syntopic *P. buergersi wauensis* by its more widely spaced stridulatory file teeth (Fig. 11), about 10 teeth against >20 per 0.25 mm in the mid part of the file respectively). Also, the shorter file and its lower number of teeth (about 100 in *P. pipiens*, >200 in *P. buergersi*) are quite different. The slightly smaller measurements of the 3 [specimens of the] new species seem to be useful to separate it from *P. buergersi*. Another difference is in the anterior margin of the elytron, which tapers apically straighter in the new species: this margin is more roundly narrowing apically in *P. buergersi* (s.l.). The general greenish coloration of the few available males of the new species is more mixed with rufous brown than in *P. buergersi*. However, the colour pattern of antennae, tympanal margins, fore tibiae, pronotum and elytra of *P. pipiens* and *P. buergersi* are similar except for the spots of the elytra, which are less obvious in the new species.

Separation of the new species from *P. apterus* and *P. pusillus* is clearly shown by the strongly reduced hind wings, the basally instead of distally darkened antennal segments, the more widely rounded tip of the elytra, Rs vein reaching the elytron margin behind its tip and the distally less narrowing male subgenital plate in the latter two species.

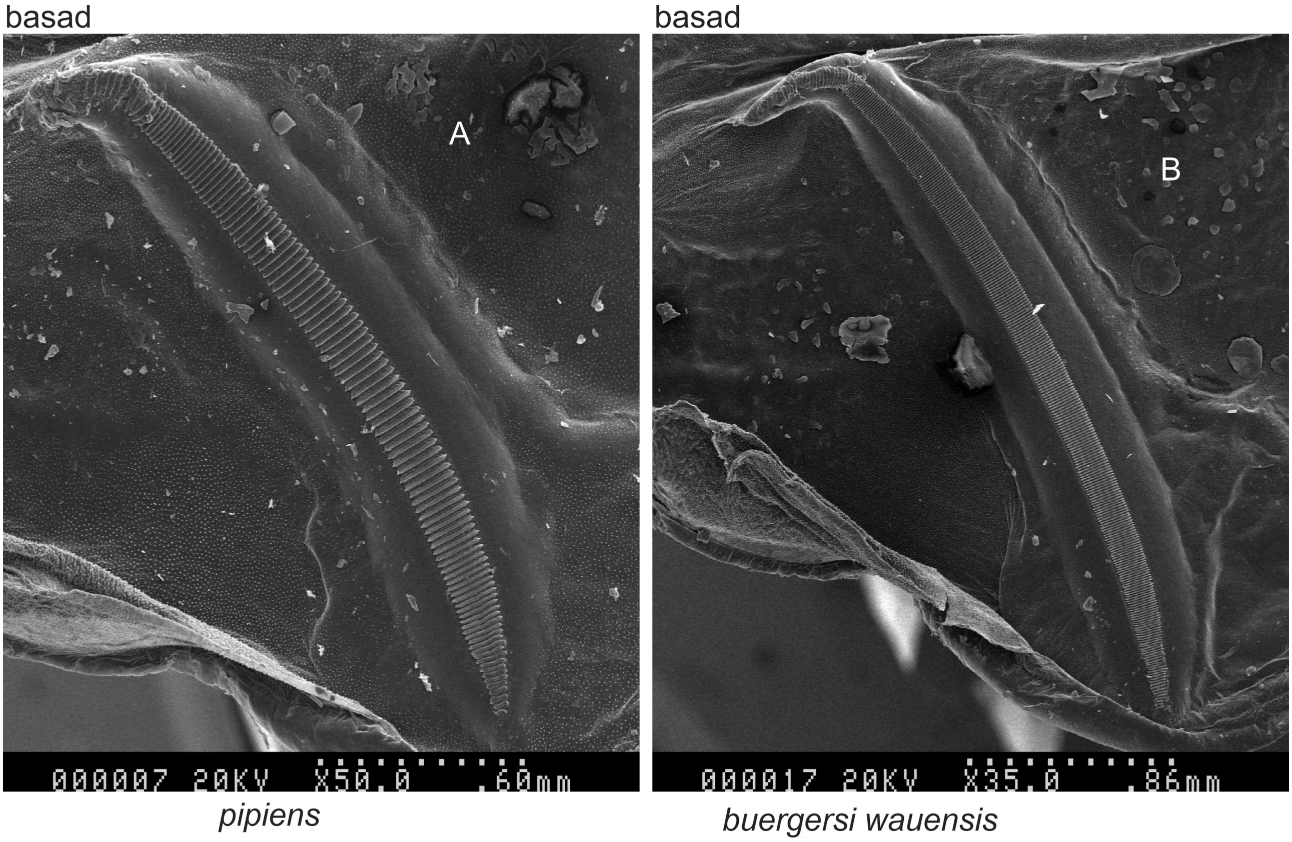
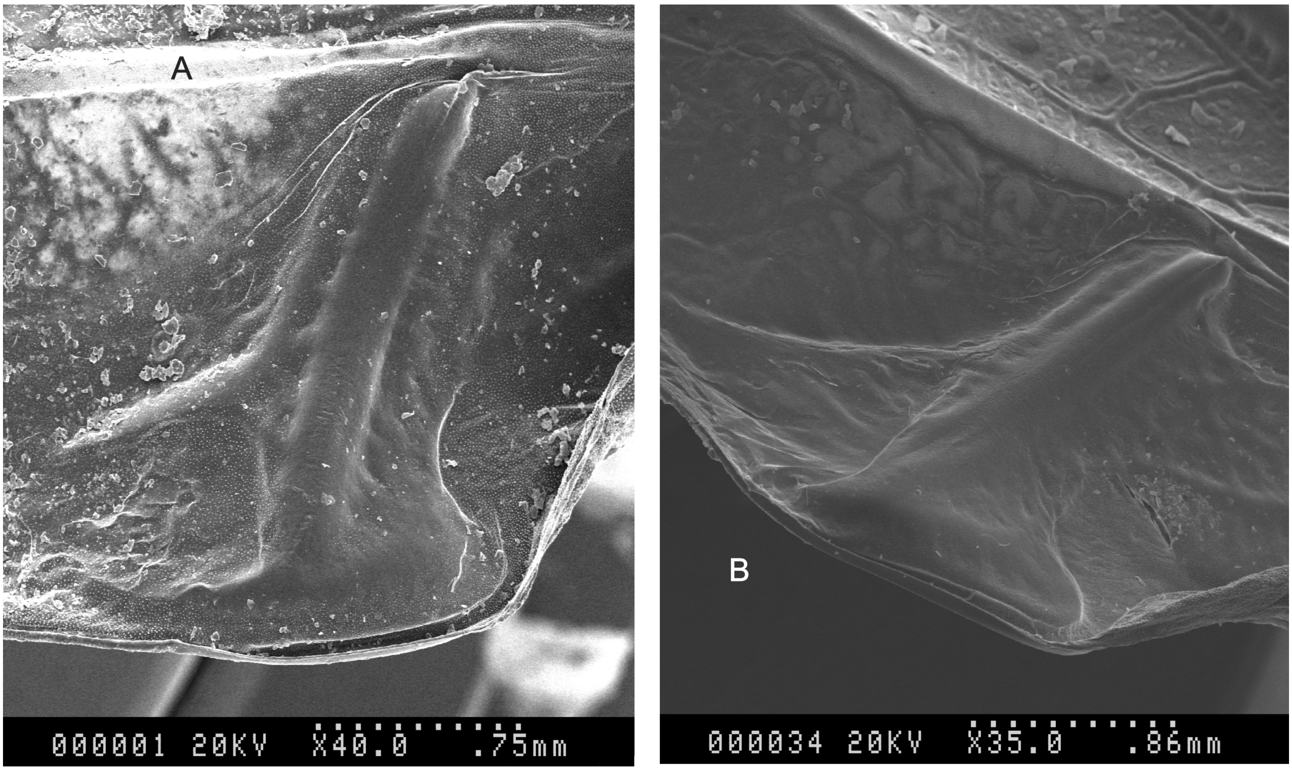
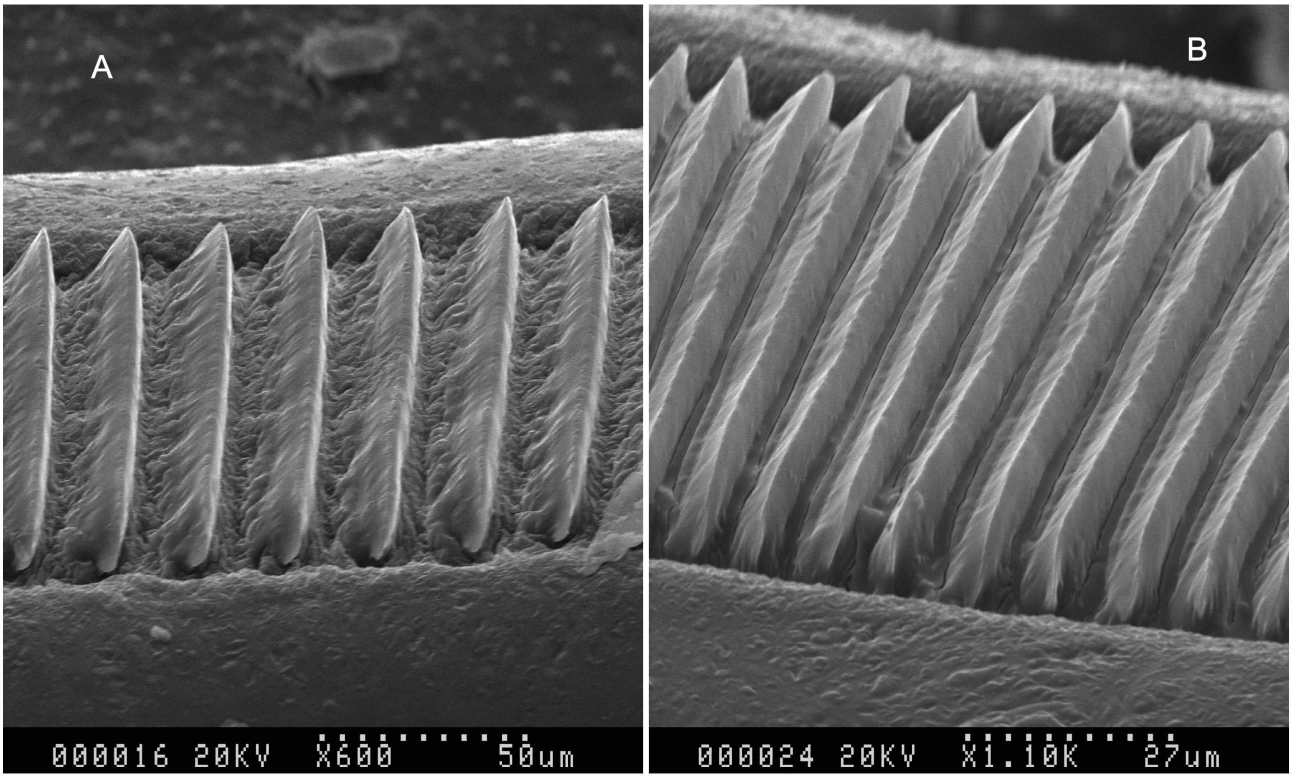


FIGURE 11. SEMs comparing files *Paraphyllomimus* spp.; view of left tegmen underside: A) *P. pipiens* **sp. nov.**; B) *P. buergersi wauensis* **ssp. nov.**; greater tooth density of *P. buergersi wauensis* is congruent with longer sinusoid song pulses.



pipiens *buergersi wauensis*

FIGURE 12. SEMs comparing scrapers *Paraphyllomimus* spp.; view of right tegmen underside, scrapers low in foreground; broadly flattened transverse vein conveys forces to and from each scraper; vestigial file absent: A) *P. pipiens* **sp. nov.** B) *P. buergersi wauensis* **ssp. nov.**



pipiens *buergersi wauensis*

FIGURE 13. SEMs *Paraphyllomimus* spp. file teeth close-up, no midbreadth tooth inflection: A) *P. pipiens* **sp. nov.** gullet nodules present; B) *P. buergersi wauensis* **ssp. nov.**, no gullet nodules.

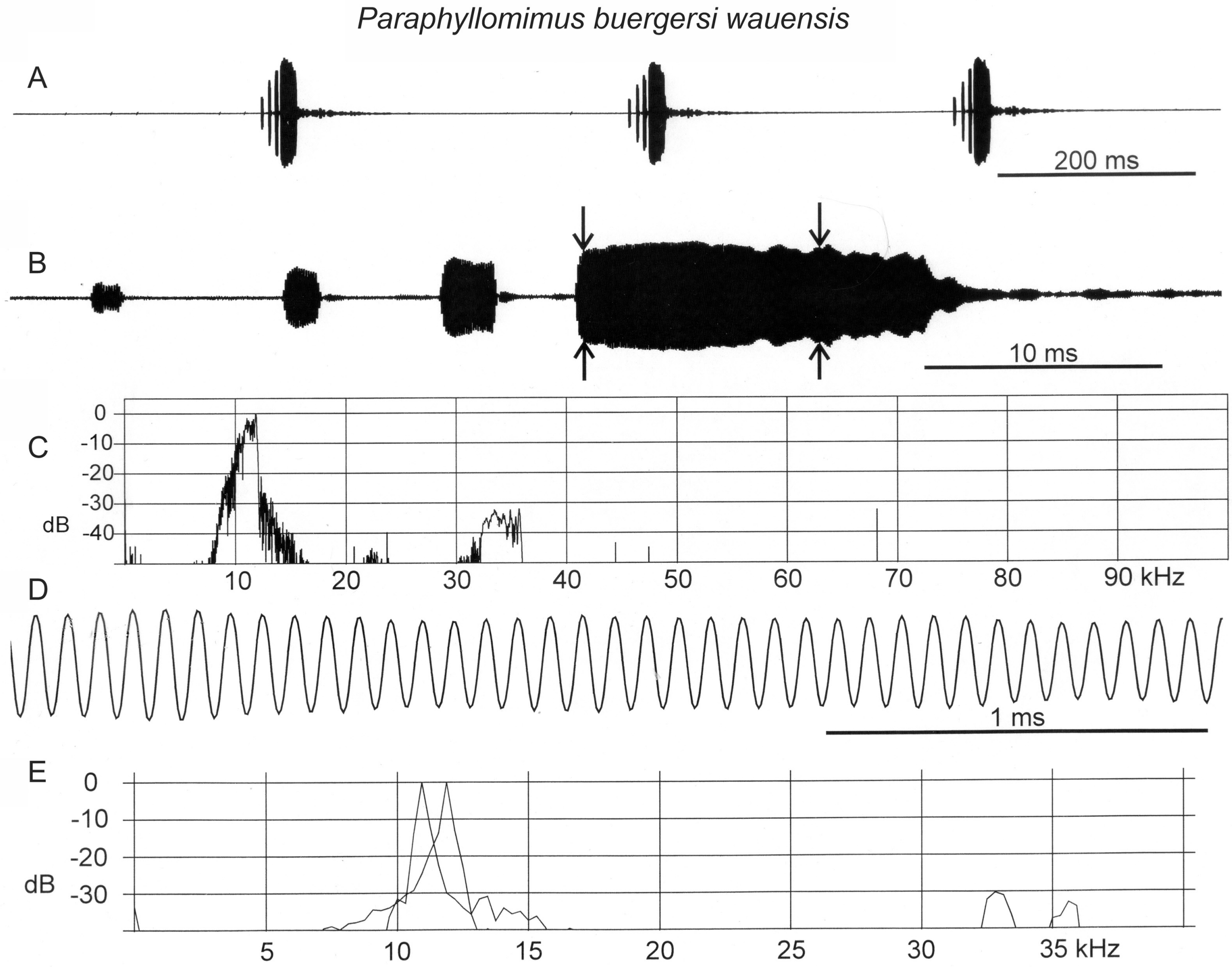


FIGURE 14. *P. buergersi wauensis* **ssp. nov.** acoustic analysis: A) 3 calls from sequence; B) One call at higher time resolution, three shorter pulses building in amplitude and duration precede a sustained pulse of almost 20 ms; C) Power spectrum of call, weak harmonic of 13 kHz fundamental ~34 kHz; D) Strongly sinusoid (high-Q) time sample from final pulse; E) Upward sliding FM of ~1 kHz, limits shown by overlain power spectra; FFT calculated on each of 512-point samples taken from the prolonged pulse at times indicated by arrows in FIGURE 14B.

Distribution. Known only from Mt. Kaindi near Wau, Morobe District, NE New Guinea. *P. pipiens* and *P. buergersi wauensis* sing perched on understorey vegetation within earshot of each other at the higher elevations of Mt. Kaindi in undisturbed forest.

Stridulation. At 20°C a recorded male had a mean call period of 1.5 s (n =24 consecutive calls). The field name 'zipper' arose from the several short pulses comprising each call, these giving a human listener an impression of infrastructure. Though the pulses of *P. pipiens* are much shorter than those of *P. buergersi wauensis*, they still leave a tonal impression when 'sample-rate slowed'. The first trace of Fig. 15A, is one complete song. Its 4 pulse groups each consist of a series of short sinusoidal pulses such as that shown in Fig. 15D, this latter being the penultimate pulse of Fig. 15B. The last pulse group of A is shown in B at higher resolution, with Fig. 15D as a very high resolution of the penultimate pulse in B.

The FFT spectrum (Fig. 15C) is calculated upon the entire trace of Fig. 15B. Peak frequency is near 10kHz with a low-Q somewhat broadened carrier peak, as one might expect with these less sustained pulses. The spectrum of the penultimate pulse of Fig. 15B is shown in Fig. 15E with a higher Q peak at 14 kHz.

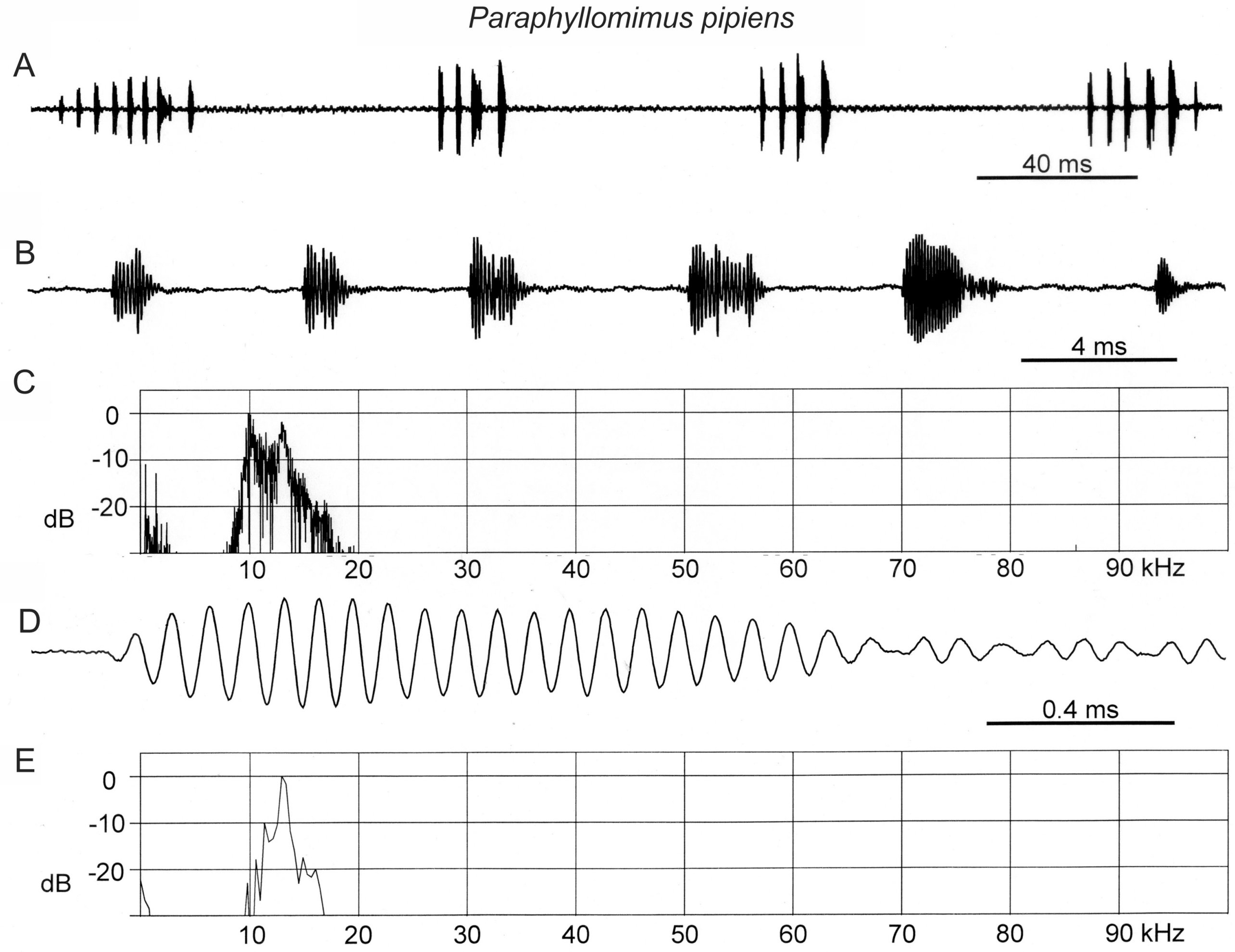


FIGURE 15. *P. pipiens* **sp. nov.** acoustic analysis: A) 4 calls, each of 4–6 cleanly time-separated pulses; B) Single call at higher time resolution; C) Fourier power spectrum of time sample in B; sound energy confined to audio between 9 and 16 kHz; D) Waveform of a single pulse, a decaying sinusoid; E) Spectrum of time sample D, peaking near 13 kHz.

Mecopodinae Walker, 1871

Mecopodinae

Charisoma Bolivar, 1903

Type species: *Charisoma karschi* Bolivar, 1903 (by monotypy). Bolivar described this monotypic genus after specimens from Sattelberg, Morobe Dist., NE New Guinea. Some of these specimens have been lost by fire (Budapest Museum 1950), but one male and female syntype could be traced in Bolivar's collection (Paris 1994) (Madrid Museum, V. Llorente in litt. 1997) and one topotypic female in Willemse's collection. Material of *Charisoma* is very scarce (Beier 1966). Since its description only a single female has been reported (C. Willemse 1933).

The generic diagnosis of two males from Mt. Kaindi near Wau (Morobe District) and a single female from Koroba (S. Highlands District) before us is obvious. However, mainly by insufficient data in the description of *C. karschi* (Bolivar 1903 = Caudell 1916 = in Latin) their conspecificity with *C. karschi* appeared doubtful. This made a comparison with Bolivar's typical specimens necessary.

Charisoma karschi karschi Bolivar, 1903

(Fig. 18A)

Specimens studied. Lectotype male (here designated): "N. Guinea, Biro, 1899", "Sattelberg, Huon Golf", "Charisoma karschi"; "**Gen. nov.** Mecopodidarum" (MNCN).

Other specimens studied: 1 female (paralectotype): similar locality labels as lectotype (MNCN), (MNCN); 1 female (topotype): "Sattelberg, Huon Golf, N. Guinea, Biro 1899".

Systematics. Both syntypes have been studied by Dr. V. Llorente. The male has been selected as lectotype. Additional data for this specimen are as follows (V. Llorente in litt. Dec. 1997). Fastigium of vertex wide, medially sulcate, laterally folded, these folds extending anteriorly and convergently towards fastigium frontis, in frontal view forming a pair of triangular plates, separated from each other by distinct median sulcus (Fig. 18A). Mirror of right elytron large, longer than wide, elliptical with basal margin straight; fold of mirror narrow, extending slightly dorso-anteriorly over depressed mirror. Stridulatory file with shortest distance between most proximal and distal tooth 3.21 mm, greatest width of teeth in mid part 0.37 mm, number of teeth over 160, proximal teeth much closer set than distal ones, spacing widest in mid third with about 8–9 teeth per 0.25 mm.

Measurements. (In mm) (male lectotype): length of body 20.5; width of fastigium of vertex 1.6; diameter eye 1.13; length of pronotum 4.53; length elytron 17.8, max. width 7.3; length of mirror 4.71, width 3.25; length of hind femur 17.

Distribution. Known only from Sattelberg, Huon Golf, Morobe District, NE New Guinea. The record of a female from NW West Irian (C. Willemse 1933) should be confirmed by an associated male.

Stridulation. Unknown.

Charisoma karschi 'goggle eye' undescribed subspecies

(Figs 16, 17B, 18B, 19)

Specimens studied. Holotype male: "PNG, Mt. Kaindi near Wau, 30 viii 1981, G.K. Morris" (Depository NBC Leiden, missing).

Other specimen studied: 1 male (paratype) with similar labels as holotype (Depository NBC Leiden, missing).

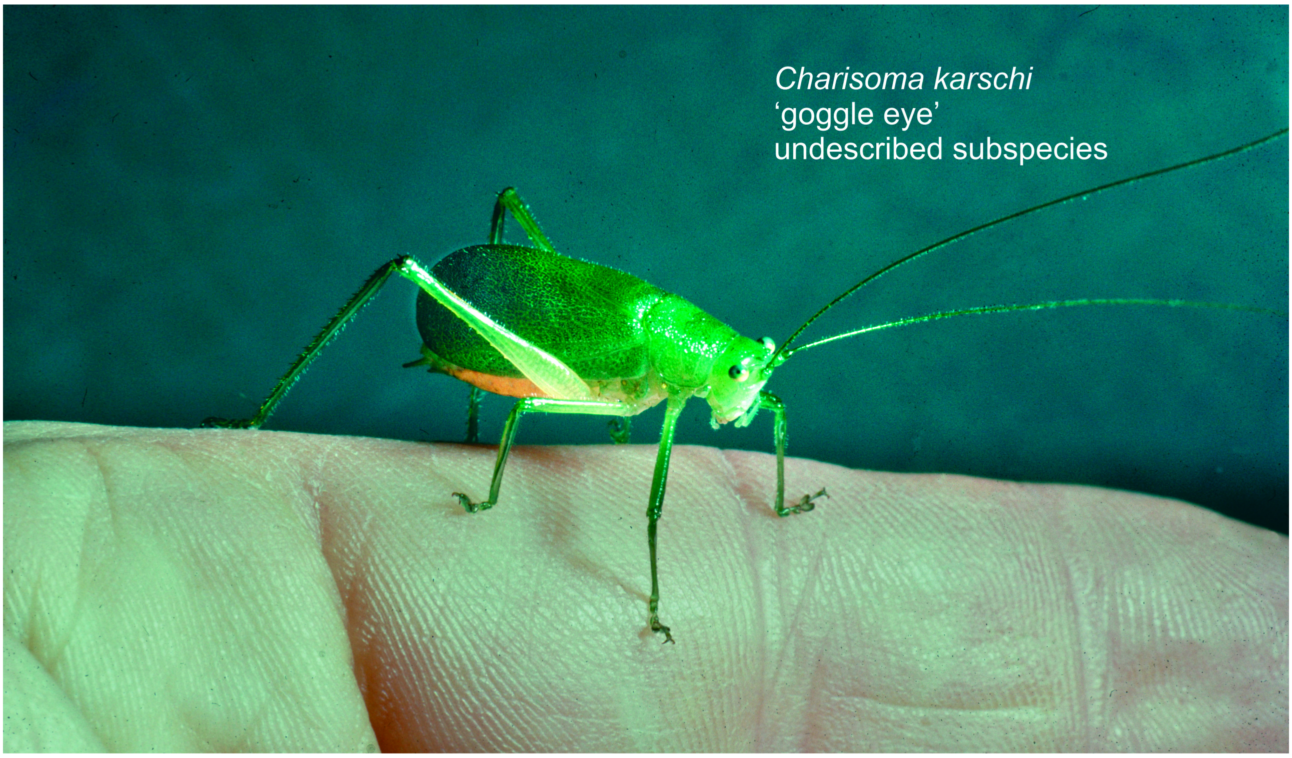


FIGURE 16. *Charisoma karschi* 'goggle eye' **ssp. nov.**, male stands on finger.

Description. Male.—General appearance as in Figs. 16, 17. Size smaller than nominate form. Fastigium of frons tubercle-like. Fastigium verticis transverse (1.2–1.3 mm), distinctly divided into right and left halves, each half consisting of a rounded tubercle-like inflation medially and a laterodorsally extending narrow fold which does not extend anteromedially (Fig. 18B). Eyes conspicuously globose, slightly stalked, in dorsal view greatest diameter of eye 1.1 mm of stalk 0.9 mm. Pronotum as in nominate form but smaller, surface impressopunctate, anterior margin very slightly rounded, posterior margin weakly excised, disc flat without lateral carinae, laterally roundly merging into lateral lobes, also in metazona. Thoracic auditory spiracle small, comparatively inconspicuous, not covered by pronotum. Prosternum with a pair of spines. Elytron scarcely reaching tip of hind femur, thick, somewhat rigid, convex with weak cubital hinge along stridulatory area; not transparent, archedictyon in basal half of elytron including all of costal area densely covered with numerous droplet-like semitranslucent areolae, in distal half increasingly striated with numerous elongate narrow semitranslucent tiny cells; elytron quite wide at base, anterior and posterior margins almost straight, the latter in apical third obliquely converging towards narrowly rounded tip; venation reduced to main veins, Sc and R rather divergent in basal third, convergent in mid third and almost touching each other there and thus creating a fusiform area, in apical third again weakly divergent and reaching tip of elytron; R with two or three pectinate branches, these and distal part of M running straight, parallel and at about similar distance from each other reaching the posterior margin. Stridulatory area folded along Cu1, triangular, venation of this area of left elytron consisting of archedictyon all over except for the file; file in dorsal view not inflated, in ventral view almost straight, concave in profile, slightly fusiform, shortest distance between most proximal and distal teeth 2.9 mm, greatest width in mid part 0.23 mm, number of teeth about 140, proximally closer set, spacing widest in mid third about 7 per 0.25 mm; stridulatory area of right elytron with large mirror which is longer than wide, elliptical with basal margin transverse and straight; fold of mirror narrow, extending slightly dorsoanteriorly over the depressed mirror, its outline almost straight.

Supra-anal plate simple, convex, posterior margin evenly rounded. Cercus slightly tapering apically, cylindrical, weakly incurved with a strongly incurved apical spinule. Subgenital plate narrowing posteriorly, hind margin with deep U-shaped excision, the posterior processes bearing quite short styli.

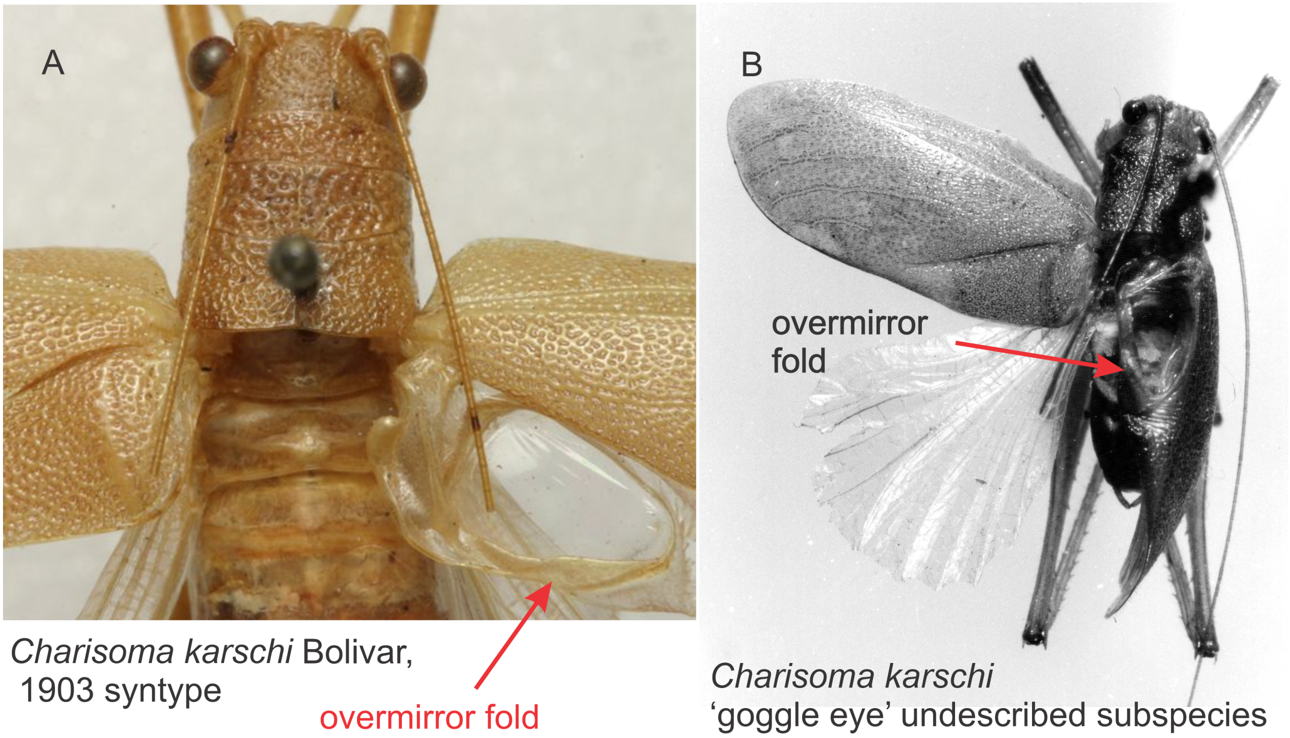


FIGURE 17. A) *Charisoma karschi* Bolivar, 1903 male syntype, dorsal view of strigin of deployed tegmina, arrow to modest overmirror fold; photo from OSF; repository Museo Nacional de Ciencias Naturales, Madrid; B) *Charisoma karschi* 'goggle eye' **ssp. nov.** (F. Willemse intended holotype male).

Tympana of fore tibiae narrow oval, completely open on either side. Fore coxa with dorsal spine, mid and hind coxa unarmed. Fore legs unarmed except for both knee lobes provided with a single spine each and presence of a tiny apical spine of dorsoexternal keel of tibia. Mid legs also with single-spined knee-lobes, ventral keels of tibia bearing some spines. Hind femur with a few spines in distal half of both ventral keels, knee-lobes also single-spined.

Coloration uniformly green except for eyes and tips of tibial spines dark brown and brownish flush over distal striated part of both elytra.

Female.—see below.

Measurements. (In mm) (male n = 2): body length 16.0 & 15.7; width of fastigium verticis 1.2 & 1.3; eye diameter 1.1 & 1.1 plus stalk 0.9 & 0.9; pronotum length 4.1 & 4.3; elytron length 13.5 & 15.1; max. width of elytron 7.0 & 6.7; mirror length 3.8 & 4.1 width 2.6 & 2.7; length strid. file 2.9 & 3.0, max. width of teeth 0.225 & 0.290, spacing in mid part 7 & 8 teeth per 0.25 mm, total number of teeth 138 & 143; length hind femur 13.2 & 13.0.

Distribution. Known only from Mt. Kaindi near Wau, Morobe District, NE New Guinea.

Comments. In fading evening light attention was drawn to this species by its calls. These came from trees bordering the repeater station atop Mt. Kaindi. The first male of two captured was taken by climbing 4–5 m up a tree. The singer was disturbed into silence by the climber several times, but readily returned to his song. He was secured by a clumsy grab that deprived him of a leg. A second male was collected later about 1 m from the ground, an anomaly of perch since no calling was heard coming from that low down.

The Mt. Kaindi males are apparently smaller than typical *C. karschi* and the lateral folds of the fastigium verticis do not extend towards the fastigium of frons. Differences of the stridulatory apparatus may refer mainly to smaller size of the elytra in *C. karschi* ‘goggle eye’ **ssp. nov.**

The difference in size, but particularly the remarkably distinct fastigium of vertex of the Mt. Kaindi specimens justify taxonomic recognition of the latter form. As further comparison of their songs is not yet possible, we propose to rank the new taxon at subspecific level, *C. karschi* ‘goggle eye’ **ssp. n.**

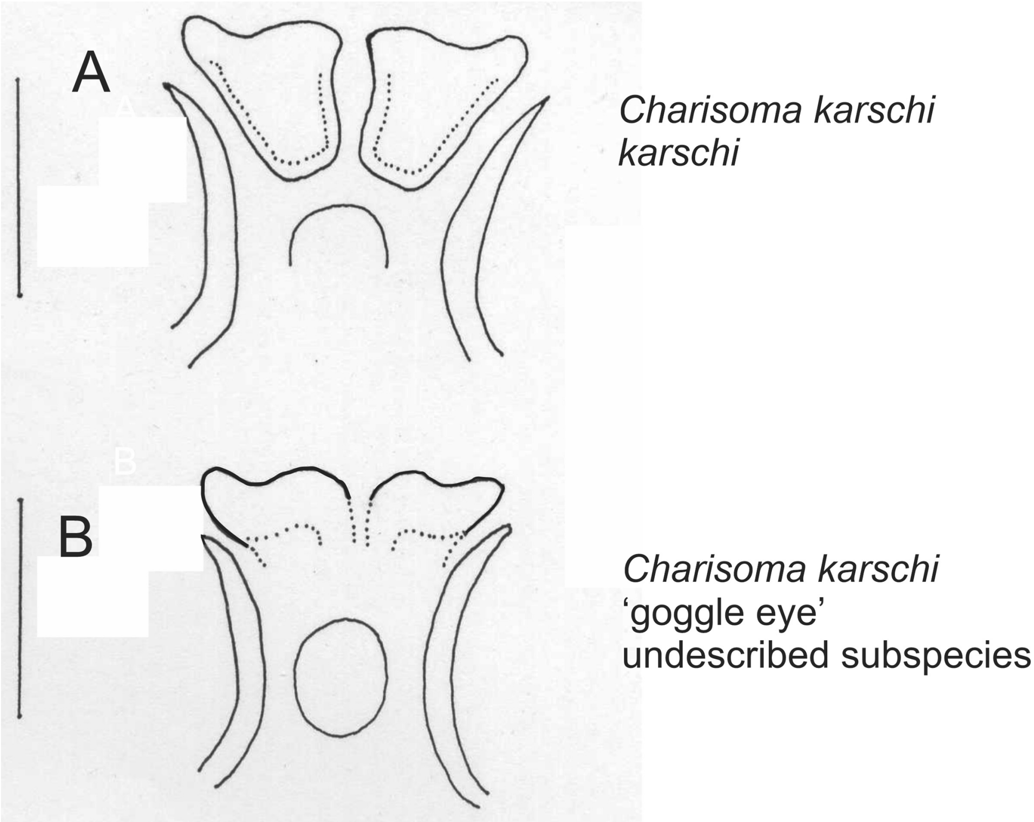


FIGURE 18. Compared fastigia of vertex *Charisoma* spp. (scale 1 mm): A) *C. karschi karschi* Bolivar, 1903 lectotype male; B) *C. karschi* ‘goggle eye’ **ssp. nov.** (Fer Willemse intended holotype male).

We have before us a single female from Koroba, Southern Highlands District 13 x 1960. Its size and fastigium of vertex disagree with the female of nominate *C. karschi* before us but fit perfectly these characters of *C. karschi* 'green goggle'. By lack of an associated male, however, we abstain from further identification.

A photo available on the Orthoptera Species File (Fig. 17A) shows a dorsal view of the right tegmen sound field of the syntype male in the Madrid Museum. In this species there is only a very small cantilevered overmirror fold, spanning the anal margin of the somewhat rearwardly ovoid mirror speculum.

Stridulation. The song of *Charisoma karschi* 'green goggle' is a succession of well-spaced 5-train calls. Song period of a singer at 20°C was close to 1.2 s. One call is shown in Fig. 19A. It lasts about a quarter second and consists of 4–6 rather dense trains of pulses, most commonly 5. The first pulse train is lower in intensity and shorter in duration. The train period (Fig. 19A) is about 50 ms.

Because what we here term a pulse often overlaps its neighbours i.e., is not cleanly isolated by down time, the waveform of this insect's stridulation has a 'string of beads' appearance (Fig. 19C). In each single train (Fig. 19B) we can count ~70 variably contiguous pulses. (See the 8 pulses of Fig. 19BC.) The insect's file has ~140 teeth. So one might guess that each 'bead' reflects scraper play across two teeth. (Alternatively, or in addition perhaps posit two specular oscillations per each tooth-scraper event?) As Fletcher (1992) says, if the slip rate of the scraper falls just below that needed for resonance, then slipping from one file tooth to the next "may take place before the vibration from the previous slip event has died away" (Fletcher 1992). Pulses should then overlap. The overall effect is a great number of sinusoidal waves which repeatedly start and decay but never extend to a sustained resonance. This repeated onset and falling away would add side bands which would explain why the spectrum (Fig. 19D) tends toward a band rather than a high Q carrier.

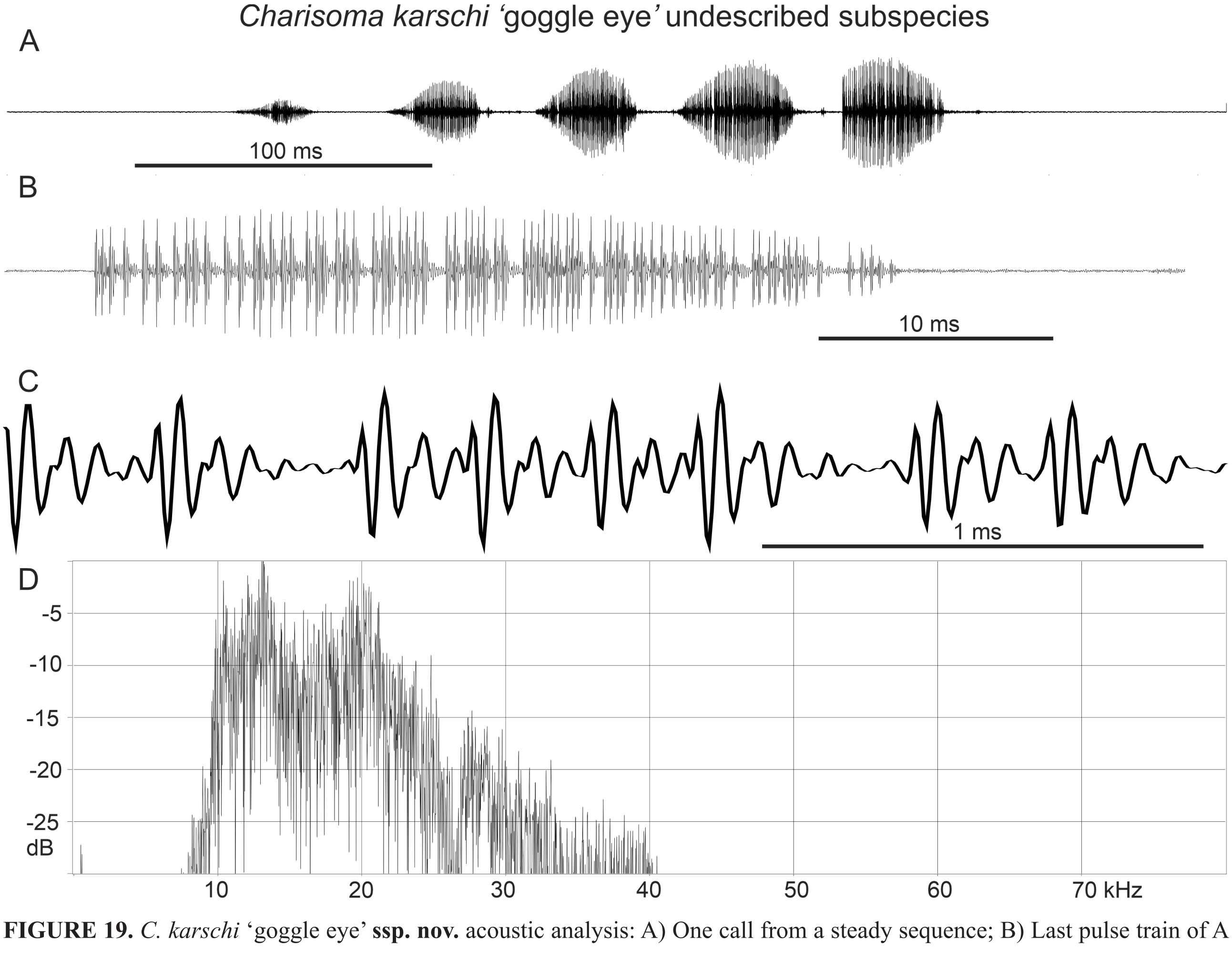


FIGURE 19. *C. karschi* 'goggle eye' **ssp. nov.** acoustic analysis: A) One call from a steady sequence; B) Last pulse train of A at higher resolution shows ~70 variably recurring pulses; C) time sample from middle of train in B showing 8 pulses in more detail; D) Fourier power spectrum a 15-kHz wide band between 10 and 25 kHz, produced by, transient stridulation.

Spectral frequencies occur in a high-audio band whose longer wavelengths begin sharply at 10 kHz (Fig. 19D); this carrier band remained intense to the beginning of the ultrasonic in one singer but rolled off appreciably in the other. The spectrum Fig. 19D is a FFT calculated upon the signal sample in B. The microphone in use for these records is a B&K 4135 attached to a 2203 sound level meter, so the spectrum above 40 kHz is inaccurate. But spectra made with the QMC recording system showed no sound energy above 40 kHz, so we have left the axis extending to 70kHz in the figure.

Eumecopoda Hebard, 1922

Type species: *Mecopoda cyrtoscelis* Karsch, 1888 by original designation.

Under this genus about 7 taxa have been arranged (Hebard 1922, Beier 1966). Two of them, *E. reducta* Hebard, 1922 and *E. walkeri* (Kirby, 1891), occur in the Philippines, *E. moluccarum* (Griffini, 1908) in the Moluccas, *E. superba* (Bolivar, 1898) known only from "Hassam" and Mansinam (NW West Irian) (Bolivar 1898, Griffini 1908) and the widespread type-species *E. cyrtoscelis* from the Aru Islands through all of New Guinea to New Britain. The taxa *E. karschi* and *E. regina*, both Kirby, 1891, are considered subspecies of *E. cyrtoscelis*, the former occurring in Queensland, the latter in Duke of York Islands.

The specimens collected in the surroundings of Wau represent two species, a larger one referring to *E. cyrtoscelis* and a smaller one, which has apparently not yet been described.

Eumecopoda cyrtoscelis (Karsch, 1888)

(Figs 22–25, 30, 31, 82AB)

Specimens studied. PNG, Wau W.E.I. 30 vii & 4 viii & 23 viii 1981, remnant forest understory, G.K. Morris 3 males; Bulolo Gorge, McAdam Nat. Pk., 28 viii 1981, G.K. Morris (1 female). (Depository NBC Leiden).

Systematics. .The specimens agree with the nominate form.

Habitat. Found on low vegetation alongside forest paths. Both *Eumecopoda* spp. descended to the bottom of their cages during the day becoming immobile. But when disturbed they reacted explosively: Dita was very effectively startled when she investigated one inert male that suddenly leaped away. Once it gets dark the insects climb back up in their cages and begin to sing.

Stridulation. Each *E. cyrtoscelis* call continues for several seconds at a time (Fig. 30A) and each call initiates with single high intensity sound (see arrow in Fig. 30A). At increased time resolution these calls are seen to be composed of two sorts of simple sine waves, i.e., two different carrier frequencies (Fig. 31A–C). There is a less intense higher frequency and a more intense lower frequency. Both carrier frequencies, 3.1 and ~6.7 kHz, lie in the low audio range and are harmonically related, alternating rather than co-occuring, so providing an example of resonance stridulation together with sequential frequency modulation. Both species are very loud to healthy human ears. On first hearing calls in the field we remarked on the song's odd quality, perhaps a response to the rapid alternation of the two close harmonics.

This would appear to be an instance of resonance stridulation. Yet the presence of the overmirror fold and a large terminal swelling blocking the basad terminus of the file, the lack of typical katydid count in file teeth: these are oddities of strigin morphology that suggest a differently functioning sound generator. See the Discussion for an attempt to imagine the workings of this strigin.

The spectral peaks (Fig. 30D) are quite high-Q even though the pulses are comprised of only two dozen waves. Yet there is little or no transient distortion. Perhaps this is because the pulses build slowly and slowly decay (Fig. 31BC). "The amount of transient distortion varies as a function of the time required for the amplitude to rise from zero to maximum or to decay from maxiumum to zero. …slowly rising and slowly decaying signals are characterized by less transient distortion than signals for which the amplitude rises and decays very quickly" (Speaks 1992).

Eumecopoda pumila sp. nov.

(Figs 20, 21, 26–29, 32, 82CD)

Specimens studied. Holotype male: "29.viii.1981 Mt. Kaindi lower slopes PNG", "nr Wau PNG 81-3 coll. G.K.Morris" (Depository NBC Leiden); Allotype female: as first label of holotype (Depository NBC Leiden); Paratypes: PNG nr Wau, Mt. Kaindi, 1.viii (one male) & 19.viii (two males).1981, G.K.Morris; PNG, Wau W.E.I., 21.viii 1981 G.K.Morris (1 male).

Additional paratypes: Papua New Guinea, Madang District, Kaironk, Dec. 1971–Jan. 1972 Coll. J.I.Menzies (two males); New Guinea, Uniba, Upper Minj River Valley, Western Highlands, ca 6200 ft, 17.viii.1963. W.Vink (1 male 1 female).

Description. Male.—As type species of genus but appearing smaller with shorter and relatively broader elytra and wings (Figs 20, 21). Fastigium verticis transverse, truncate anteriorly, faintly depressed from above. Pronotal disc strongly divergent, flat, lateral margins deeply cut by transverse sulci, anterior margin ranging from weakly concave to very slightly convex, posterior margin broadly rounded with or without a very obtuse median tubercle. Thoracic auditory spiracle narrows, elliptical, comparatively large (as in type-species), greatest diameter (height) 1.3 mm, hidden by ventroposterior part of pronotal metazona.

FIGURE 20. Male *Eumecopoda pumila* **sp. nov.**, Habitus in dorsal aspect, smaller of the two *Eumecapoda* spp.

Tip of elytra, when flexed, ranging from not quite reaching to just surpassing tip of hind femur; tip of hind wings commonly not extending beyond elytra, at most scarcely beyond it. Elytron relatively wide, anterior edge apically strongly convex, posterior edge apically also strongly recurved but further apically scarcely sinuate, both edges creating apically a reduced pointed tip. Stridulatory area triangular, as in type-species; left elytron with file of normal shape, slightly fusiform, weakly concave horizontally and vertically, distance between most proximal tooth and distal tooth 3.1–3.2 mm, widest teeth in mid-part 0.33–0.34 mm, spacing widest in mid half about 8–9 teeth per 0.25 mm, total number of teeth 104–111; most of stridulatory area of right elytron transparent, 'mirror' speculum elongate elliptical and strongly depressed towards its posteroapical angle and there covered dorsally by strongly sclerotized but not inflated shell-shaped cantilevered fold (OMF), with straight to slightly convex outline. Hind wing also short and wide; anterior edge strongly curved apically; posterior edge remarkably convex, tip at distal end of MPa (Ragge 1955) not or only obtusely pointed; stronger sclerotization of tip and distal part of MPa area scarcely present. Legs and abdominal terminalia as in type species, but smaller. Coloration as in type species, commonly quite dark brown.

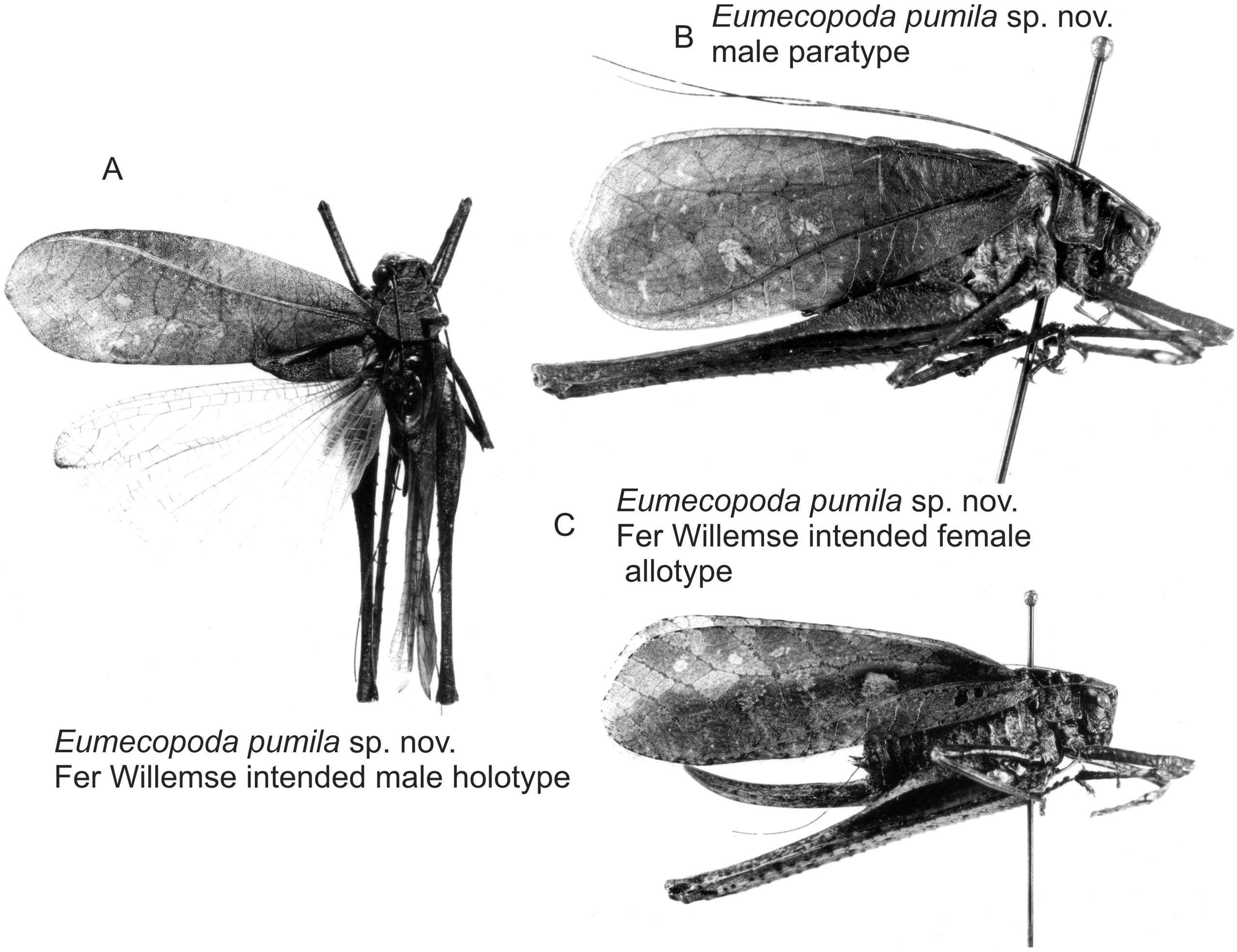


FIGURE 21. *Eumecopoda pumila* **sp. nov.**: A) Habitus in dorsal view, male holotype; B) Habitus in lateral view, male paratype; C) Habitus in lateral view, female allotype.

Female.—As male, slightly larger.

Measurements. (Length in mm) (male n = 8; female n = 2): body male 21.0–25.0, female 27.0–28.6; pronotum male 6.0–6.2, female 7.0–7.5; elytron male 31.0–34.0, female 40.5–43.1; max. width elytron male 11.3–14.0, female 15.5–17.8; hind femur male 28.0–30.0, female 34.8–35.0; ovipositor 19.0–21.0.

Etymology. Named for its size, *pumilus* = dwarfish.

Distribution. Known from the districts of Morobe, Madang and W. Highlands, NE New Guinea.

Habitat. Perches to sing beside forest paths on low vegetation.

Comments. The new species is readily recognizable from all other taxa of the genus and especially from sympatric *E. cyrtoscelis* by its smaller dimensions and the relatively short elytra and wings which scarcely reach the tip of the hind femora and show a blunt apex, the very tip of the elytra located more posteriorly. The elytra in *E. cyrtoscelis* (length male 47–62, female 64–69 mm) surpass the tip of the hind femora (length hind femur male 38–44, female 46–51mm) ranging from almost to ample pronotal length, while the hind wings commonly extend clearly beyond the apex of the elytra when flexed.

Stridulation. The stridulatory apparatus of *E. pumila* differs from that in *E. cyrtoscelis*: the file in the latter commonly slightly longer (2.9–3.9 mm), slightly wider (0.35–0.4 mm), with fewer teeth (53–68), these more widely spaced (4–5 per 0.25 mm) and more robust. Bouts of steady stridulation lasting several seconds (Fig. 32A) are interrupted with pauses of a second or so. Listening to the playback of a recorded signal slowed by a factor of 8,

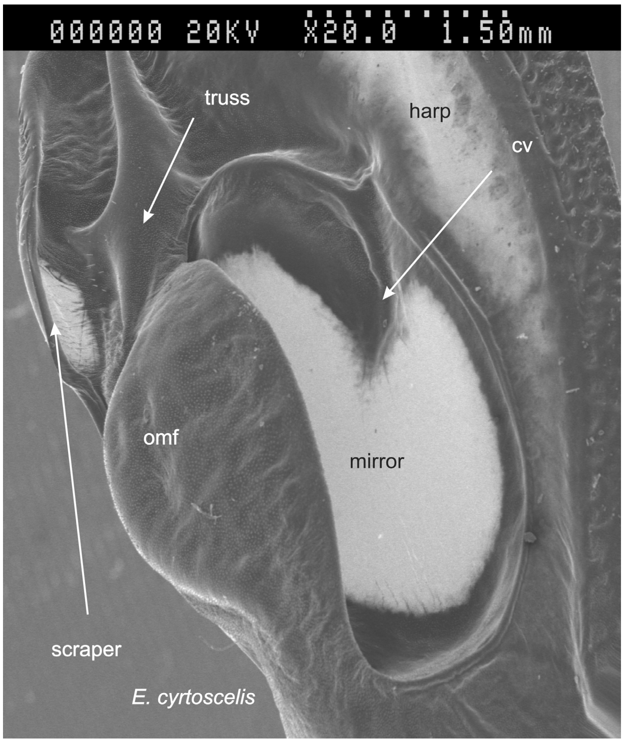


FIGURE 22. *Eumecopoda cyrtoscelis* (SEM). Dorsal aspect of right tegmen shows mirror speculum below cantilevered 'over-mirror fold' (omf); wing base to upper left. Two-side charging of speculum and small area behind scraper indicates their thinness. Short but strong unguiform curved vein (cv) projects into the speculum.

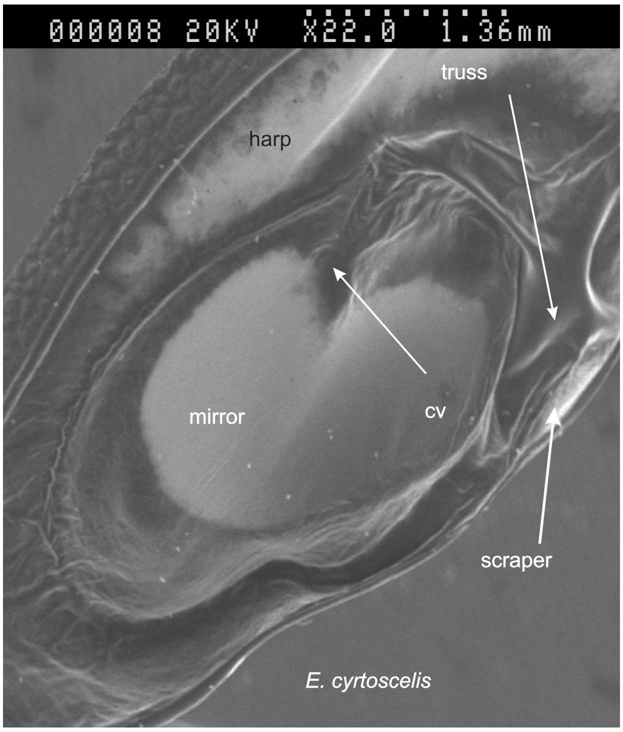


FIGURE 23. *E. cyrtoscelis* (SEM). Oblique view ventral aspect anal region right tegmen, shows charging ovoid speculum and harp; wing base (and scraper) upper right.

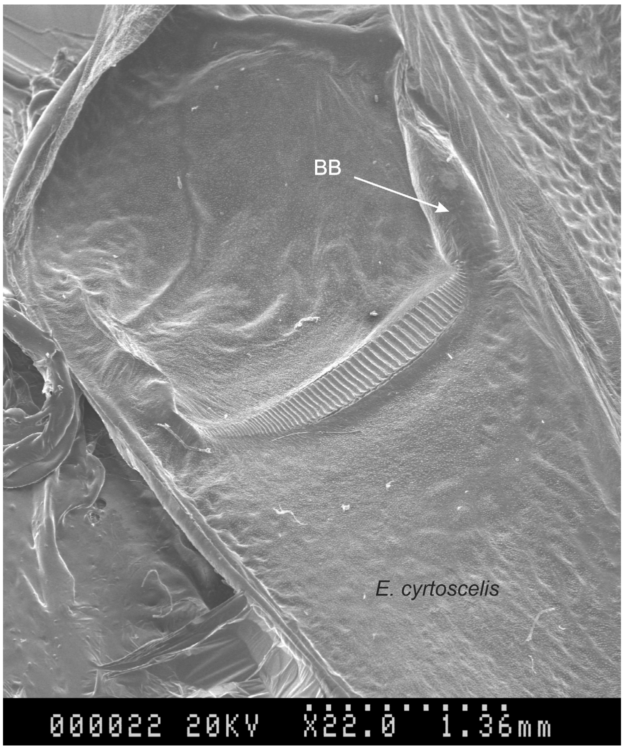


FIGURE 24. *E. cyrtoscelis* (SEM). File of left tegmen seen in ventral aspect; basad file vein bends abruptly 90° creating a large basal blockage (BB) of scraper advance.

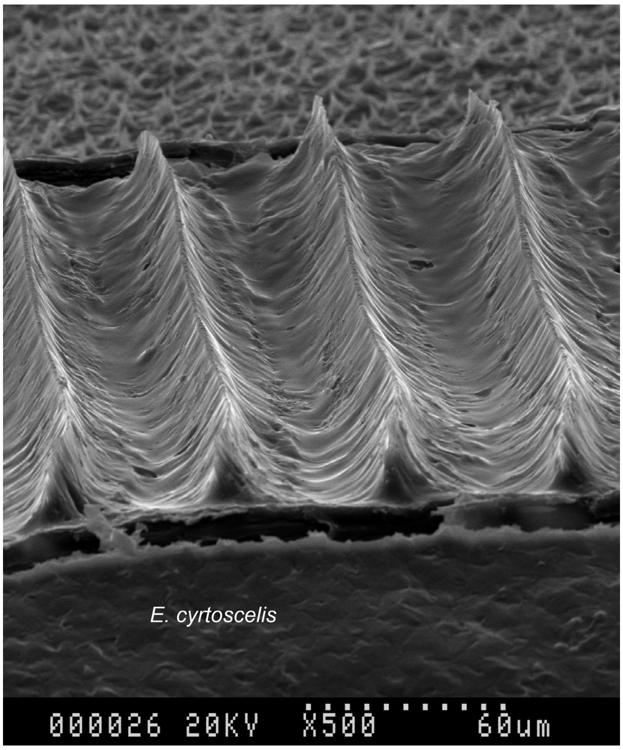


FIGURE 25. *E. cyrtoscelis* (SEM), high resolution of 4 midfile teeth.

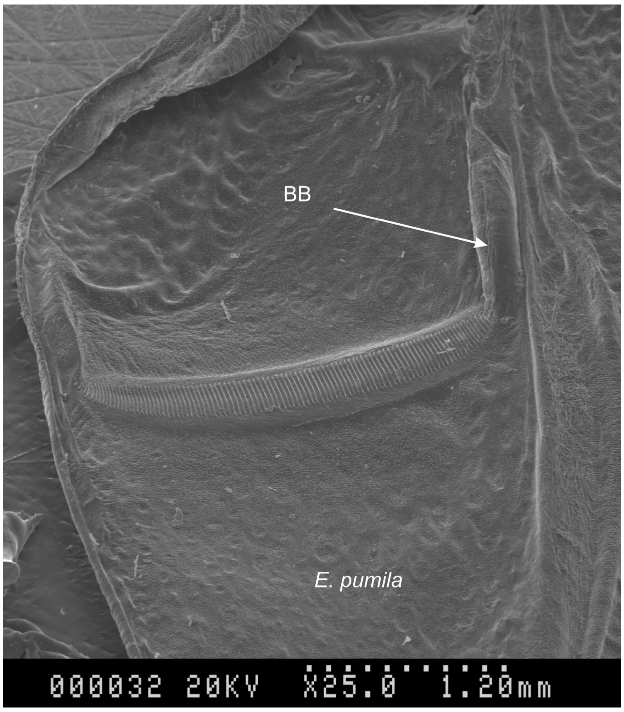


FIGURE 26. *Eumecopoda pumila* (SEM), strigin file; anal region of left tegmen, file vein bent abruptly 90° at cubitus, continuing as large toothless scraper blockage (BB).

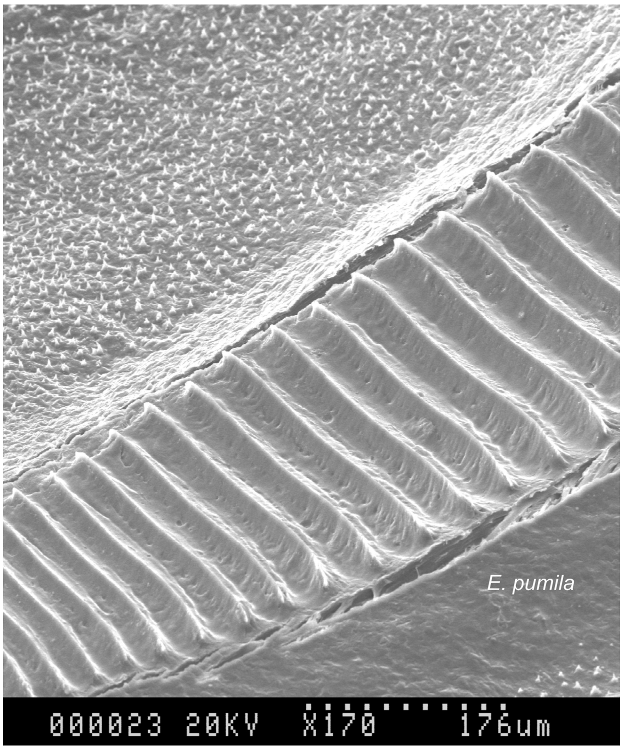


FIGURE 27. *E. pumila* (SEM), close-up of low broad midfile teeth.

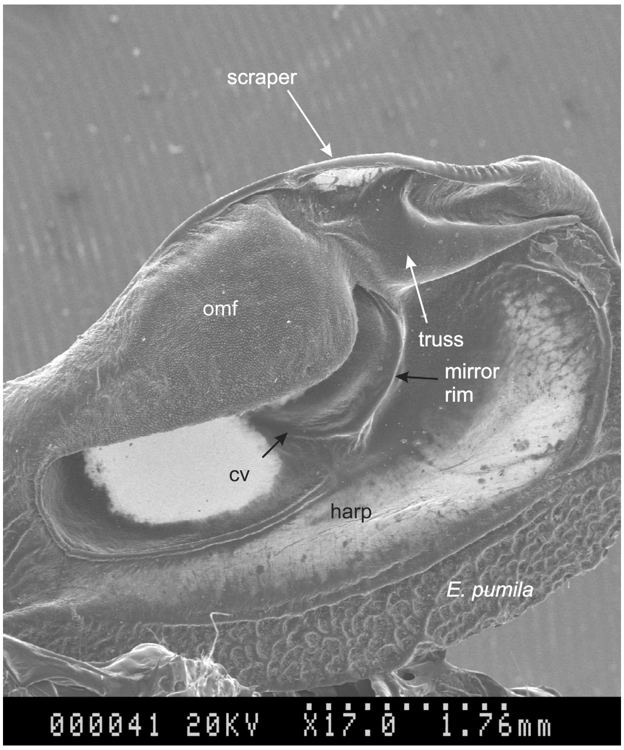


FIGURE 28. *E. pumila* (SEM) dorsolateral slightly oblique aspect of right tegmen; overmirror fold projects toward harp above part of speculum; curved vein (cv) projects into mirror; charging region indicates mirror thinness, harp also charging in part but less so; wing base to the right.

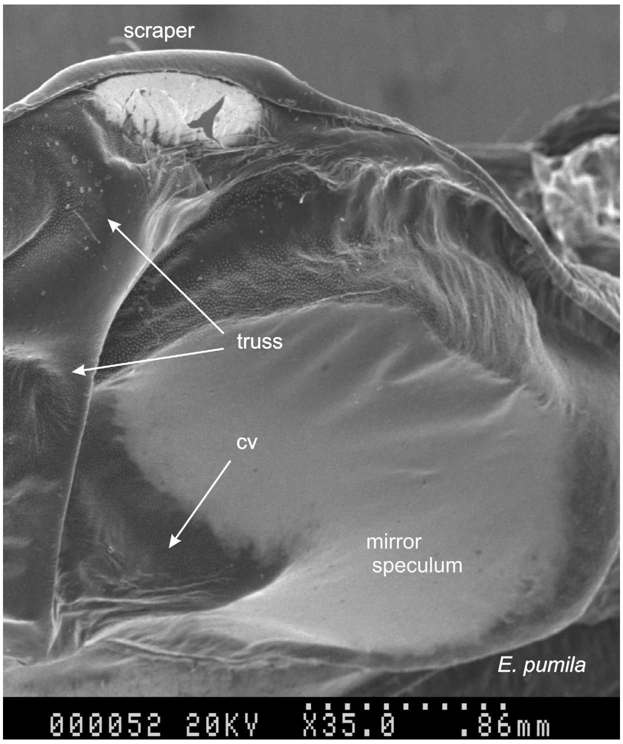


FIGURE 29. *E. pumila* (SEM), strigin in part; ventrolateral aspect of right tegmen showing speculum from below; broad transverse strut of truss braces scraper; wing base to right; note small ovoid charging wing cell immediately behind scraper at top of photo.

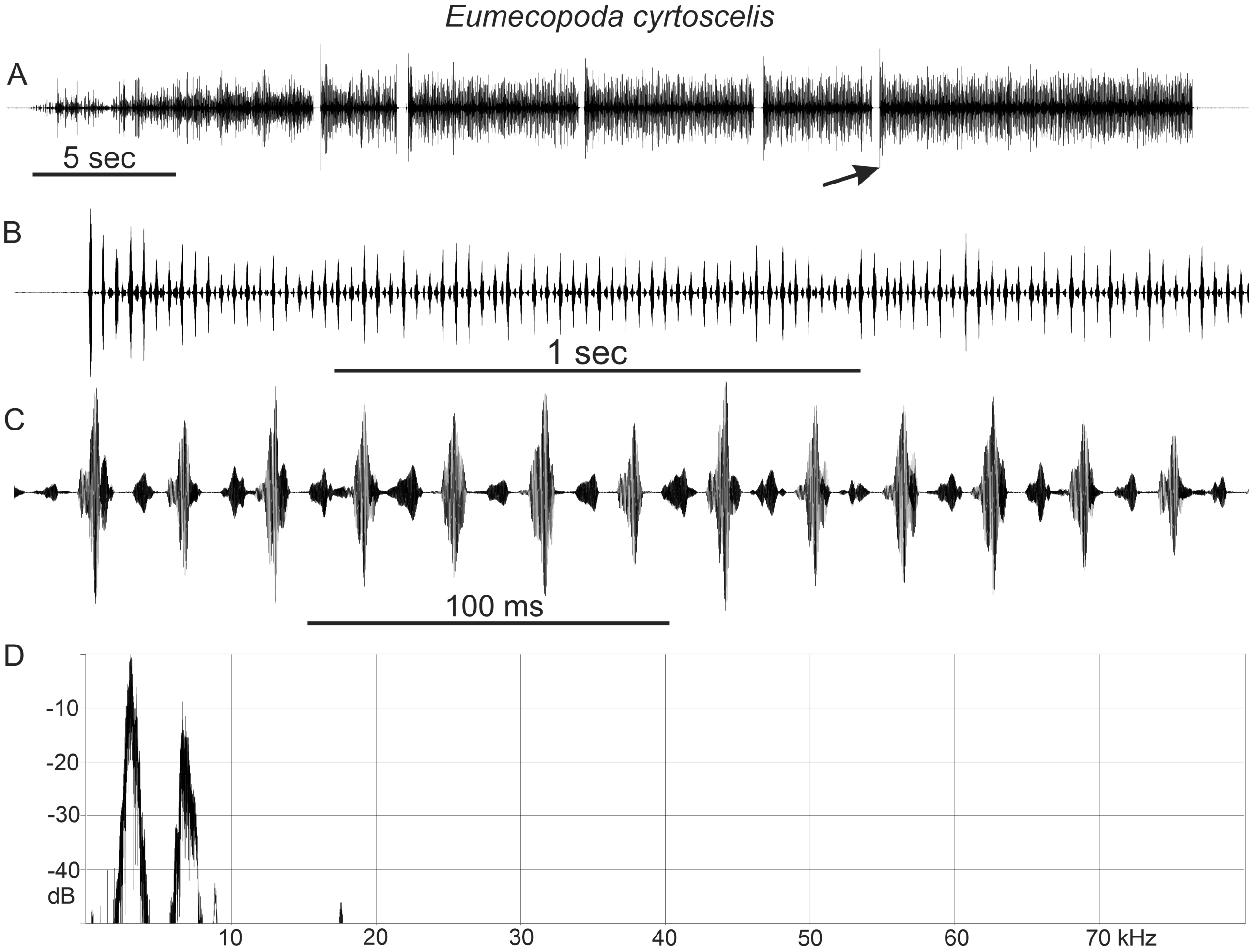


FIGURE 30. *E. cyrtoscelis* acoustic analysis: A) At coarse time resolution 5 calls follow lower intensity ‘warm-up’, each call starts with brief high-amplitude emission; B) Onset detail of the last song of A (arrow); C) higher time resolution of a portion of this fifth call; D) spectrum showing emission of two high-Q audio peaks [3.1 kHz, 6.7 kHz] separated by about 3 kHz (harmonically related); call devoid of ultrasonics.

one is aware that between each loud ‘oink-like’ squeal is another lower frequency sound. In real time in the field the insect sounds raspy, like a rough running motor, but it is nevertheless a resonant stridulator emitting a fairly long sinusoid wave train (Fig. 32B, C) with a Q_{10} of 5 calculated from the spectrum of Fig. 32F. The most intense of these trains—a pulse—shows a stereotyped amplitude envelope (Fig. 32B, C) which builds, maximizes then falls away more slowly than it builds; this pulse precedes a drawn out decay (Fig. 32C) which is in turn followed by the quiet pulse (Fig. 32C,E). Slow rise and fall is perhaps contributing to reduced transient distortion as was the case in *E. cyrtoscelis*.

Most call energy is in the low audio, centred on 7 kHz (Fig. 32H) hence loud to human ears. *E. pumila* (Fig 32FGH) show a frequency modulation of about 2400 Hz—between 4.6 kHz and 7.1 kHz; compare Figs 32D and 32E. There is a very weak sound peak at 20 kHz (Fig. 32H) but no relevant ultrasonics. Unlike *E. cyrtoscelis* in *E. pumila* a harmonic relationship is not apparent between the audio peaks, but again the insect makes two low audio range resonant pulses typical of resonant stridulation. The specimen whose song was used in the figure consistently produced a low amplitude pulse between each major pulse, but this was less well defined in a second singer we recorded.

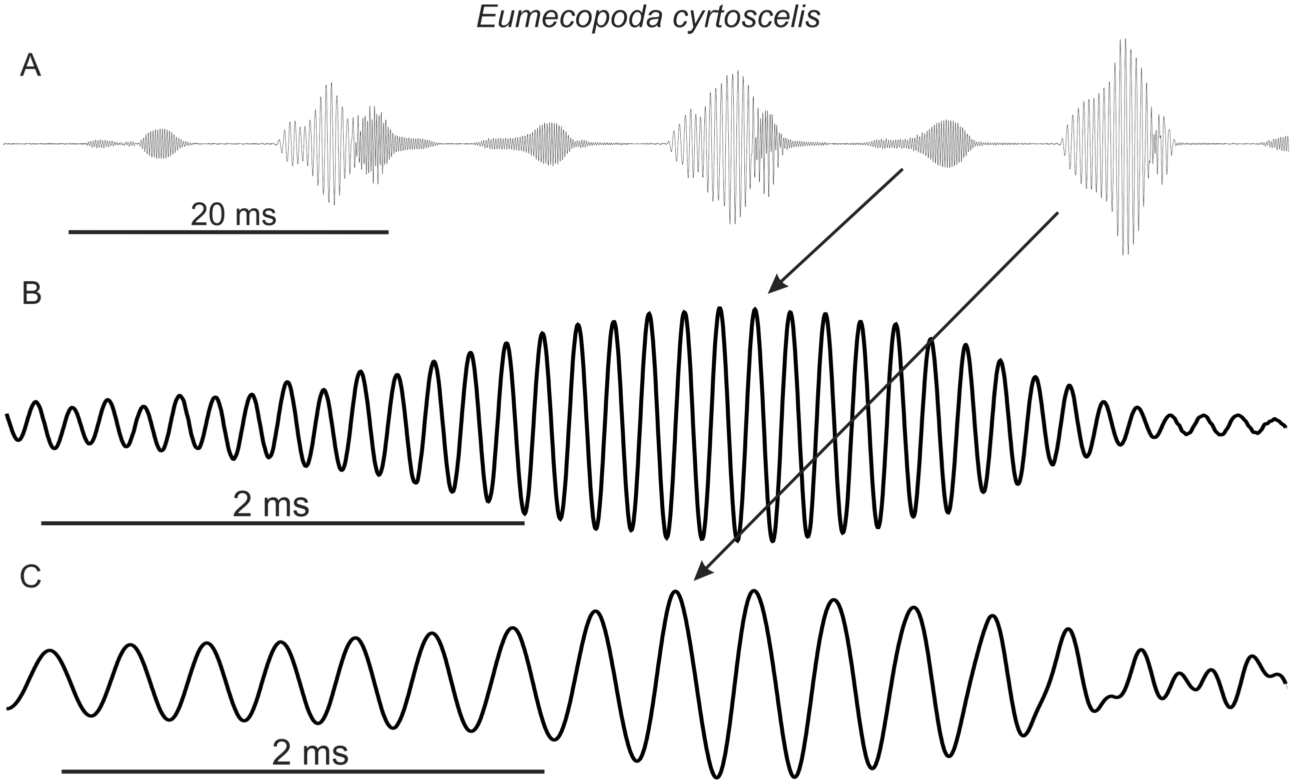


FIGURE 31. *E. cyrtoscelis* acoustic analysis: A) 3 pulse pairs of alternating low and high-magnitude sinusoids; B) lower amplitude pulse in A has higher frequency wave; C) higher amplitude pulse in A has the lower frequency wave.

Sexavaini, Karny, 1924

Sexava-group of genera, *Segestidea*

Two mecopodine species, found together on Mt. Kaindi and closely allied to each other, could not be identified to any known taxon, neither genus nor species. They could be placed with confidence in the *Mossula*-group of genera and will be described below. At the same time, it became clear that with the exception of the *Sexava* group of genera, the arrangement of the remainder of the Sexavini into either the *Mossula* or *Phricta*-group of genera or even the tribal classification of Mecopodini, is sometimes arbitrary, resulting in unexpected resemblance of some taxa which have been arranged quite distantly from each other. Two examples are noted here. Monotypic *Phrictaeformia* C. Willemse, 1961, arranged under the *Phricta*-group (C. Willemse 1961b, Beier 1966) is much the same as monotypic *Huona* Kuthy, 1910, arranged under the *Mossula*-group (Kuthy 1910, Karny 1924a, Kaestner 1934, C. Willemse 1961b, Beier 1966). Monotypic *Kheilia* I. Bolivar, 1898 is arranged under the nominate tribe of Mecopodini (Beier 1966), but seems to be identical to monotypic *Albertisiella*, erected by Griffini (1908) for *Diaphlebus acanthodiformis* Brunner v. Watt., 1898 and classified under the *Mossula*-group of genera (e.g., Karny 1924a, C. Willemse 1961b, Beier 1966). Apparently, part of the subfamily is much in need of revision.

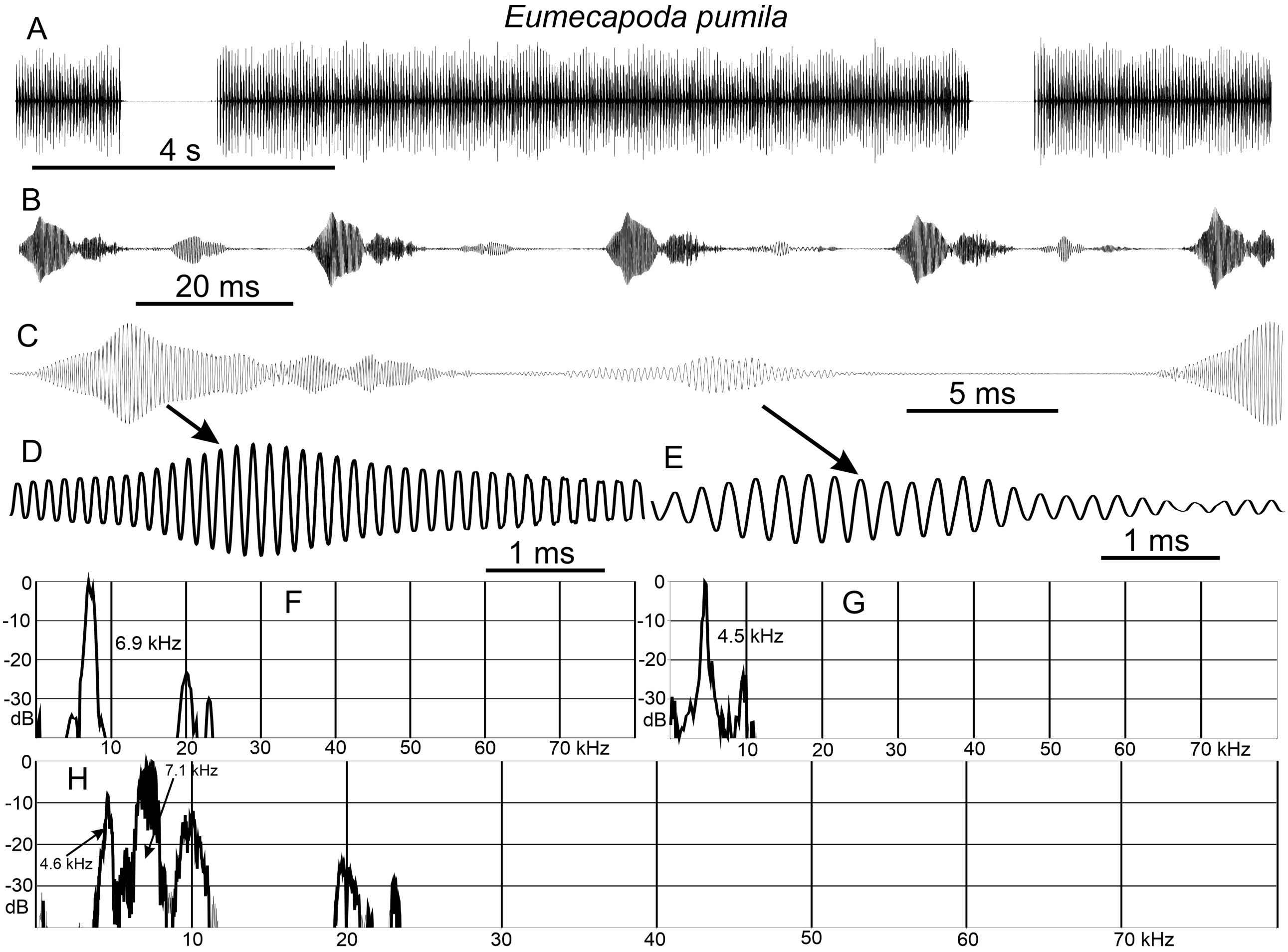


FIGURE 32. *E. pumila* acoustic analysis: A) Coarse time resolution of one complete time-domain emission amid parts of two others; B) 5 phonatomes, each pairing a more sustained more intense pulse with a fainter less stereotyped following pulse; C) higher resolution of one complete phonatome from B shows sinusoid nature of pulses; D,E) [arrows from C] indicate higher resolution sinusoid waveforms at two audio frequencies; F,G) Fourier power spectra of D and E time samples respectively, F a high-Q peak of 6.9 kHz for more intense pulse, G a high-Q peak of 4.5 kHz for less intense pulse; H) Spectrum of multi phonatome time sample in B shows both low-audio frequency peaks.

***Segestidea novaeguineae* (Brancski, 1897)**
(Figs 33, 34)

Specimens studied. (1 male) Papua New Guinea, McAdam Nat. Park, Bulolo Gorge, 28 viii 1981, Coll. G.K.Morris.

Systematics. The male fits perfectly the redescription (F. Willemse 1977, 1979).

Comments. Common name palm katydid. Several *Sexava* spp. are pests of Oil Palm (Page 2005).

Distribution. The locality of this species is covered by the distribution as mapped in F. Willemse (1977, 1979).

Stridulation. Sustained over many seconds, the buzzes of the single recorded male (Fig. 34A) time resolved to regularly repeated wave trains of about 60 ms duration (Fig. 34B) with a regular period of a quarter second (0.25 s). The trains are characterized by a highly erratic amplitude envelope (Fig. 34B). Spectrum frequencies formed one broad aggregate in the audio range (Fig. 34D): for 10 averaged calls this aggregate centred on 10.0 kHz. Though the spectrum is markedly low Q, the waveform of the pulse is not a train of distinctly time-separated transients and at higher time resolution these are seen to be almost sinusoid (Fig 34C); visible are distortions of the sine waves which might be the result of overloading the recording equipment or alternatively of a low sampling rate.

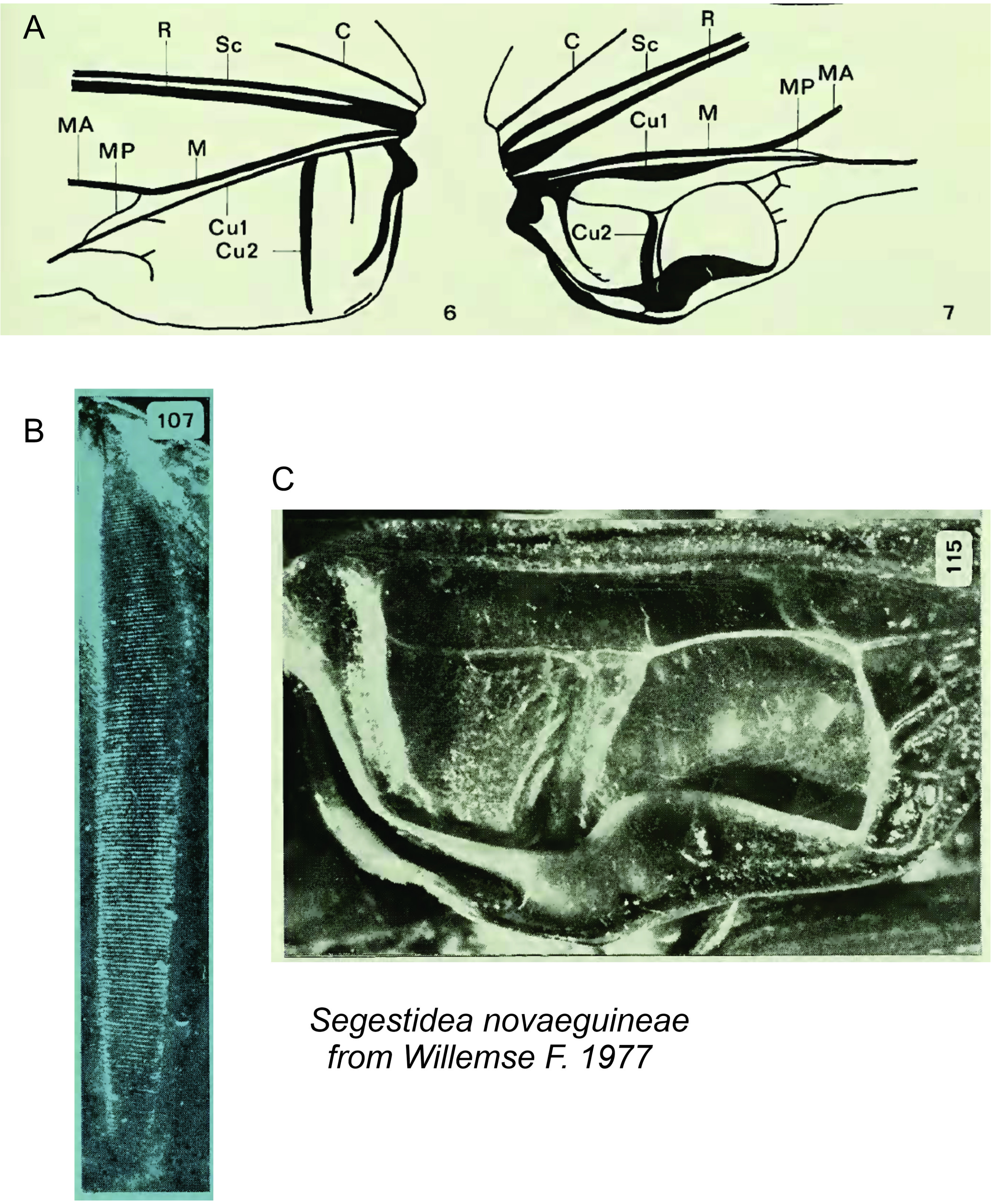


FIGURE 33. *Segestidea novaeguineae* strigin: A) Figs 6,7 from F. Willemse 1977 clarifies venation posterior to Cu2 contributing to overmirror fold; B) Fig. 107 from F. Willemse 1977, straight file of many broad teeth, note absence of basal block; C) Dorsal aspect of right tegmen strigin showing fold cantilevers only modestly over mirror.

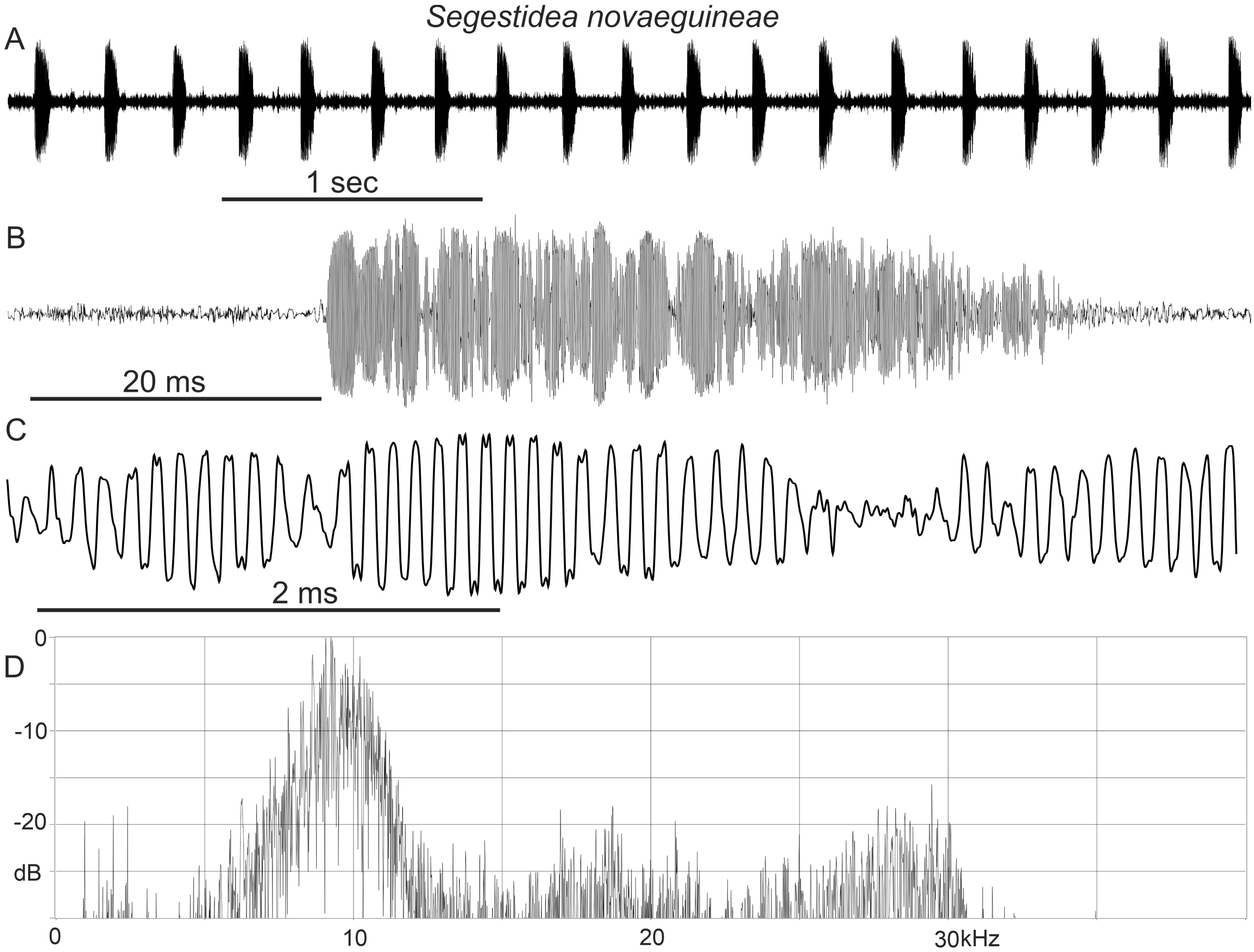


FIGURE 34. *Segestidea novaeguineae* sound analysis: B&K 2203 SL meter and 4165 ½" B&K microphone, equipment insensitive above 40 kHz. A) Coarse time resolution of song shows 19 phonatome emissions; B) One such phonatome at higher time resolution showing characteristically variable amplitudes; C) Time domain sample excerpt from B at high resolution; D) Spectrum of the sound in B, single broad low-Q peak centred on 9.4 kHz.

A related species *Sexava femorata* C. Willemse, exhibits mandibular stridulation as a protest sound. A restrained female moved her labrum to and fro, sliding it "vertically over the anterior surface of her mandibles" (Lloyd & Gurney 1975). Working with a recorder (Uher 4000 Report L) limited to the audio frequency range these authors found sound spectral energy for this defensive strigin near 3.5 kHz.

Mecopodinae, *Mossula*-group of genera

Rentziella gen. nov.

(Figs 35–38, 40–44)

Type-species *Rentziella rufa* **sp. nov.** here designated.

Description. Male.—Size comparatively small. Head with fastigium verticus short, projecting horizontally, strongly narrowing anteriorly, tip acute and from there extending downward as sharp keel joining fastigium frontis. Eyes globose. Pronotum short, surface irregularly coarsely rugose, without spines or tubercles, deeply cut by two transverse sulci, pro- and mesonotum slightly convex from above, metazona from above slightly depressed in the middle, laterally somewhat raised; disc roundly merging with lateral lobes in pro- and mesozona, in metazona angularly inserted; anterior margin slightly convex, ventro-anterior angle narrowly, ventroposterior angle broadly rounded; posterior margin of lateral lobe without humeral sinus, margin of disc truncate to faintly convex. Prosternum with two, basally wide, slightly divergent spines; meso- and metasternal lobe obtusely pointed. Thoracic auditory spiracle narrow, inconspicuous, not covered by pronotum, diameters 0.4- and 0.1-mm. Elytra wide, remarkably coriaceous and almost not pliable, when flexed reaching just beyond tip of abdomen and close to base of hind knee, considerably overlapping each other dorsally. Venation strongly reduced, replaced by dense archedictyon, only Sc and R well visible, widely separated from each other, running about parallel, reaching anterior margin near the tip. Stridulatory area strongly folded along Cu1, remarkably large, extending posteriorly along proximal half to third length of elytron and laterally along two thirds of basal width of elytron; stridulatory file of left elytron as seen from above just recognizable; mirror of right elytron large, elongate with a prominent overmirror fold. Hind wing well developed, cycloid, as long as elytron. Fore coxa with dorsal spine of variable and moderate size, mid and hind coxa unarmed. Legs from normal size and length to slender and long, armature moderate, knee-lobes with a single spine, those of fore legs small; fore tibia with an outer and inner dorsal apical spine, tympanum oval, completely open, no trace of a fold. Supra-anal plate with posterior margin slightly excised. Cercus slightly tapering distally, slightly hairy, incurved apically, tip rounded with a tiny hook-shaped superimposed tooth. Subgenital plate elongate, with a weak median keel, posterior margin deeply v-shaped excised giving rise to a pair of processes terminating into styles.

Female.—As male, slightly larger. Elytra less wide. Subgenital plate broad, posterior margin rounded with a shallow median incision. Ovipositior short, strong, basally widest, upcurved, lower margin scarcely crenulate, tip acute.

Comments. From the pointed fastigium verticis, the absence of spines, tubercles, teeth or other processes of the pronotum and the well-separated Sc and R veins of the elytra, the genus belongs to the *Mossula*-group of Mecopodinae. The combination of open tibial tympanum, the undivided fastigium verticis, the short elytra, the single-spined knee lobes and short ovipositor, exclude almost all known genera of the group.

FIGURE 35. *Rentziella rufa* **sp. nov.** Habitus, insect on glass.

A few genera only remain to be discussed. *Ocica* Walker, 1869 is represented by 5 species: *Ocica lutescens* Walker, 1869 (type species), *Ocica nitida* and *Ocica* lineata (both Redtenbacher, 1892), all three from Fidji Is., *Ocica salomonis* (C. Willemse, 1940) from Solomon Is. and *Ocica karschi* (Karsch 1891, Karny 1920, Kevan 1987) from Caroline Is. The new genus has been compared with *Ocica lutescens*, *Ocica nitida* and *Ocica salomonis*.

In *Ocica* the fastigium verticis is weakly sulcate dorsally and separated from the fastigium frontis, the pronotal surface much smoother, the dorsum of the metazona roundly not angulately merging with its lateral lobe, elytra less coriaceous with wider archedictyon and folded along R (resembling the Sympaestria-group of Phaneropterinae) and the legs conspicuously slenderer and long and the ovipositor also longer and less curved. It is noted here that *Ocica nitida* could well be synonymous with *Ocica lutescens* and that from the quite peculiar male abdominal terminalia the generic arrangement of *Ocica salomonis* under *Ocica* should be considered doubtful.

FIGURE 36. *Rentziella. rufa* **sp. nov.** Habitus, insect on fist.

Dasyphleps Karsch, 1891 is monotypic (Beier 1966): *Dasyphlebs novaeguineae* (de Haan, 1842) described after two females from "Southwest New Guinea collected by Muller" [translated from Dutch] (de Haan 1842). The species is poorly known. A century and a half later, further material is still not available. Also, Karny (1920) in his study of de Haan's types gives but little more information on its morphological characters. The syntypes are now before us, two females in bad condition (Leiden Museum) (Fig. 39). The species was thought to belong to the *Mossula*-group (Karny 1924a, C. Willemse 1961b, Beier 1966). However, the pronotum (Fig. 39CD) presents tubercle-like processes at the lateral margins of the dorsum, one in the pro-, a divided one in the meso- and one in the anterior part of the metazona, which agrees more with the arrangement under the *Phricta*-group of genera. Apart from the distinct pronotal lateral keels, *D. novaeguineae* differs from *Rentziella* in the not raised [flush?] pronotal metazona, very slender and long legs, the strongly stylate eyes, the knob-like fastigium verticis, the shorter elytra not reaching the tip of the abdomen, in lacking any indication of main veins and in the narrower thicker ovipositor. The history of the nomenclatural validity of generic ranking of *Dasyphleps* is complicated (e.g., Redtenbacher 1891; Karny 1920, 1924a; Beier 1966; Kevan 1987). In addition, comparison of *Dasyphlebs novaeguineae* with a male before us representing *Diaphlebus bivittatus* Redtenbacher, 1892 makes clear that these genera are very close.

Going through other genera of Mecopodinae, the new species has also been compared with *Gressittiella* C. Willemse 1961. This monotypic genus, however, has a strongly different pronotum, provided with conspicuous thorns scattered over its surface and is therefore considered as belonging to the *Phricta*-group of Mecopodinae. The male elytra, however, are of a strikingly similar appearance. Though the elytra in *Gressittiella* are still shorter with coarser archedictyon, the stridulatory file is much the same. The file of the latter presents also a transversely placed, raised ridge at the distal end upon the hind margin of the wing and only spacing and number of teeth are different between *Gressittiella* and *Rentziella*.

Etymology. Named [by Fer Willemse] in recognition of the distinguished orthopterist David Rentz.

Rentziella rufa sp. nov.

(Figs 35–37AC, 38, 43)

Specimens studied. Holotype male: 29.x.1963, Aiyura Amomonta, EH PNG 5600 ft J.H. Barrett, ex Pandanus; separate label: n. 29218; Eastern Highlands District NE New Guinea (Depository NBC Leiden).

Allotype female: 23.viii.1959, Aiyura Akuna, EH PNG 6000 ft, J.H.Barrett, ex Pandanus; Eastern Highlands District NE New Guinea (Depository NBC Leiden).

Paratypes: (1 male) 28–30.xii.1966, Aseki Bulolo, Morobe District PNG; (1 male) 23.viii.1959, Aiyura (Akuna), 6000 ft; (2 males) 29.x.1963, Aiyura Amomonta 5600 ft J.H. Barrett; MKMM follow: (F. Willemse intended holotype male) "19.viii.1981, Mt. Kaindi 'Gress. Russet' see file ablat. [file teeth ablated] PNG"; (FW intended allotype female) "19.viii.1981, Mt. Kaindi PNG"; (4 males, 2 females) "19.viii.1981, Mt. Kaindi PNG"; (1 male) "30. viii.1981, Mt. Kaindi PNG". Paratypes (6 males 3 females) from Mt. Kaindi; 'G.K. Morris' absent from labels.

Description. Male.—As generic description. Elytra remarkably strongly coriaceous, when flexed widely overlapping each other dorsally and even enveloping tip of abdomen on ventral side; R and Sc already separated from each other at base, running parallel at 1 mm distance from each other, M indicated. Stridulatory area wider than pronotal width of 6.5–7 mm; total width of elytron 10–11 mm and stridulatory area 10–12 mm long, being half total length of elytron; stridulatory file of left elytron remarkably long, about 6 mm, in ventral view about straight, strongly widening from proximal end, widest teeth in mid part 0.40–0.45 mm and further distally only slightly tapering again, distal end at posterior margin of elytron and provided with a transversely placed inflated ridge; in profile concave throughout its length, mostly in proximal third; spacing of teeth very narrow proximally (e.g., 25 teeth per 0.25 mm) increasingly wider towards the mid part (4–5 teeth per 0.25 mm) and further distally again slightly closer (5–6 teeth per 0.25 mm); number of teeth in proximal third about 80–100 followed by about 50 more widely set and functional teeth until distal end of file. Mirror of right elytron roughly oval shaped, length about 6 mm, width about 4 mm, deepest point about 2 mm and provided along posterior margin with a strong elongate fold (overmirror fold) of about 2 mm width (Fig. 37C).

Legs of normal length, mean ratio length of pronotum to length of hind femur 1:3.6. Fore femur unarmed, mid femur with 2–3 spines on ventro-external keel in distal area, hind femur with 6–9 spines along ventro-external keel.

General coloration reddish brown. Base of pedicel, antennal scrobae, clypeal suture and hind edge of genae black. Lower margin of pronotum black. Some males from Mt. Kaindi have a green pattern as follows: frons, genae, scape and pedicel, distal end of femora and all tibiae dark olive green except very tip of tibiae; first two tarsal segments brown, last one also green, coxae may also be partly green.

Female (Fig. 38C).—Slightly larger than male. Elytron less broad but of similar length, reaching almost tip of ovipositor and hind knee. Subgenital plate and ovipositor as described. Coloration as in male but green pattern absent. Clypeal suture, hind edge of genae, lower part of antennal scrobae, articulation between scape and second antennal segment and ventral margin of pronotum blackish. Apical half of ovipositor dark brown.

Measurements. Length in mm (male n = 11, female n = 4): body male 24.5–26.1, female 25.2–30.3; pronotum male 4.7–4.9, female 5.0–5.7; elytron male 19.3–21.1, female 20.1–25.9; hind femur male 16.3–18.5, female 19.2–21.0; ovipositor 10.5–11.6.

Etymology. Named for its reddish-brown general coloration.

Distribution and Habitat. Known from Mt. Kaindi near Wau and Aseki-Bulolo, both Morobe District and the surroundings of Aiyura, Eastern Highlands District, NE New Guinea.

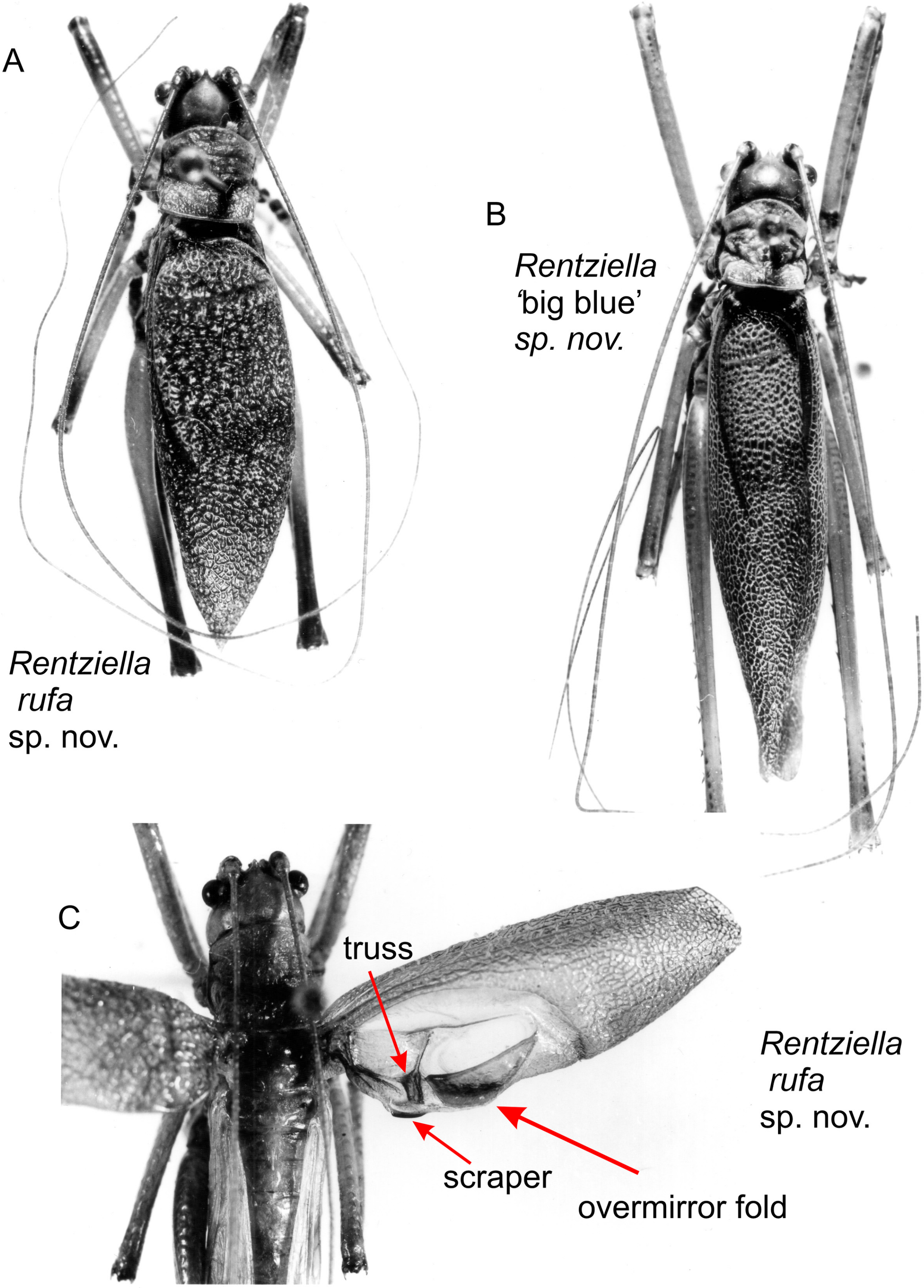


FIGURE 37. A) *Rentziella rufa* **gen. & sp. nov.**, habitus of male dorsal aspect (Fer Willemse intended male holotype, type of genus); B) *Rentziella* 'big blue' **sp. nov.** undescribed species, habitus of male (F. Willemse intended male holotype); *R. rufa* male with extended right male elytron right male elytron showing overmirror fold (paratype).

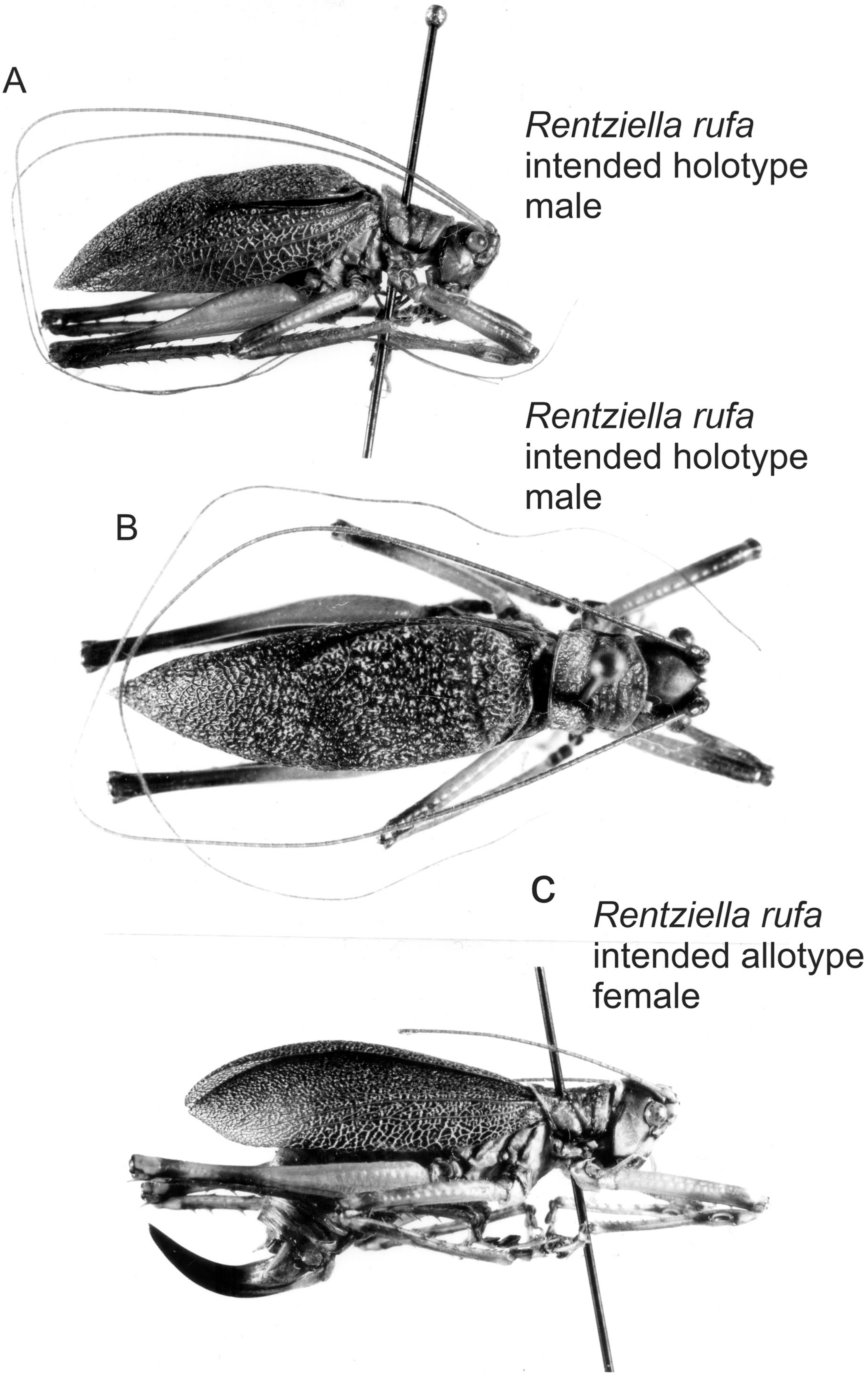


FIGURE 38. *Rentziella rufa* **sp. nov.**: A) male holotype (chosen by F. Willemse) in lateral aspect; B) same specimen viewed dorsally at different magnification; C) *Rentziella rufa* **sp. nov.** (F. Willemse intended female allotype).

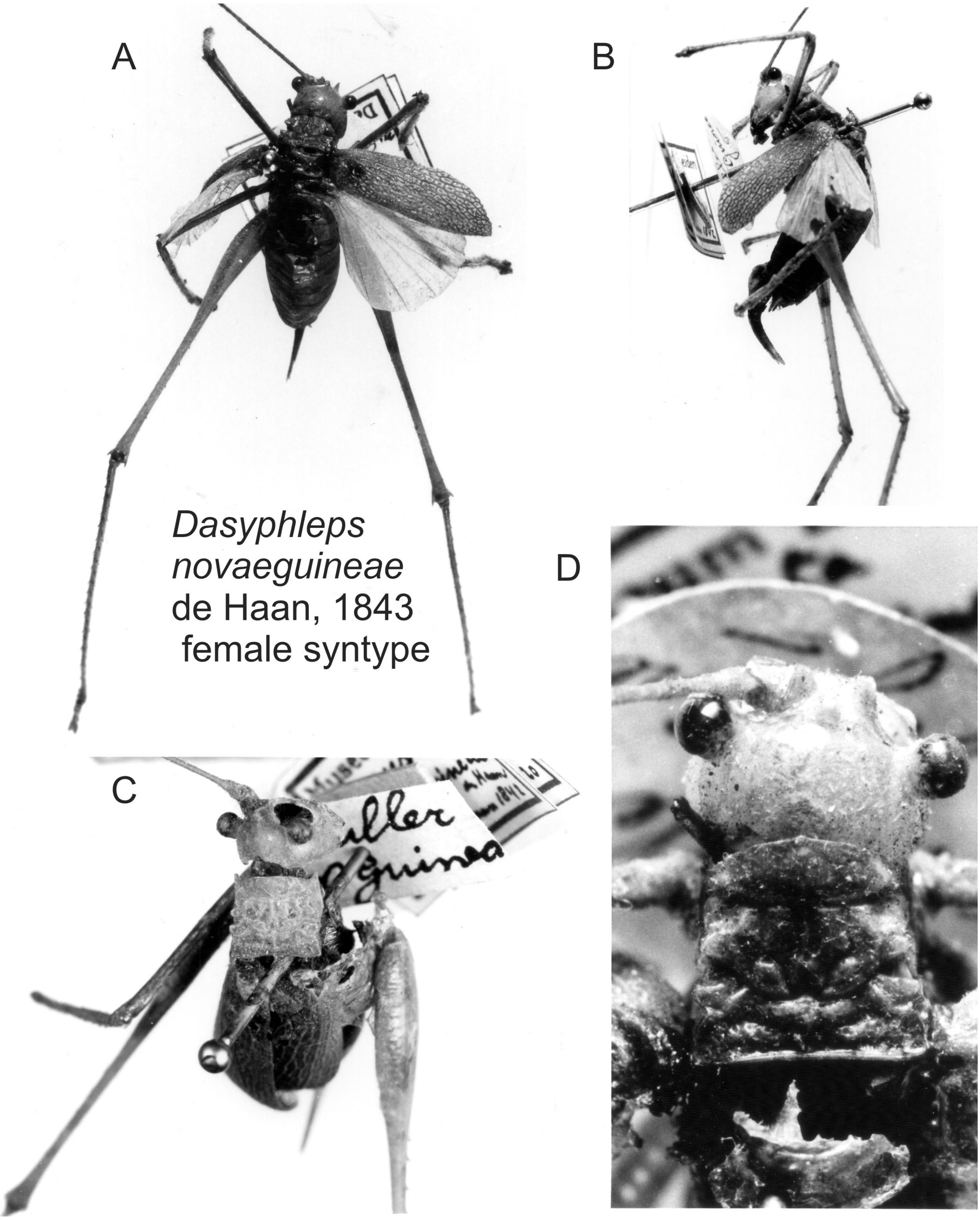


FIGURE 39. *Dasyphleps novaeguineae* (de Haan, 1842) all same specimen: A,B) Habitus female syntype; C,D) dorsal views pronotum (all same specimen).

Comments. Discrimination of this species from other mecopodines, particularly from members of the *Mossula* group, has already been pointed out above under the discussion of the genus.

Stridulation. Four different males contributed to measurements of song structure and the values given here are averages of a sample of 10 calls from each of these males. The species employs transient stridulation. The song is a sequence of pulse trains (Fig. 43A). Each train (apparently a one-way file run) has an average duration of 160 ms and includes >100 transient pulses, which is roughly in accordance with the observed high tooth density of the file (see above). Time-discrete throughout, pulses begin from a remarkably low amplitude becoming more intense very gradually, giving an evenly rising amplitude envelope over the first >2/3 of the train (Fig. 43AB). (The train's stereotyped shape recalls a child's top.) The pulse train period is 723 ms on average. Each transient pulse starts in a complex wave of higher frequencies (Fig. 43D) which ends with a more sinusoid lower frequency wave (Fig. 43C); this is unusual for transient stridulators. This sinusoid wave is responsible for the low audio frequency band centred on 6.6 kHz (Fig. 43CF) as confirmed by time and spectral domains (Fig 43EF). Low ultrasonics extend in a band from the high audio to just beyond 30 kHz (Fig. 43C).

In Canada on Dec. 13, 1981, sound levels of a still vigorous male were measured at 20 cm lateral aspect insect body to microphone tip. We used a B&K 2204 sound level meter on impulse mounted with a ¼" microphone. Ten readings on the left and ten on the right gave an average of 94.6 dB on the left and 102.8 on the right, a difference in lateral sound fields of 7.7 dB. This sound level asymmetry is consistent with the open side of the overmirror fold.

Rentziella 'big blue' undescribed species

(Figs 37B, 40–42, 44)

Specimen studied. Fer Willemse intended holotype male: Papua New Guinea, Mt. Kaindi: 19 viii 1981, Coll. Glenn Morris (NBC Leiden, MKMM). Specimen discovered missing from NBC Leiden 2024.

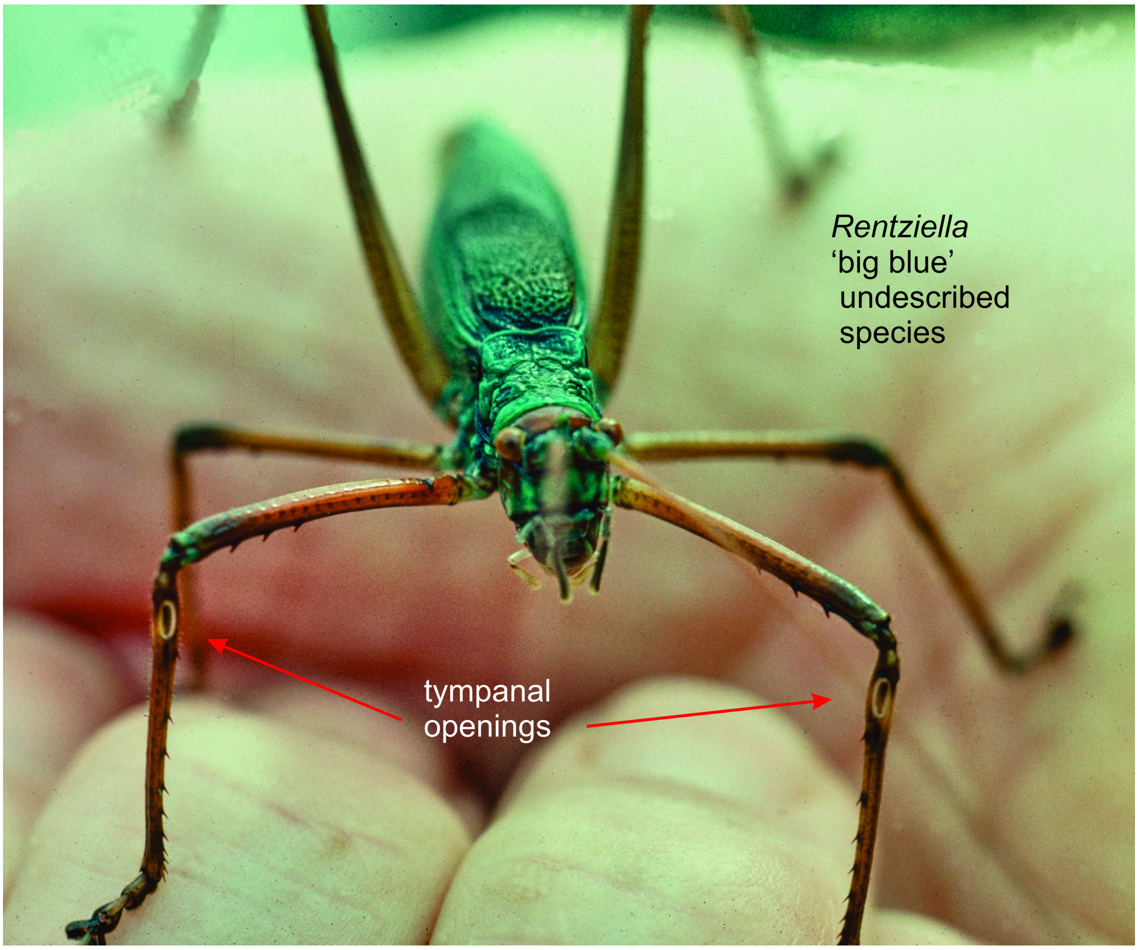


FIGURE 40. *Rentziella* 'big blue' **sp. nov.** undescribed species, frontal aspect with white-rimmed oval tympanal openings on foretibiae.

Description. Male (Fig. 37B).—Differing from genus type-species as follows. Size larger. Surface of pronotum less coarsely rugose, fore margin convex. Meso- and metasternal lobes more pointed. Elytra less coriaceous, relatively less broad, not extending so far ventrally as in type-species, tapering apically, tip narrowly rounded, main veins more recognizable; stridulatory area as wide as pronotal width (about 5 mm) and slightly longer than third of elytron length (11 mm); file of left elytron less concave ventrally, shortest distance between proximal and distal end 4.4 mm, widest in mid and distal parts, 0.25 mm, distal end provided with transverse raised ridge, total number of teeth about 100, in proximal fourth very closely set, in remainder more widely and almost evenly distributed, 6 teeth per 0.25 mm; mirror of right elytron elongate, length 5.2 mm, width 3.4 mm, with 1.5 mm wide fold (OMF) covering mirror from above. Legs comparatively slender, ratio pronotal length to length of hind femur 1:5. Fore coxa with a strong spine. Ventro-external keel of fore femora with 3, of mid femur with 2, of hind femur with 8 and ventro-internal keel of hind femur with 5 spines. General coloration pale brown. Head from above reddish brown; scape, ventral part of scrobae, clypeal suture and ventral margin of pronotum blackish as in type-species. Left posterior angle of pronotal dorsum with green flush. Venation of elytra, including archedictyon, dark brown dorsally, pale brown laterally.

Female.—Unknown.

FIGURE 41. *Rentziella* 'big blue' habitus in more lateral aspect.

Measurements. Length in mm (male n = 1): body 32; pronotum 5.6; elytron 29; hind femur 28.

Distribution and habitat. Known only from one male specimen taken on Mt. Kaindi near Wau, Morobe District, NE New Guinea. It was found perching on *Pandanus* in earshot of the type species of the new genus *Rentziella rufa*.

Searching at night up and across Mt. Kaindi's eastern face we discovered a narrow path. It wound generally higher diagonally across the mountain, emerging onto the access road to the summit about 600 paces below the microwave repeater station. This trail was very steep in some places "with 'steps' of barefoot-pounded mud between tree roots; it took us the whole way through undisturbed montane forest. Over several hours we stopped frequently to capture accessible *Paraphyllomimus* spp. At one point the trail sloped a little downward and passed by huge *Pandanus* plants. Specimens of *Rentziella* both *rufa* and 'big blue' were perched in amongst the edge-serrated *Pandanus* leaves, detected by the slow agitation of their very long antennae (Fig. 42) waving in the light beam. We were able to effect capture by gingerly pulling down the appropriate *Pandanus* leaf and encouraging the insect into the mouth of a net held below. Initially we also took a (large colourful) female of *R*. 'big blue', but it escaped during transfer to a vial. My expletives did not preclude the taking of a male that had orginally been perched quite near this female. He emitted a loud protest sound on being trapped within the net. The moon, past full but still more than half, emerged from clouds giving the forest a silvery white appearance. It was quite bright, at times penetrating down to the trail. Once out on the road under a clear sky we no longer needed our flashlights. The summit and the walk down the road to the station was bathed in moonlight and banks of white cloud lay between the folds of the hills and out in the valley of Eadie Creek. (excerpted from the daily journal of Aug. 19).

FIGURE 42. *Rentziella* 'big blue' on entomologist shows long antennae to advantage.

Comments. Specific distinction from type-species *R. rufa* as given in the description: bigger size, proportions and texture of the male elytra and its slenderer legs are obvious. We are not fully convinced of its congeneric state.

Stridulation. This insect called with a period of about 1 sec. One such call is shown in Fig. 44A, a train of >60 irregularly time-separated pulses, creating overall a 'time symmetric' amplitude envelope rising (first half) then falling (second half). The pulses of the train, as shown in higher time resolution (Fig. 44C) also build and decay symmetrically, rather than having the exponential decay of its congener *R. rufa*. The dominant carrier near 7 kHz (Fig 44B) is almost the same as *R. rufa*. Spectral frequencies are all in the audio with an intense peak centred on 6.7 kHz. Perhaps more than one tooth contributes to each sinusoid making up the pulse. Scraper velocity is presumably below that necessary to sustain a many-waved prolonged 'resonant' pulse.

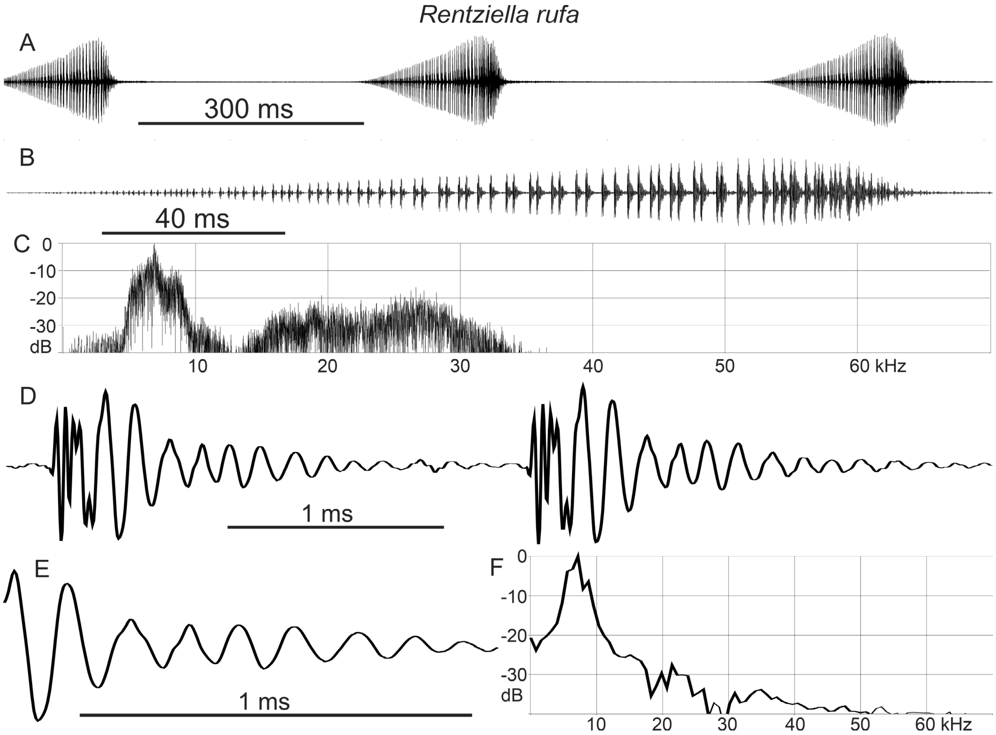


FIGURE 43. *R. rufa* acoustic analysis: A) 3 phonatomes (= pulse trains) from call sequence, ~3 calls/s [d 10cm 21.5°C, QMC]; train increments steadily for most of its duration; B) 3rd train in A at higher time resolution indicates transient stridulation; C) Fourier power spectrum of phonatome in B shows low-Q carrier peak centred at 7 kHz; D) high-resolution time sample from the train in B of 2 successive pulses separated by 2.2 ms, complex wave train of each tooth event repeats in high and low frequency wave forms; E) time sample of one pulse's following waveform; F) spectrum of time sample in E showing 7 kHz peak.

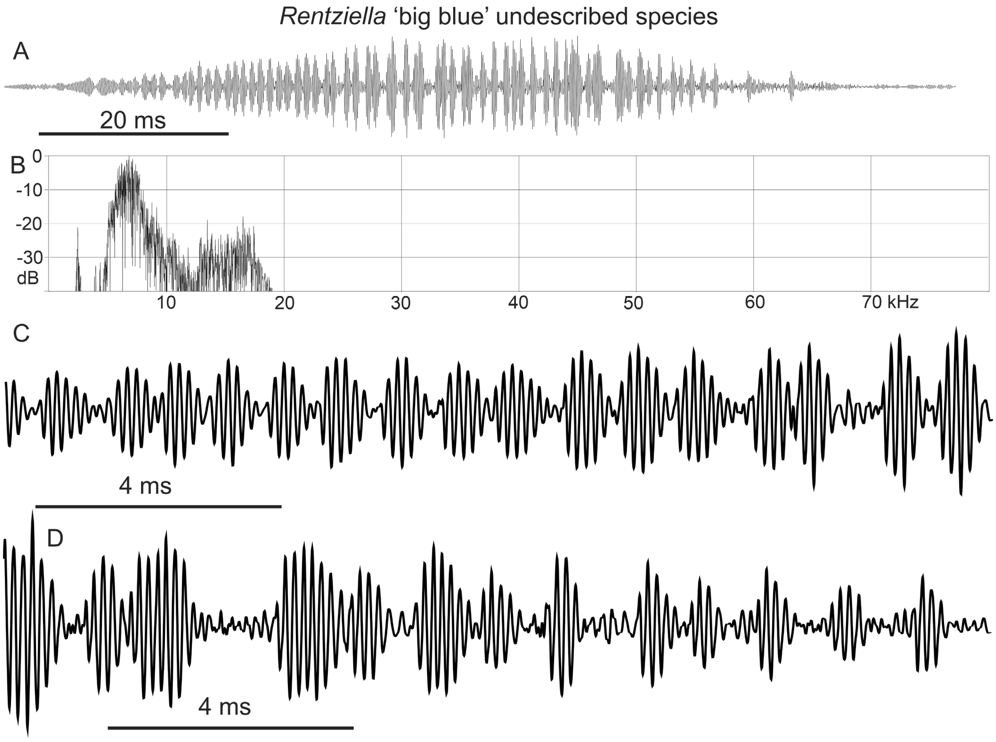


FIGURE 44. *Rentziella* 'big blue' acoustic analysis: A) one phonatome (= pulse train); B) Fast Fourier transform of power spectrum showing most intense carrier a low-Q peak near 6.7 kHz, ultrasonics absent; C,D) at higher time resolution pulse waveforms appear as variable-amplitude sinusoids suggesting multiple tooth events per pulse.

Conocephalinae

Agraeciini

Salomona Blanchard E., 1853

Salomona ustulata Redtenbacher, 1891
(Figs 45, 51, 52)

Specimens studied: 4 males, 1 female PNG, McAdam Nat. Park, Bulolo Gorge, 28 viii 1981, (G.K. Morris NBC Leiden, MKMM).

Systematics. The specimens fit fully the diagnosis in Redtenbacher (1891), Karny (1926, as *S. lambda*) and especially as given in a synopsis of this large genus by C. Willemse (1957). The reliability of a number of characters could be underlined, among others frons, male cercus, measurements, pattern of coloration. Opportunity is taken here to give some details of the strigin in this species. The left file in ventral view (Fig. 51) straight, fusiform, widest part in distal fourth, length 1.9 mm, in profile sinuate with its most bulging part also in distal 4th; number of teeth about 58, most of them regularly spaced, about 7 teeth per 0.25 mm but distally (towards posterior margin of elytron) more closely set. 'Mirror'/speculum of both elytra short trapezoid, length 1.4 mm, greatest width 1.8 mm along proximal edge which is close to and parallel to the file: membrane transparent, bordering veins without modifications, no fold. The cell bordering the mirror (the harp) distally, and that anteriorly, widened and transparent. Titillators with outer pair of sclerites as a left and right triangular-shaped sclerotized sheet; inner one medially strongly sclerotized, strongly divergent basally, scarcely divergent apically, the latter with tip simply rounded.

Distribution and habitat. The locality of the series at hand is in between the two already known, Mt. Lamington near Kokoda in the south and Sattelburg, Huon Gulf in the north. Calling at height from trees.

Comments. Type species of the genus *Salomona is S. marmorata* (Blanchard,1846) by original monotypy.

FIGURE 45. *Salomona ustulata* Redt., 1891: adult female.

Stridulation. Readily audible to a human listener, this insect's song recalls the regularity of a ticking clock and 'ticker' was its assigned field name. Silent intervals of several seconds (e.g., 4 s, Fig. 52A) separated tick bouts, a dozen or so ticks per bout. There is a very stable tick period of about 300 ms (Fig. 52B). Forming the substructure of the ticks are trains of scarcely time-separated sinusoid amplitude fluctuations (Fig. 52C, E). Time separation of pulses in this species is far less distinct than that seen with *Salomona* 'darth'. This appears to be a kind of subresonant stridulation, with teeth engaging at just below the repetition rates needed for sustained resonance. The spectrum, in keeping with the waveform is relatively low Q with a broad peak occupying much of the higher audio and centred near 13 kHz.

***Salomona* 'darth' undescribed species**

(Figs 46–50)

Specimens studied. Holotype male: Papua New Guinea, WEI, Coll. G.K. Morris, 25 viii 1981 (NBC, L) missing 2024).

FIGURE 46. *Salomona* 'darth' **sp. nov.**: habitus of male lateral view, (intended male holotype).

FIGURE 47. *Salomona* 'darth' **sp. nov.**: frontal view. Male's vivid head colours inspired field name of Darth Vadir.

Paratypes: PNG, WEI, 4 viii 1981 (male) & 12 viii 1981 (male), G.K. Morris (NBC, L), missing 2024).

Description. Male.—Relatively small for the genus but thickset (Figs 46–48). Head a little wider than pronotum; frons (Fig. 48C) with outer furca and lateral keels indicated as rugose keels, no inner furca and median keel, surface in middle dull, with very fine and sparse impressed points and lines, subocular area and lateral part of head with some transverse, irregular low ridges. Fastigium of vertex shorter than length of scape, tip acute and downcurved, dorsobasally with a minute tubercle, ventrobasally joining acute tip of fastigium of frons.

Pronotum slightly longer than broad, surface of lateral lobes a little impressopunctate; anterior margin dorsally almost straight, laterally rounded; posterior margin dorsally slightly rounded, laterally almost straight; ventral margin very weakly sinuate, anterior angle broadly rounded, posterior angle narrowly, almost rectangularly rounded. Thoracic auditory spiracle as described above under S. *ustulata*, 1.3 X 0.4 mm.

Wings extending well beyond abdomen and hind knees, reaching basal third of hind tibia. Elytron strongly tapering apically, greatest width in basal fourth; Sc and R nearly straight and parallel to hind margin of elytron; C area in basal third as wide as remainder of elytron, in mid third strongly tapering and in apical third narrow.

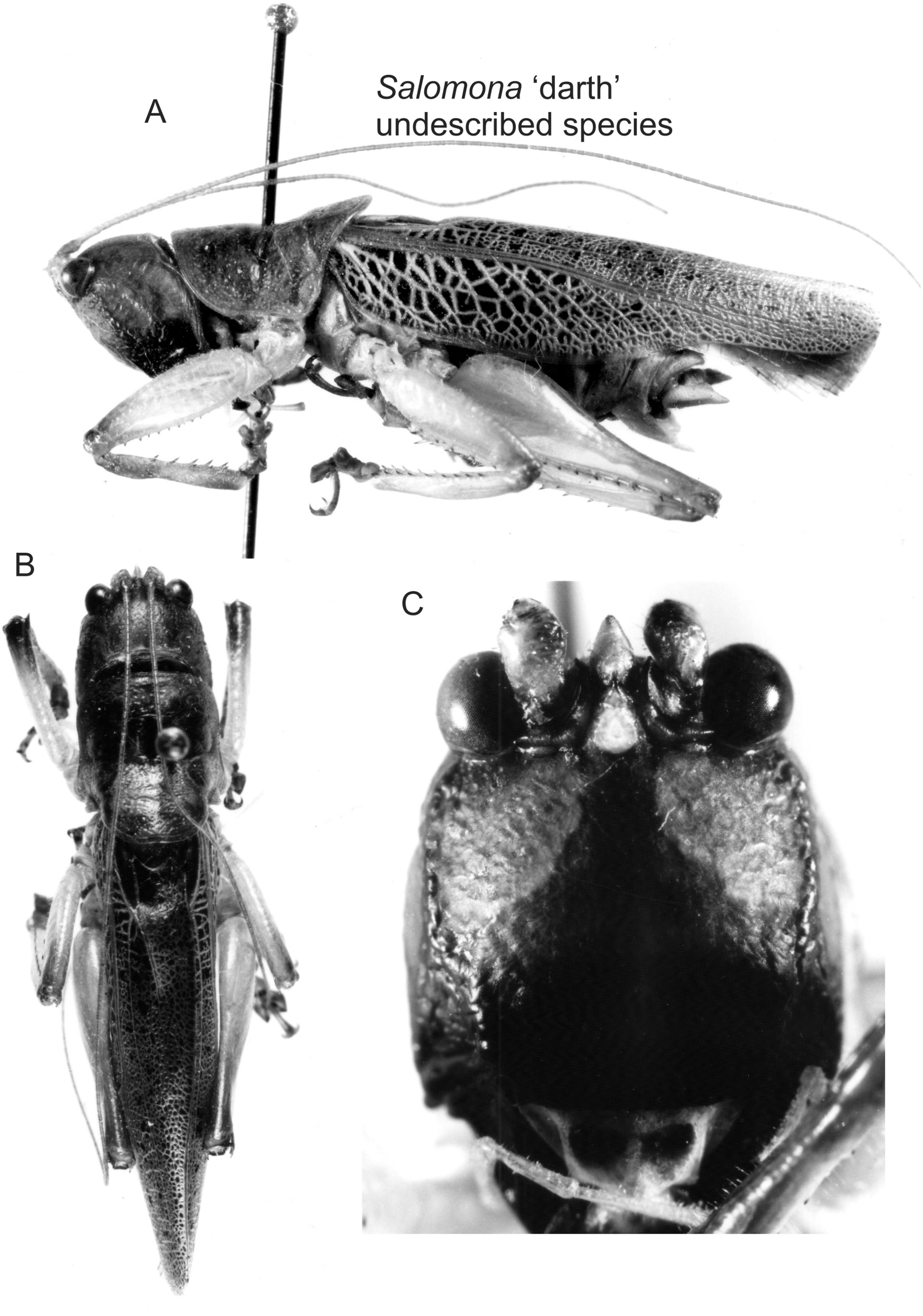


FIGURE 48. *Salomona* 'darth' **sp. nov.** undescribed species: A) Lateral aspect habitus, Fer Willemse intended paratype male; B) dorsal aspect habitus, intended holotype male; C) frontal view of head paratype male.

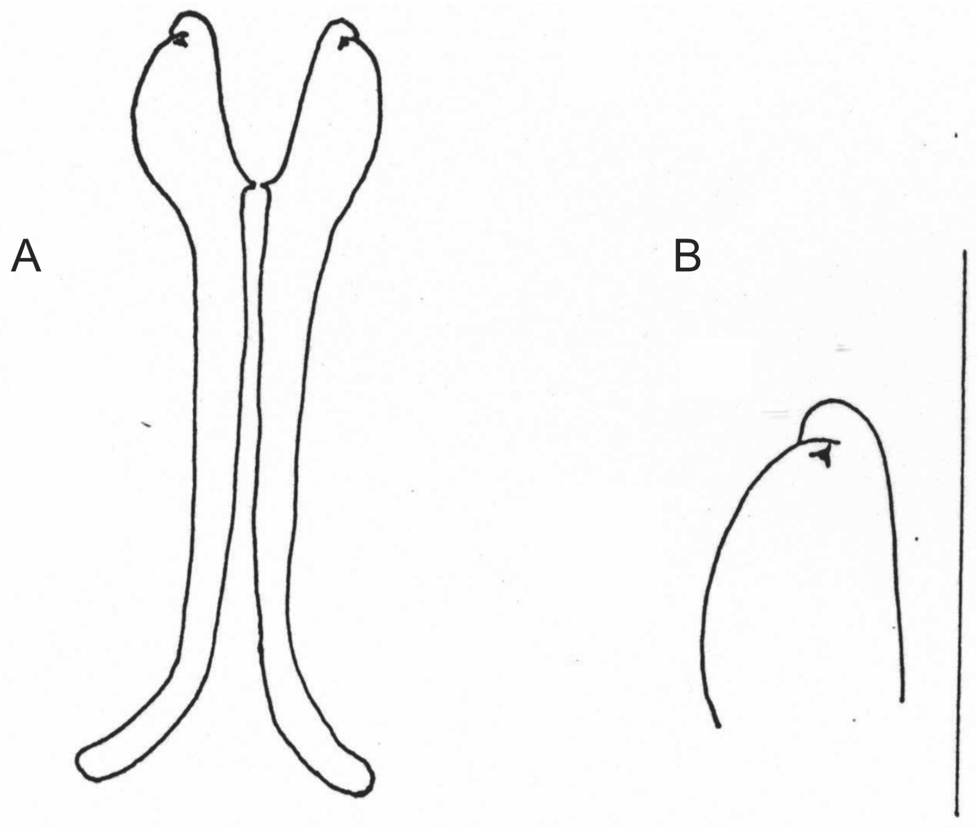


FIGURE 49. *Salomona* 'darth': A) titillators in ventroapical view; B) same, tip enlarged; scale of B 1 mm.

Stridulatory area of both elytra of similar appearance; mirror as long as wide (1.8 mm), basal and lateral edges straight, apical edge broadly convex; left stridulatory file narrow, slightly fusiform, length 1.9 mm, at widest 0.16 mm in distal third, in ventral view straight, in profile slightly concave in proximal and almost straight in apical half; total number of teeth about 46, distally closer set, spacing in mid part 6 teeth per 0.25 mm.

Legs remarkably short and thick. Fore femora with 5 spines on both ventral margins; mid femora with 2 basal spines on ventro-internal and 5–6 spines on ventro-external margin, hind femora with 8–9 spines on ventro-external margin, internal side unarmed. Internal knee-lobes of fore and mid femora spined, external ones obtuse; both inner and outer knee-lobe of hind femur spined. Internal and external tympanum of fore tibia slit-like.

Tenth tergite tapering apically into a pair of short obtuse, down-curved processes separated from each other by a broad U-shaped median emargination. Cercus thick, short, in apical fourth tapering into a strong obtuse tooth; external side straight with weak lontgitudinal depression; internal side expanded medially, in its midpart forming a large process slightly flattened dorsally, slightly concave ventrally and showing a strongly sclerotized ridge with 3–5 teeth at its top. Subgenital plate longer than broad, ventral surface with a short median keel apically, posterior margin widely V-shaped emarginated, styles slender. Outer pair of titillators forming a weakly sclerotized triangular sheet. Inner pair of titillators bar-like structures, basally divergent and widened, tip provided with a tiny median tooth (Fig. 49AB).

General colour olive green (Figs 46, 47). Head dark olive green, ventral parts of cheek and frons dark reddish brown, clypeus pale yellowish with a pair of brown spots, mandibles black, labrum carmine red, median ocellus creamish, eyes brown, fastigium of vertex yellow, scape brown. Antennae pale brown, unicolorous or distal margin of proximal segments dark brown. Pronotum and remainder of thorax of general colour. Elytron with basal parts of main veins and their bordering archedictyon greenish, remainder of venation creamish, membrane of basal part of C area and scattered spots over remainder of elytron infuscate. Abdomen and legs from pale green to pale brown, armature of legs with tips dark brown. Dorsal side of fore tibia between tympana and all tarsi brown.

Female.—Unknown.

Measurements (Length in mm) (male n = 4): body 31–34; pronotum 9.0–9.3; fore femur 8.3–8.8; mid femur 7.7–8.4; hind femur 14–15; elytron 24–28.

Comments. The new species is readily recognizable by its thickset appearance with short legs, strongly tapering elytra, sculpturation of the frons, shape of cercus and its green coloration. The short robust appearance, short legs and the short and strongly tapering elytra are, among the genus, only shared with *S. buergersi* C. Willemse, 1959, known from "Malu", Sepik River. Male cercus, sculpturation of face and coloration however are quite distinct.

Distribution and Habitat. Known only from the type-series collected by G.K. Morris and D. Klimas, originating from the surroundings of Wau, Morobe District, NE New Guinea. Singing in trees on institute grounds; one male apprehended by GKM by climbing several metres up a tree.

Stridulation. Like its congener *S. ustulata*, *S.* 'darth' constructs a long-lasting buzzing song (Fig. 50A) from trains of incompletely time-separated sinusoid pulses (Fig. 50D). The song is irregularly interrupted by pauses in both species. The trains of *S.* '*nameless*' are less stereotyped, than those of *S. ustulata*. Four such trains are shown in Fig. 50B and part of one at higher resolution in Fig 50D. These pulse trains repeat with a stable period of about 80 ms (Fig. 50B). Unlike *S. ustulata*, the fluctuations in amplitude allow one to distinguish the pulses. Thus Fig. 50D shows about 8 poorly time-spaced pulses. As with the two *Rentziella* species, this insect seems to be making short sinusoids at a velocity of the scraper falling just below that needed for resonance and with perhaps more than one file tooth contributing to each poorly time separated pulse.

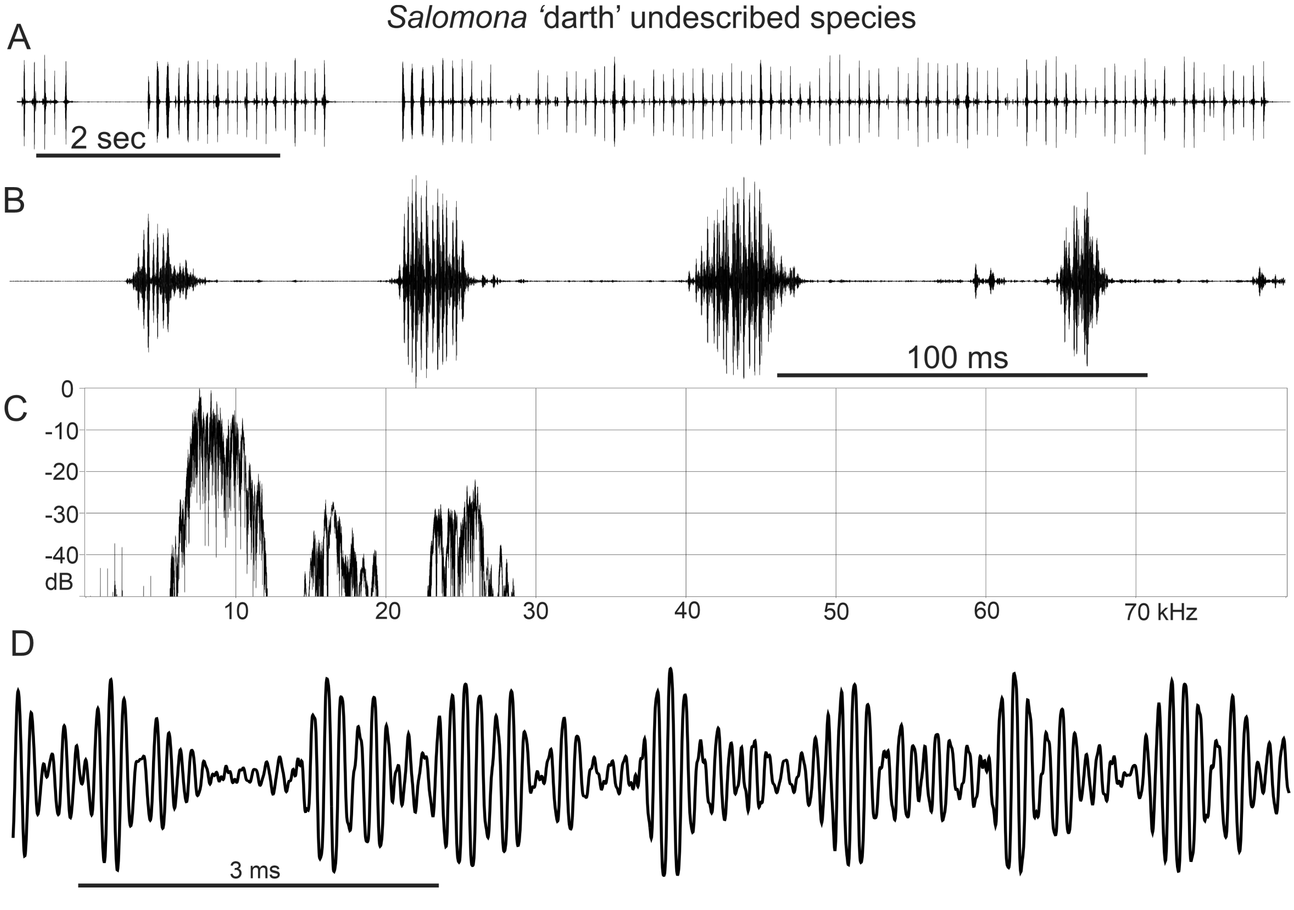


FIGURE 50. *Salomona* 'darth' acoustic analysis: A) Calls at coarse time resolution [dorsal 13 cm 17.5°C QMC] short to long trains of contiguous transient pulses; B) 5-phonatome time sample chosen to reflect train variations; C) Fourier power spectrum of time sample B showing low-Q intense audio carrier band ~7–11 kHz; D) high-resolution waveform suggesting multiple tooth events per pulse.

FIGURE 51. *Salomona ustulata* stridulatory file ventral surface left tegmen.

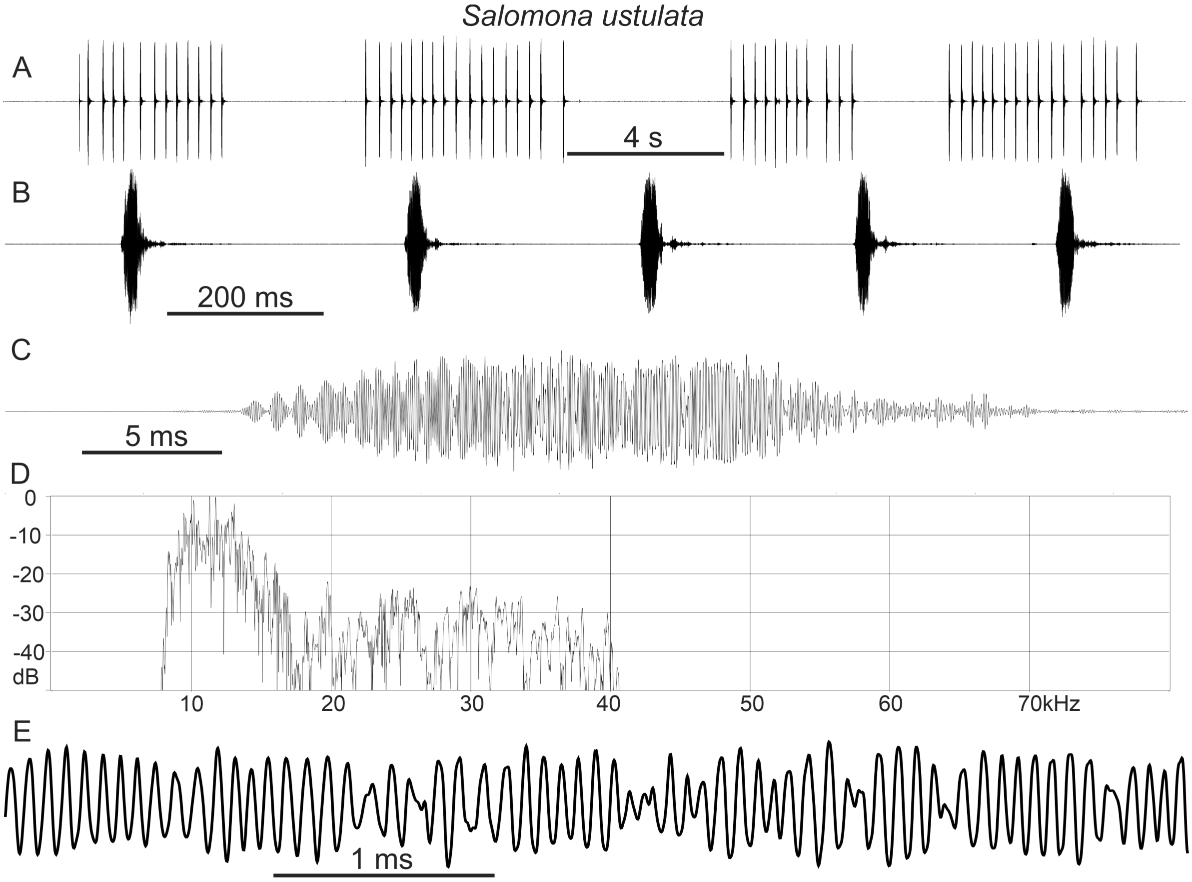


FIGURE 52. *S. ustulata* acoustic analysis: A) Four calling bouts at coarse time resolution. [dorsal aspect 11.5 cm 20°C, QMC]; song resolved by human ear as a succession of ticks; B) showing 5 such ticks; C) high resolution of one tick showing erratic amplitude envelope and run-on multiple tooth-event waveforms; D) Fourier spectrum has highest intensity audio band 8–16 kHz with lower intensity ultrasonics up to 40kHz; E) at high resolution waves almost suggesting resonance stridulation.

Philmontis Willemse, 1966

Philmontis profusus Ingrisch, 2022

Specimens studied. Holotype male: Papua New Guinea, Wau, Morobe Province, Mt. Kaindi, elev. 1230 m, 7°21'S 146° 41'E, 30. viii. 1981, leg. G.K. Morris, Depository Naturalis Biodiversity Center, Leiden (NBC).

Comments. The monotypic genus *Philmontis* C. Willemse, 1966 (type genus *Philmontis nigrofasciatus*) was expanded (Ingrisch 2022) to include 13 species. The holotype chosen for one of these species, *Philmontis profusus* Ingrisch, is an adult male specimen collected by GKM & DEK on Mt. Kaindi in 1981. Its specific name acknowledges the "rich modification" (Ingrisch 2022) of the male cerci. The recordists waited in vain for this insect to sing so there is sadly no information on its song structure.

Philmontoides Ingrisch, 2022

Philmontoides wau Ingrisch, 2022

(Figs 53–58)

Specimens studied, including holotype and paratypes. Papua New Guinea, Wau Ecology Institute (WEI)., 30 vii 1981, 4 & 12 viii 1981 on *Pandanus*, remnant forest Wau, G.K. Morris (4 males, 2 females); PNG, McAdam Nat. Park, Bulolo Gorge, 28 viii 1981 (1 female).

FIGURE 53. *Philmontoides wau*; habitus of hand-held male, dorsolateral aspect.

FIGURE 54. *Philmontoides wau*, lengthy antenna.

FIGURE 55. *Philmontoides wau*; habitus of female, lateral view.

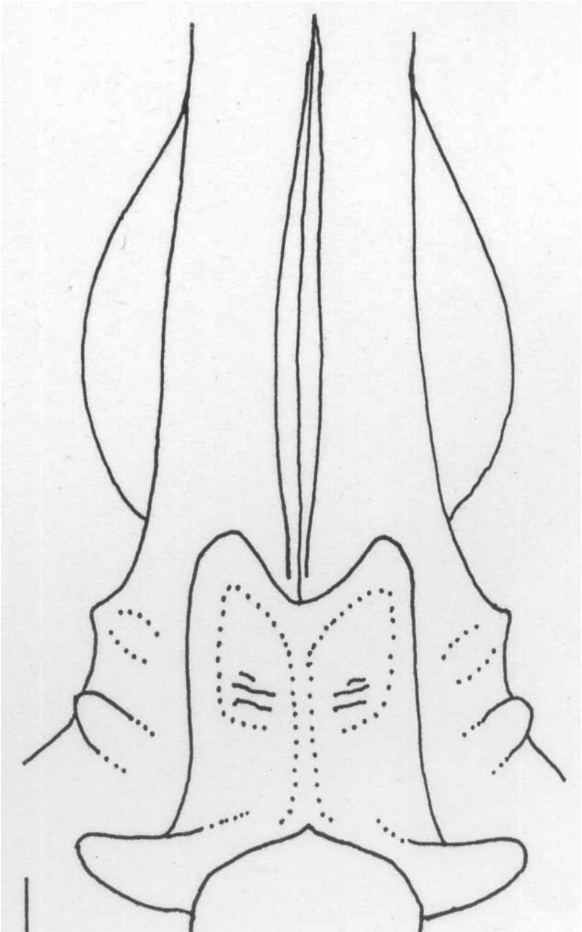


FIGURE 56. *Philmontoides. wau* base of ovipositor and subgenital plate in ventral view; scale 1 mm.

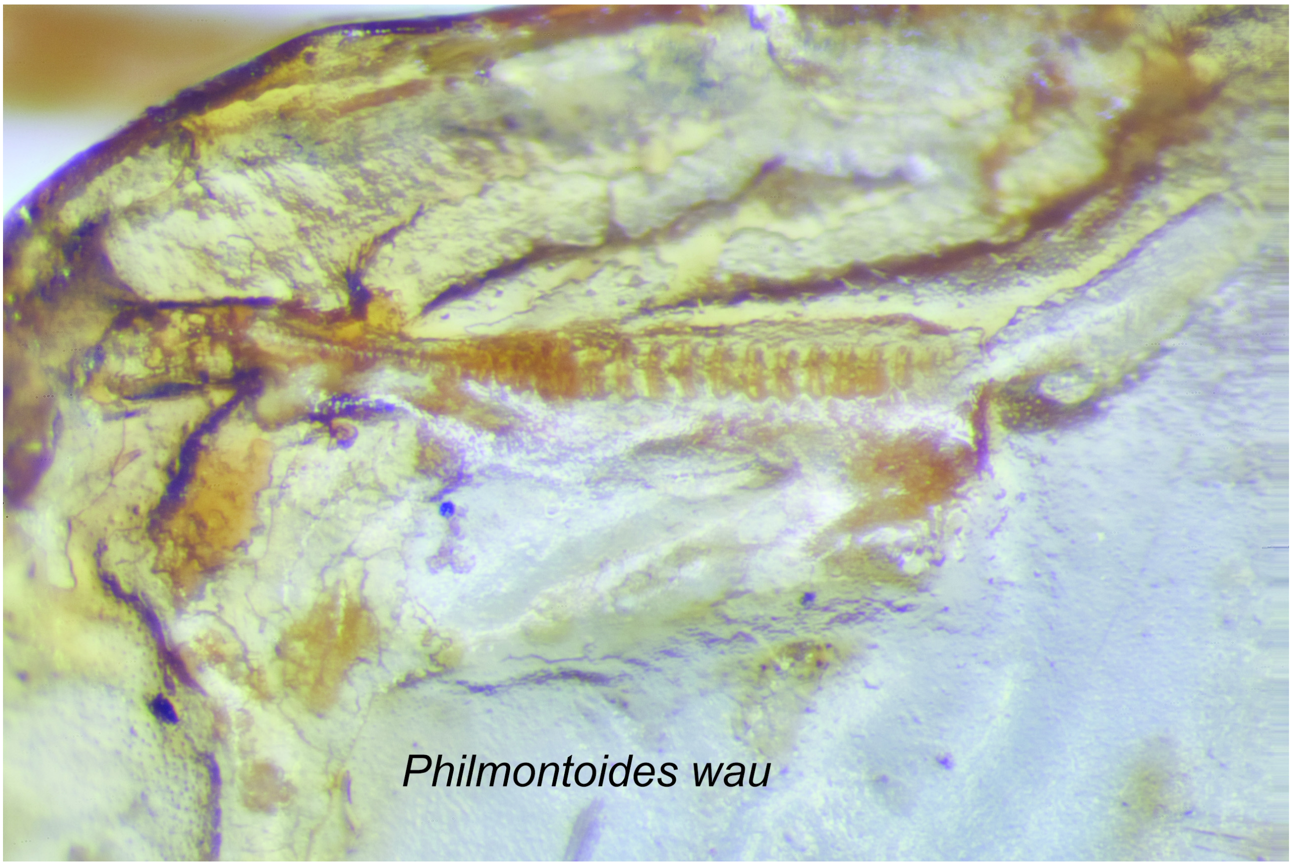


FIGURE 57. *Philmontoides wau* stridulatory file on ventral surface of left tegmen.

Comments. *P. wau* is one of 8 species grouped by Ingrisch (2022) into the genus *Philmontoides* Ingrisch, 2022. Type species of this genus is *Lobaspis hageni* Dohrn, 1905. For *Philmontoides wau* the male holotype was chosen from among specimens collected by GKM and DEK: Papua New Guinea (PNG), Morobe Province, Wau, 12 viii 1981, leg. G.K. Morris, [recording designation 81-2]. Depository: Naturalis Biodiversity Center, Leiden (NBC). Specimens found only on *Pandanus* [GKM].

Tremulation. Substrate signalling, observed as tremulation (body oscillations with or without impact, imparting vibratory substrate waves to a plant perch) is widespread among tettigoniids (e.g., Morris 1980, De Luca & Morris 1998, Hill 2008). A male and female of *P. wau* were placed together onto a *Pandanus* leaf where the male engaged repeatedly in tremulation bouts.

Stridulation.—To a human listener the song is a regular repetition of faint crackles, resembling a stereotyped precise static, so faint you must be very close to hear. The calls are relatively intense in the ultrasonic.

Song parameters are averaged from recordings of two different singers. Based on the time domain being widely spaced short sinusoid ultrasonic pulses, this is an elastic uncoupled stridulation. The carrier is a fairly high-Q ultrasonic frequency, peaking at 26.9 kHz (Fig. 58C, E). Calls repeat at a rate of about 11/s near 20°C; each call consists of a train of identical 4–8 time-separated sinusoid pulses (Fig. 58D) comprising a major pulse train. A faint (putative opening) sound/train occurs before each intense (putative closing) train.

Philmontoides has a genus-diagnostic file form (figured by Ingrisch Fig. 12H), a region of perhaps non-functional teeth extending over the file's distal third. This leaves just 15 or so broad, distinctly spaced, teeth available to make the several ~7-wave 27-kHz sinusoids, which suggests some reversals of scraper direction during a train, i.e., there are not enough teeth on a one-wave one-tooth basis to complete one whole pulse train on one closure.

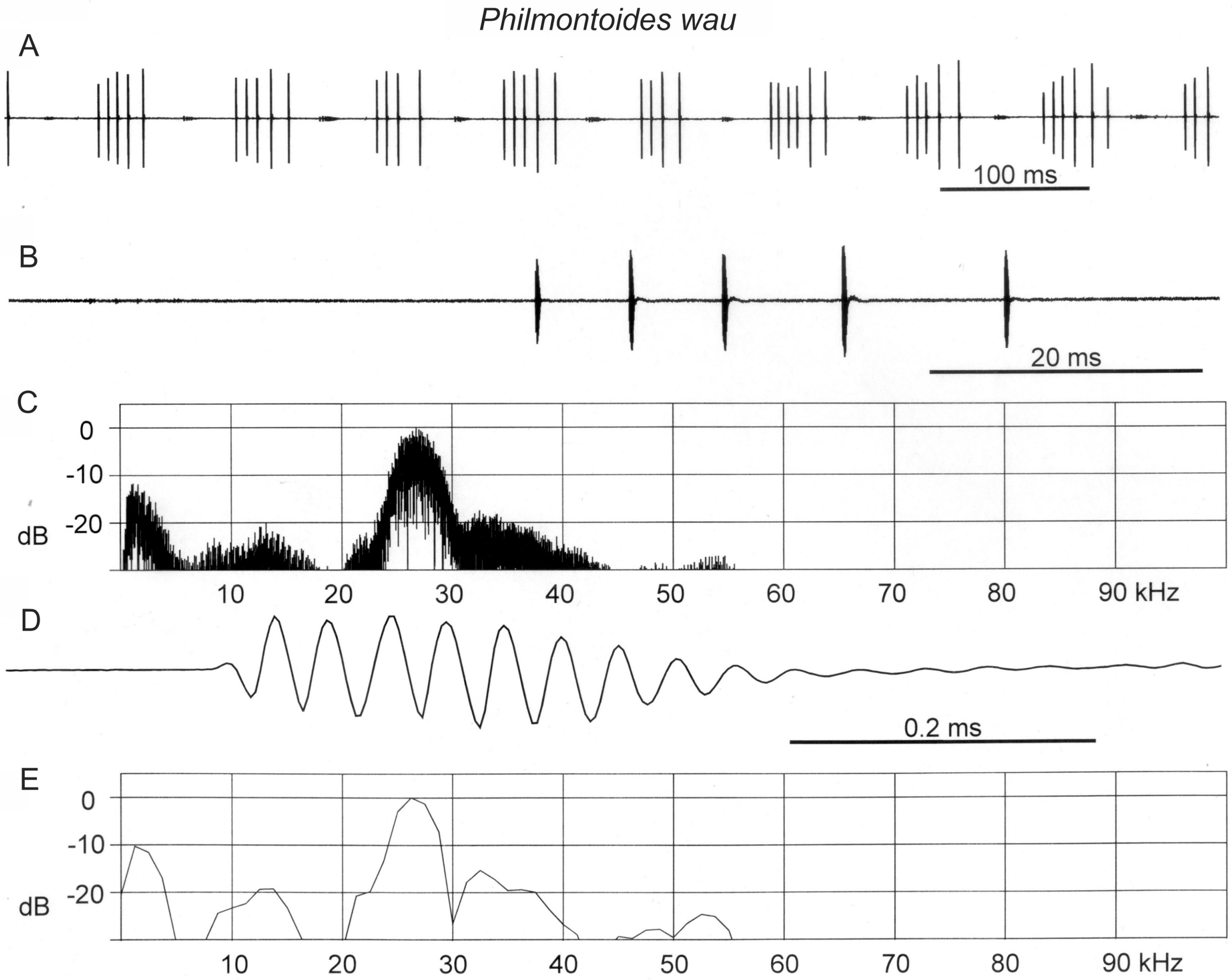


FIGURE 58. *Philmontoides wau* acoustic analysis, an example of elastic stridulation: A) time sample of 8 complete phonatomes (to-fro tegminal cycles), each comprised of a more intense (presumed) closing train of 4–6 short pulses well-isolated in time, separated by a faint (presumed) opening sound; B) 5 pulses of a closing train at higher resolution; C) Fourier power spectrum of the time sample in B; the most intense frequency is a coherent symmetric peak in the ultrasonic centred near 27 kHz; D) One pulse from B at very high time resolution showing its ultrasonic sinusoid waveform; E) Spectrum of the pulse in D shows ultrasonic peak at 27 kHz.

Parahabetia Ingrisch, 2021

Parahabetia pictifrons obtusa Ingrisch, 2021

(Figs 59–64)

Material studied. Holotype male: Papua New Guinea, Morobe, McAdam National Park, Bulolo Gorge, 7°16' S, 146°38' E, 28 viii 1981, leg. G.K. Morris, (Depository NBC, Leiden); paratype male female same data as holotype.

Measurements. (Length in mm) (male n = 2 & holotype after Karny in parens, female n = 1): body male 22.5–23 (24), female 27; pronotum male 6.5–6.6 (7.5), female 6.5; elytron male 18.2–18.5 (19.5), female 20; hind femur male 14–14 (16), female14.5; ovipositor 12.

Comments. Ingrisch in revising *Parahabetia*, names these Bulolo Gorge specimens (Ingrisch 2021) as a new subspecies of *Parahabetia pictifrons.* The name *obtusa* refers to the shape of the tips of the triangular rearward projections of the 10th abdominal tergite: their bluntness distinguishes from *P. p. acuta*.

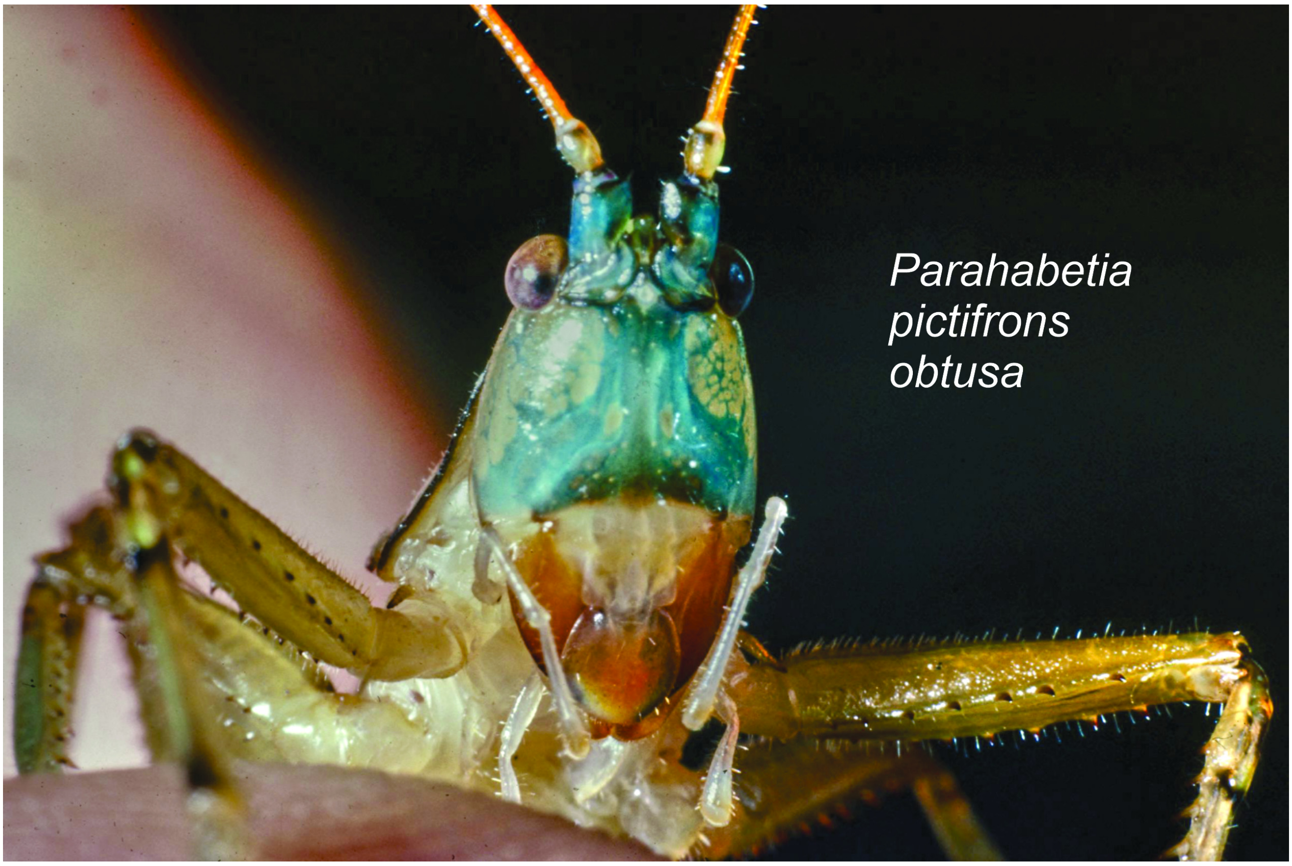


FIGURE 59. *Parahabetia pictifrons obtusa* Ingrisch, 2021: adult male in frontal aspect displays turquoise-blue markings of parts of frons, genae and antennal scapes, amber mandibles below.

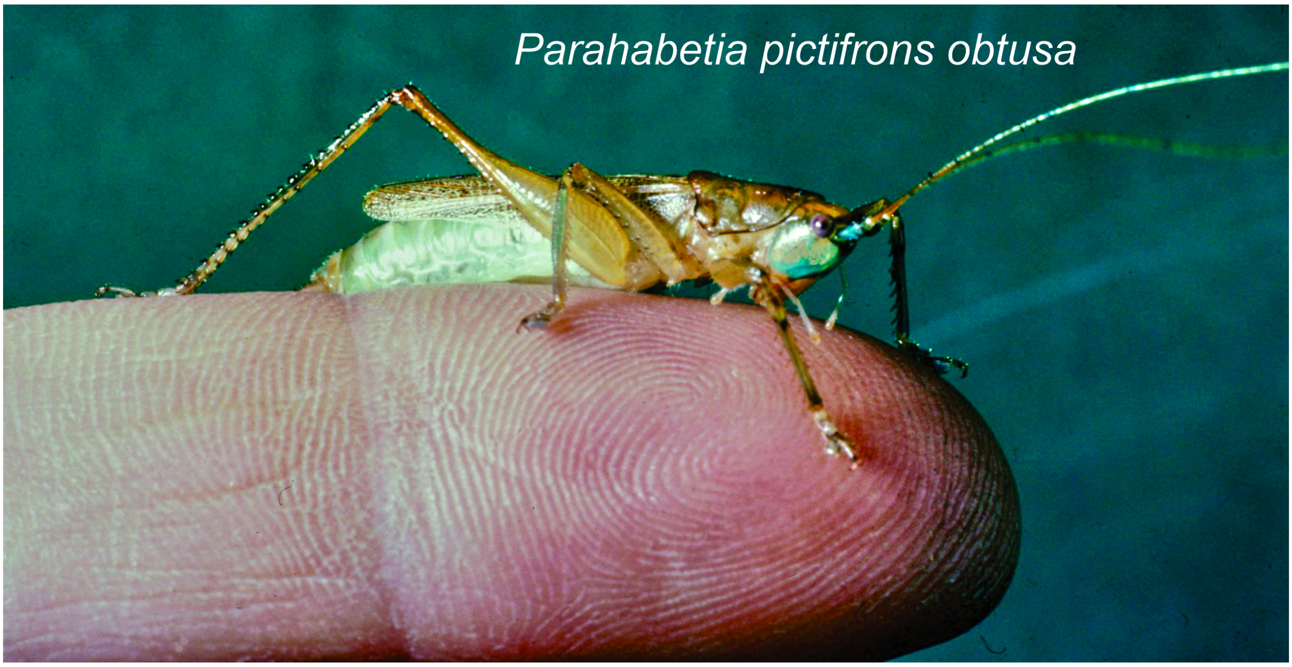


FIGURE 60. *P. pictifrons obtusa* male habitus lateral view, index finger conveys small size of the insect; amber orange colouring; Prominent pronotal bulla marks pronotal acoustic tracheal access.

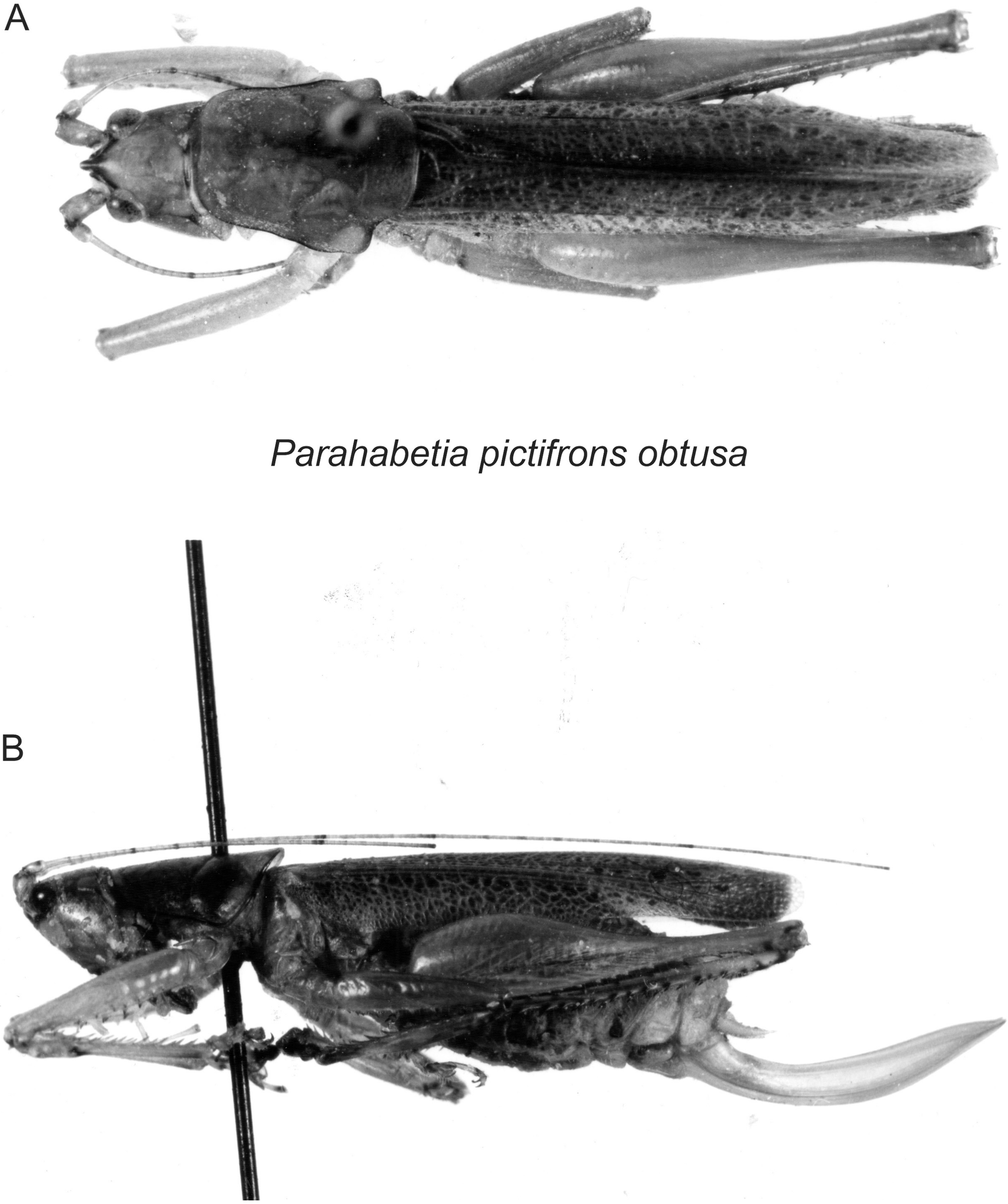


FIGURE 61. *P. pictifrons obtusa*: A) Male habitus dorsal aspect; prominent bulla on prothorax mark where sound enters en route to rear of eardrums. B) female habitus lateral aspect bearing strongly upcurved acuminate ovipositor.

In life the frons is a conspicuous blue green, as also the antennal scapes (Fig. 59). Facial colours of this sort may be adaptive in concealing the insect from colour-vision predators such as birds: as the insect faces skyward legs extended, its coloured markings blend into the colours of bromeliad leaves used as a daytime refugium. The pronotum in dorsal aspect (Fig. 61A) shows conspicuously broadened lateral lobes (bullae) at the entry to the acoustic stigma, an adaptive acoustic feature.

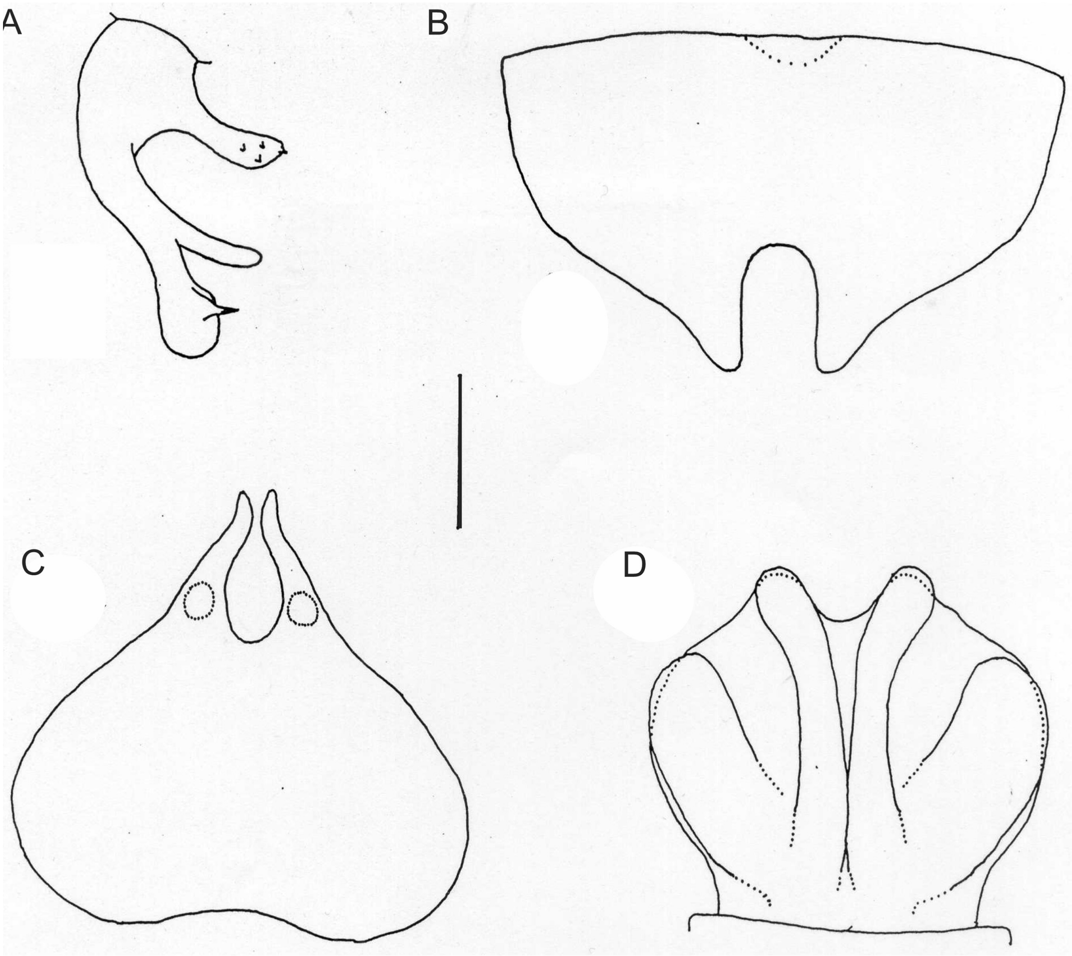


FIGURE 62. *P. pictifrons obtusa*; : A) Dorsal aspect of left male cercus; B) male last abdominal tergite, dorsal view; C) male subgenital plate ventral view, insertion of styli as stippled circles; D) female subgenital plate in ventral view (scale 1 mm).

FIGURE 63. *Parahabetia pictifrons obtusa* stridulatory file on ventral surface of left tegmen.

Stridulatory file. Male stridulatory file tiny (Fig. 63), shortest distance between most proximal and distal tooth 1.2 mm, greatest width of teeth 0.075 mm; of usual shape, slightly fusiform with proximal and distal parts curved and faintly sinuate in profile; total number of teeth 136 of which 89 are apparently functional and regularly spaced, 19 teeth per 0.25 mm.

Stridulation. A resonant stridulation, judging by the simple ultrasonic high-Q sine wave at 34 kHz (Figs 64C, D). Also there is no suggestion of elastic uncoupling apparent in this single sustained pulse (Fig. 64. B). The insect repeats these 4-ms pulses at a regular period of just under 50 ms (Fig. 64A). Each call is comprised of >140 waves which the number of apparently functional teeth—89 (see above)—is inadequate to explain as a 'one wave per file tooth event'. Something on the insect's wing is oscillating making a simple wave train at one 34 kHz frequency. How is this possible unless more than one wave is associated with each tooth?

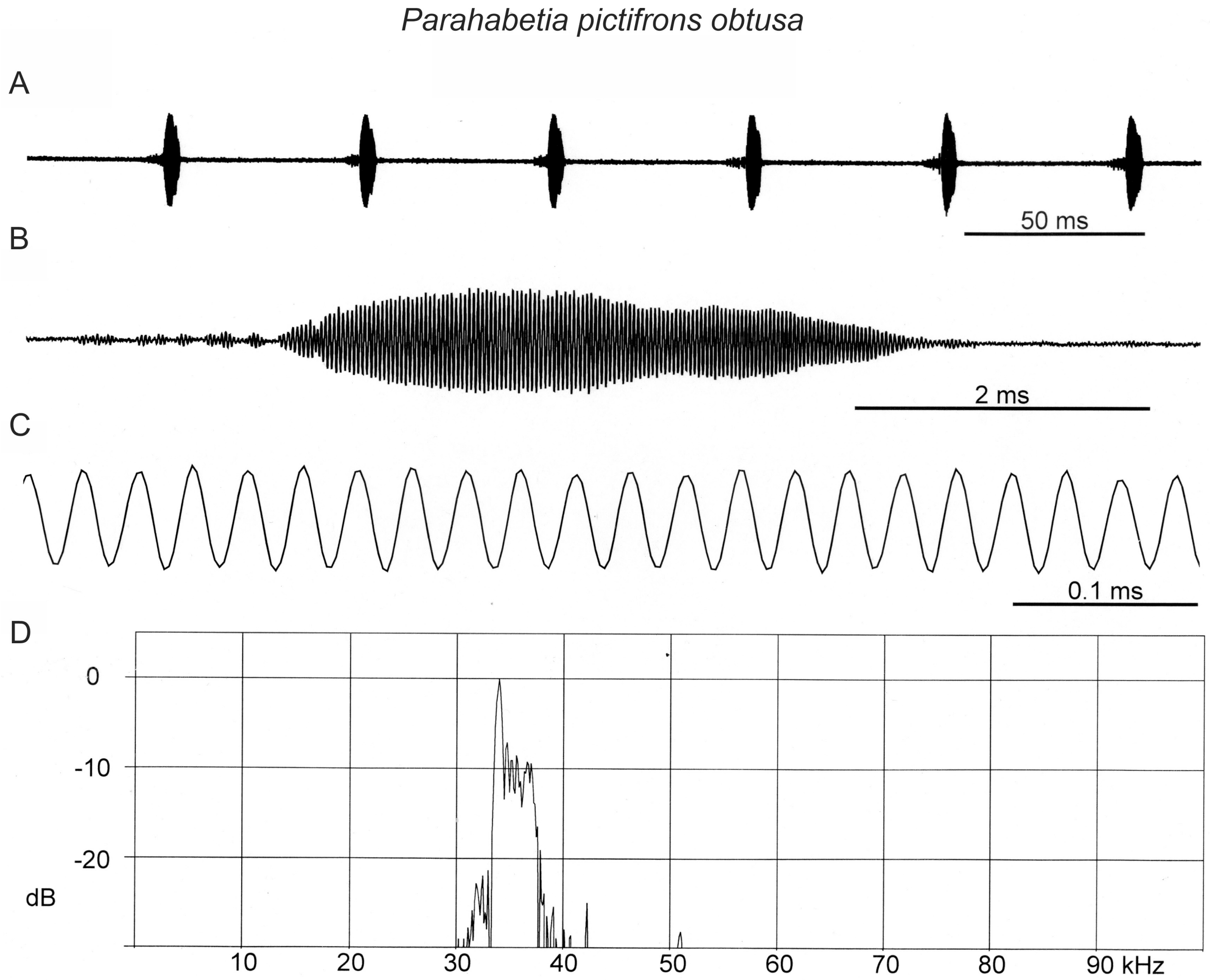


FIGURE 64. *Parahabetia pictifrons obtusa* acoustic analysis: A) Six-pulse time sample taken from the insect's call; B) One pulse at higher time resolution; C) a portion of the pulse in B showing its strongly sinusoidal tonal waveform; D) Fourier analysis shows a single high-Q ultrasonic peak in spectrum at about 34 kHz.

Glennagraecia Ingrisch, 2023

Glennagraecia curvicauda Ingrisch, 2023

(Figs 65–67)

Material studied. Holotype male: Papua New Guinea: Morobe, Wau, Mt. Kaindi, elev. 1230 m (7°21'0"S, 146°40'59.88"E), 30 viii 1981, coll. G.K. Morris, (Depository NBC Leiden). Paratype female: same data as holotype.

Comments. The male of *Glennagraecia curvicauda* is "unique for its almost completely re-curved" cercus (Fig 9F of Ingrisch 2023). These unusual cerci are evident even in the habitus photo of the live adult male holotype (Fig. 65). Diagnosis of the *G. curvicauda* female includes a subgenital plate with "huge lateral expansions" (ibid. and see his Fig. 9B), an apparent adaptation to complement the remarkable male cerci during copulation.

The pronotum of the male is dorsoventrally shallow and broadened, with a convex posteriorly rounded metazona covering the much-reduced tegminal strigin; pronotum with lateral projecting rounded humeral lobes "in about mid length" (ibid., Fig. 65).

Stridulation. Very short ultrasonic sinusoid pulses (Fig. 67A–C) and a relatively high-Q.

spectrum, peaking at 26–27 kHz (Fig. 67D), delivered (mostly) in pairs (Fig. 67A), which pair may be for convenience termed a song. Ten songs had a pulse period of 13.4 ms (Fig. 67B). Mean song period (Fig 67A) was 44.1 ms at temperatures in the low 20s. First and second pulses do not differ in their spectrum, i.e., there is no frequency modulation. This would appear to be elastic uncoupled stridulation in which each wave of the 26 kHz simple sine wave is generated by each successive tooth-scraper contact event and cuticular distortion of the scraper achieves low ultrasonics.

FIGURE 65. *Glennagraecia curvata* Ingrisch *et al.*, 2023: glistening habitus of adult male, hand indicates relatively small species. Field name 'black frons hidden tegmina'.

FIGURE 66. *Glennagraecia curvata* stridulatory file on ventral surface of left tegmen.

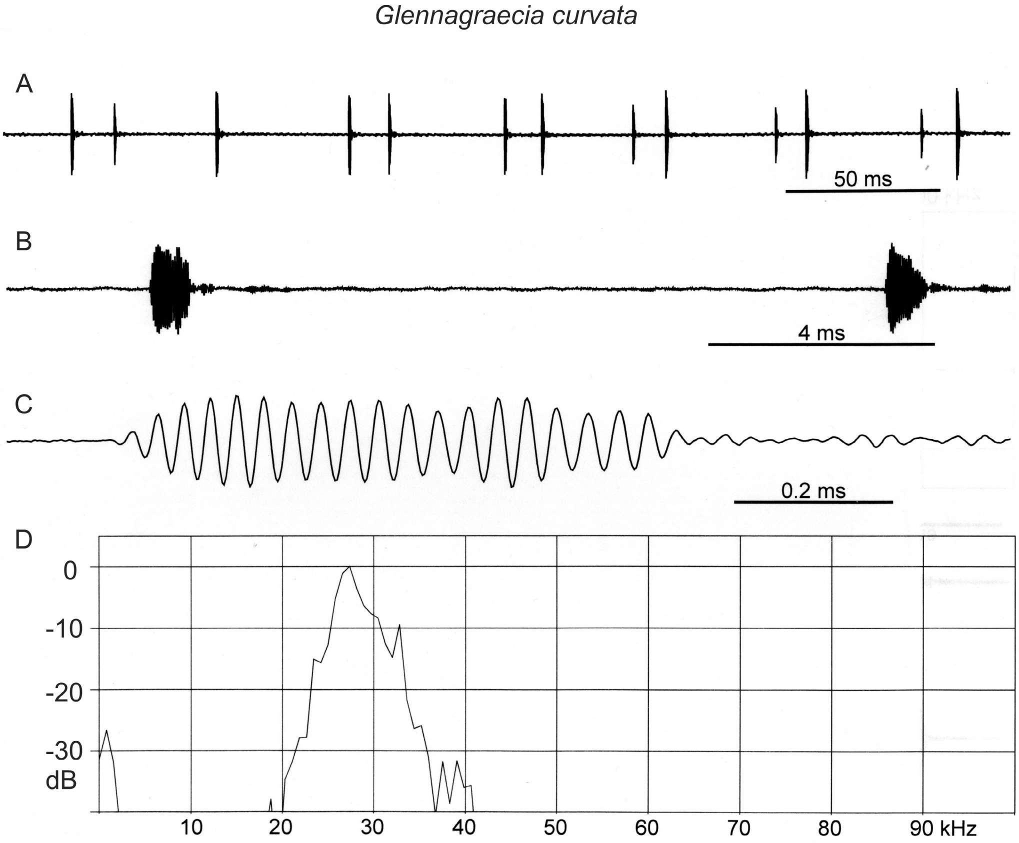
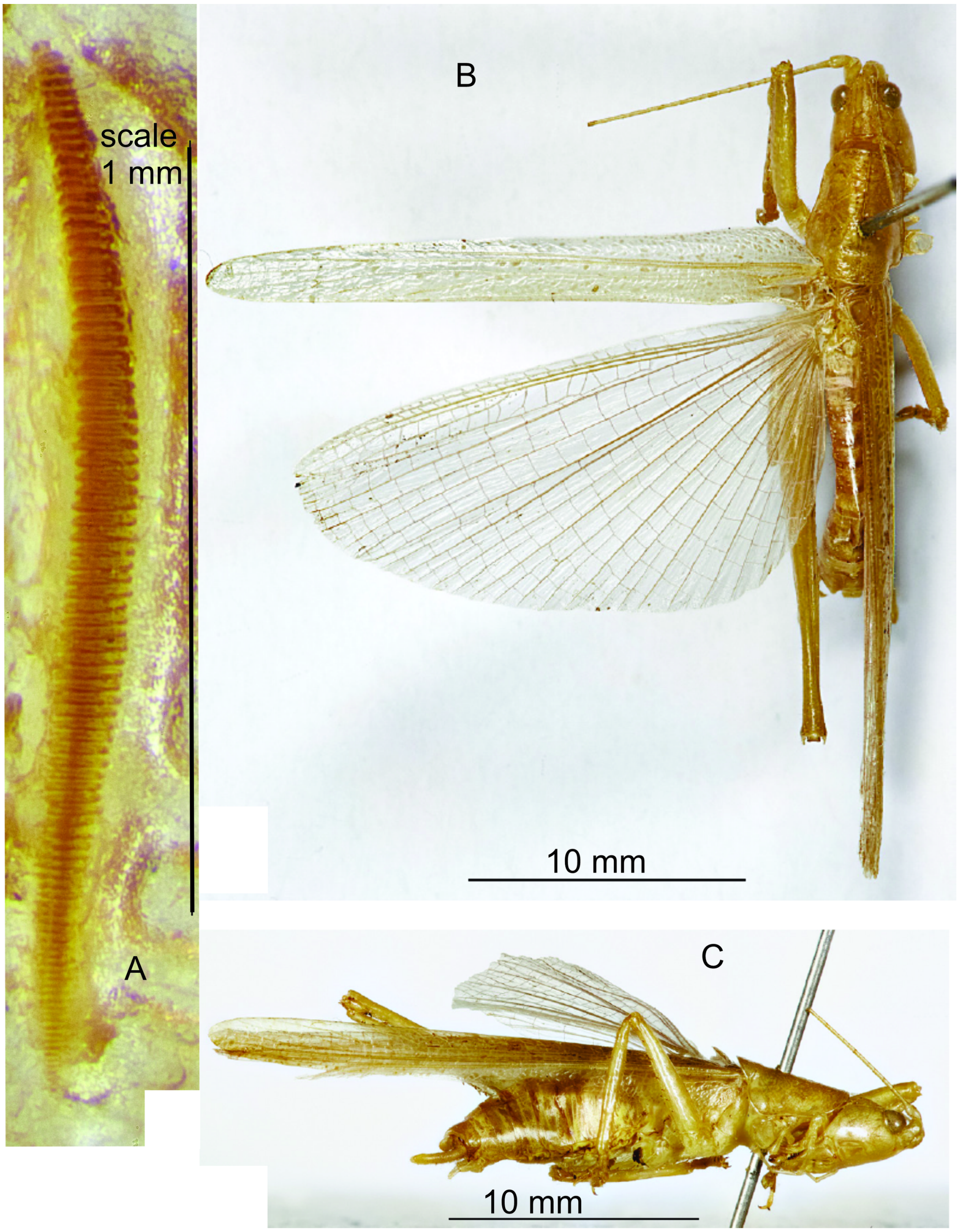


FIGURE 67. *Glennagraecia curvata* acoustic analysis, another example of elastic stridulation: A) Excerpt from a series of mostly paired short pulses, well separated in time; B) One pulse pair at higher time resolution; C) high time resolution of single pulse in B shows markedly sinusoid/tonal waveform; D) Power spectrum of time sample in D indicates a single relatively high-Q carrier frequency peak in the ultrasonic near 28 kHz.

Trichophallus **Ingrisch, 1998**

Trichophallus capillatus **Ingrisch, 2024**
(Figs 68, 69)

Material studied. Holotype male: Papua New Guinea, Wau, nr Wau Ecological Institute, 29 August 1981 coll. G.K. Morris.



Trichophallus capillatus from Ingrisch 2024

FIGURE 68. *Trichophallus capillatus* **sp. nov.** holotype male: A) Stridulatory file, scale 1 mm; B) habitus dorsal view with left wings extended; C) habitus lateral view.

Measurements. Male holotype, (length in mm): body 19; pronotum 4.8; tegmen 21.5; hind femur 12.5 mm.

Diagnosis. *T. capillatus* differs from other species of the genus described so far by the distinctive shape of the titillators on the male phallus (Ingrisch 2024).

Comments. The file of *T. capillatus* (Fig. 68).

Stridulation. Call a regular repetition of silence-separated trains of rapid-decay, single-tooth sourced, transient pulses (Fig. 69AB). The call manifests spectrally as a 25-kHz wide band of frequencies (Fig. 69C) centred near 48 kHz. The carrier frequency of this insect is entirely confined to the ultrasonic; there is no significant sound energy in the audio range. At the time resolution of Fig. 69A each train has a characteristically 'top shaped' amplitude-envelope (a shape like a toy top lying on its side): pulse peak amplitudes begin very faintly, rise steadily then fall away again slightly over the last third. Stridulatory file count of 88–93 teeth reported by Ingrisch (2024) accords reasonably with the 68 transient rapid-decay pulses in the train shown in Fig. 69B. Mean values for 10 calls of our lone singer: trains 30 ms long, repeated with a mean period of 168 ms. The transients are somewhat erratically separated in time from each other within the train (Fig. 69B).

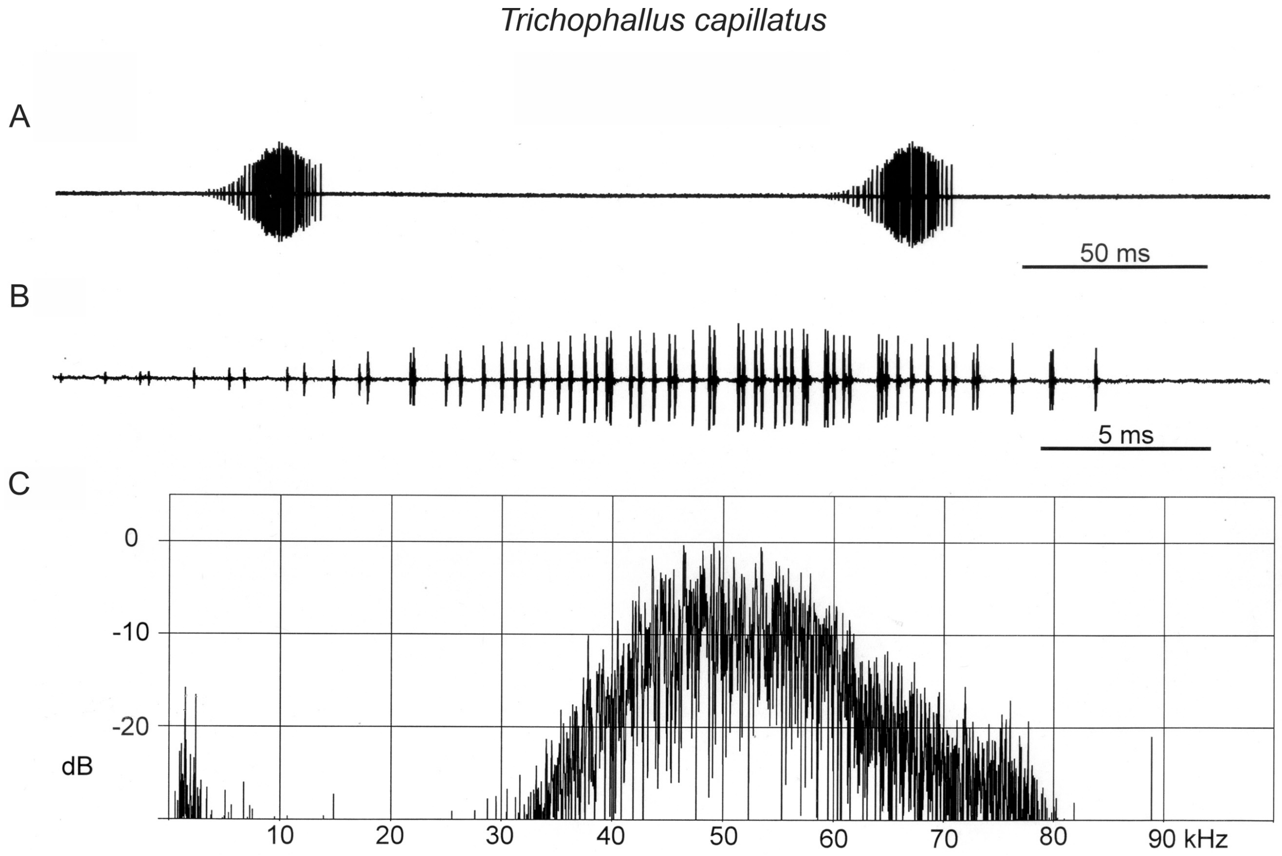


FIGURE 69. *Trichophallus capillatus* acoustic analysis: A) Two calls taken from a longer series, very faint to human ear; B) One call at higher time resolution showing train of transient pulses; C) Entirely ultrasonic broad band symmetrical spectrum, low-Q, centred near 50 kHz; recording made with ¼" B&K so flat to ~70 kHz.

Broadband spectra should not be discounted as noisy stridulatory incompetence. Bands could theoretically be adaptive through ranging: differential attenuation of frequencies with distance is accentuated by a cluttered vegetation. The spectral shape of the band could be coding for distance, so helping to detect the trespass of a neighbouring male competitor or further the success of a female localizing her mate (Morris *et al*. 2016).

Morocera Gorochov, 2016

Morocera nigrifrons Ingrisch, 2023
(Figs 70–72)

Specimens studied. Holotype male: Papua New Guinea, Morobe, Bulolo Gorge, wall outside station house, 28 viii 1981, coll. G.K. Morris (Depository NBC Leiden).

Other specimens studied: Papua New Guinea, Morobe: Wau, Mt. Missim, elev. 1120 m (7°10'S, 146°54'E), 13.ii.1963, coll. J. Sedlacek 1 ♀ (BPBM); same locality 28 viii 1981, coll. G.K. Morris (Depository NBC Leiden). PNG. nr Wau, W.E.I., 25 viii 1981, G.K. Morris (1 ♂); PNG, Mt. Missim, 18 viii 1981, G.K. Morris (1 ♀) (Depository NBC Leiden).

Comments. Ingrisch (2023) elevated Gorochov's (2016) subgenus *Morocera* to generic status. The type species of the genus is *Morocera* (*Scytocera) loriae* Griffini, 1908; a third species is *M. peniculosa*. The titillators of male *Morocera nigrifrons* have a very distinctive form (ibid, see his Fig. 2D): "…so far unique among Agraeciini (I [S.I.] have not seen a similar structure in any other species)". Over their apical half the titillators curl longitudinally, their lateral edges overlapping into submembranous stilletto-like sheaths covered in fine spicules, enclosing tufts of long hairs.

Measurements. (1 male, 2 females in mm). body: male 21, female 21.0–21.5; pronotum: male 5.5, female 5.0–5.25; tegmen: male 11.5, female 11.5–12.5; hind femur: male 10.25, female 10.7; ovipositor: female 8.0–8.5.

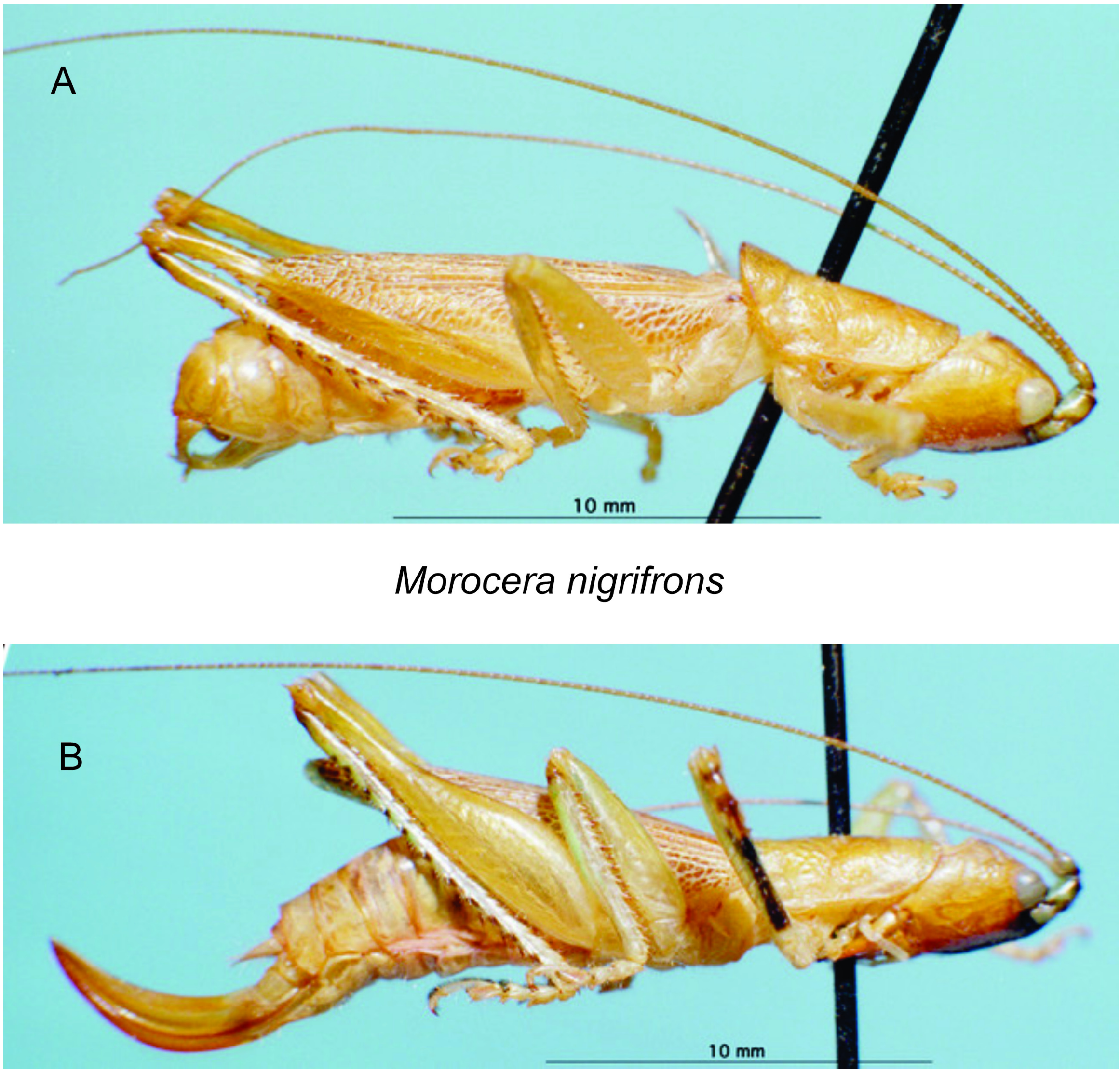


FIGURE 70. *Morocera nigrifrons* Ingrisch *et al.*, 2023: A) holotype male lateral aspect; B) allotype female lateral aspect. Field name 'black frons half tegmen'.

FIGURE 71. *M. nigrifrons* ventral view left tegmen showing stridulatory file.

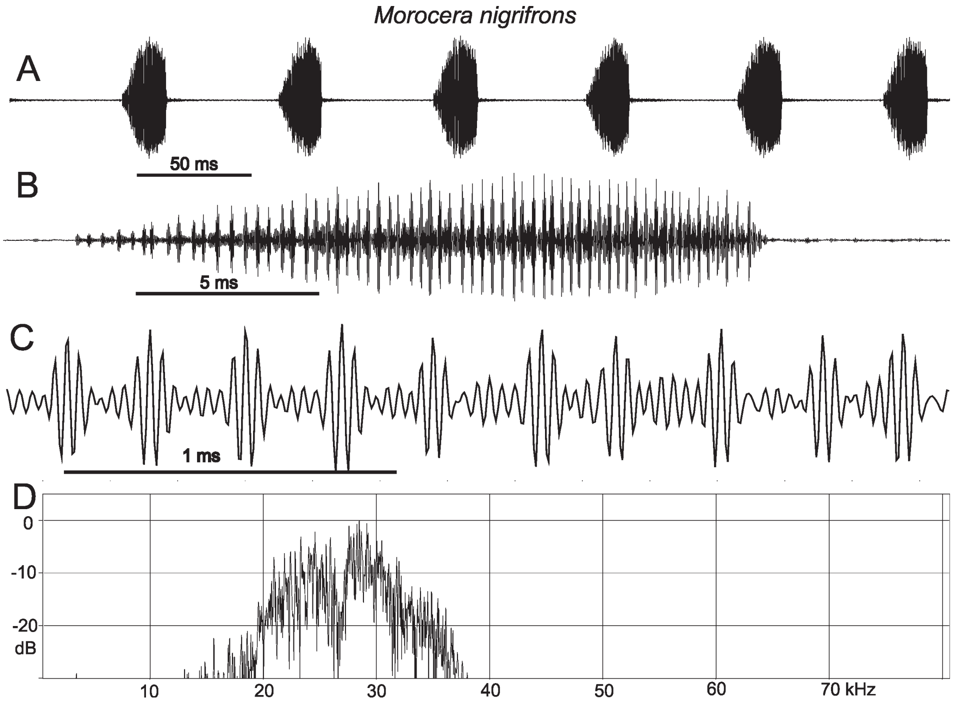


FIGURE 72. *M. nigrifrons* acoustic analysis, an example of transient stridulation: A) Three calls taken from a longer series; B) Train of multiple transient tooth events at higher time resolution; C) Spectrum mainly ultrasonic 20–35kHz, using ultrasonic-limited B&K mic ½” 4165; D) Time sample from pulse train of C showing sequential similarity of complex waveforms.

Stridulation. This insect produces transient pulses (Fig. 72D) grouped tightly together into trains (Fig. 72A,B) with a pulse-train period of 66.5 ms at low 20° temperatures. "Stridulatory file on underside of left tegmen 1.70 mm long, with 78 teeth or 45.88 teeth per mm; about the last 20 teeth very small" (Ingrisch 2023, his Fig. 2A). The number of file teeth agree reasonably with the number of pulses in the train): mean number of pulses for 10 calls of one male 65.2. Average duration of train 19.1 ms. The spectrum is a broad band (Fig. 72C) between 20 and 38 kHz with an average carrier of 28.4 kHz.

Copiphorini

Pseudorhynchus cornutus (Redtenbacher, 1891)

(Figs 73,74)

Material studied. PNG, Wau, W.E.I., 29 vii 1981, G.K. Morris (1 male); PNG, McAdam National Park, Bulolo Gorge, 28 viii 1981, G.K. Morris, identified Judith Marshall (1 male).

Systematics. The stridulatory file and other particulars of these males agree fully with Bailey's revision (1979).

Stridulation. Song loud to human ears, a steady indefinitely sustained sequence of two alternating pulse types (Fig. 75AB). The more sustained and intense pulse type of the two, at higher time resolution, shows as a repeating stereotyped complex wave (Fig. 75D). The Fourier analysis (Fig. 75C) shows energy distributed over a band from 10 kHz to almost 60 kHz, but the most intense frequencies show as a broad peak ~ 11–15 kHz.

Pseudorhynchus raggei Bailey, 1979

Specimen studied. PNG, Wau, Poverty Creek, 18 viii 1981, G.K. Morris, 'Euconoc. Spec. 2', 81-1 (1 male).

Systematics. This male fits perfectly the description of *raggei*, including that of the stridulatory file.

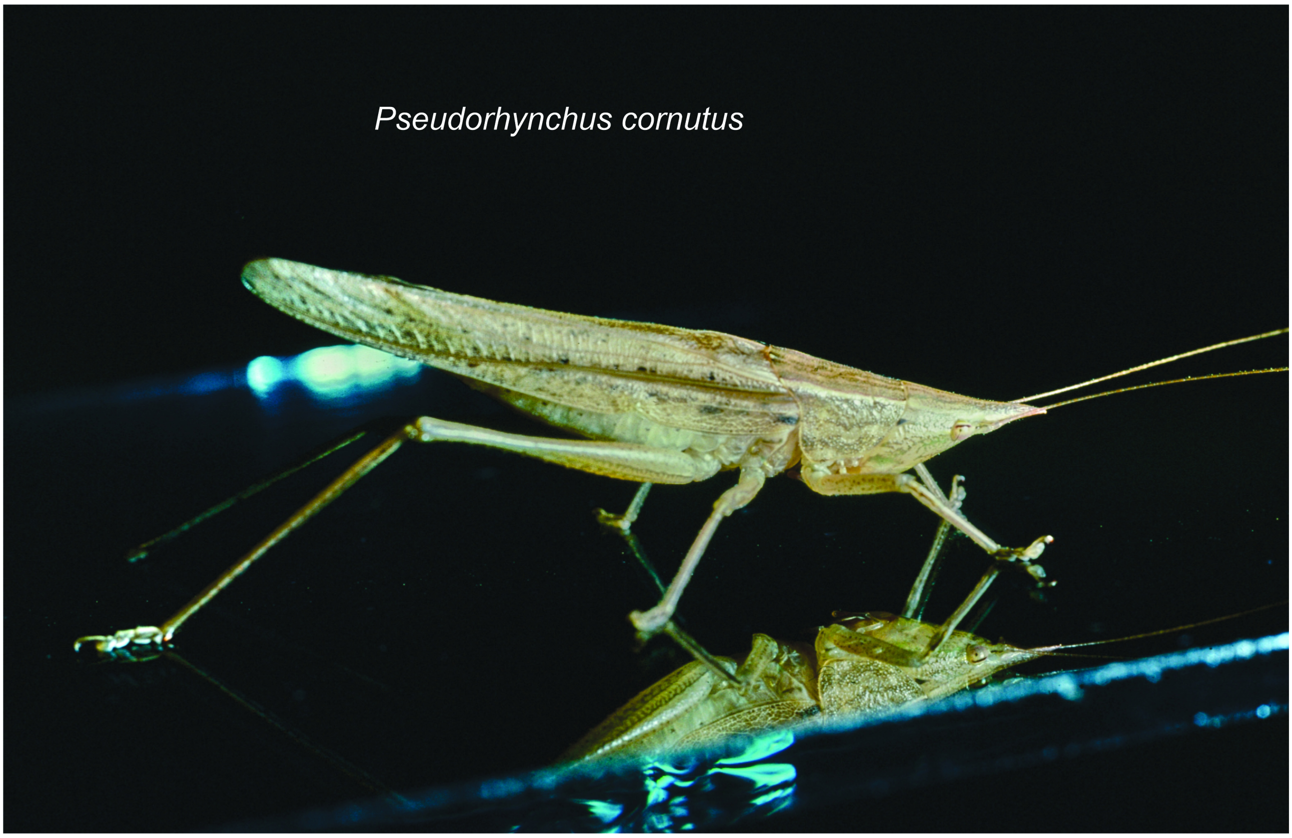


FIGURE 73. *Pseudorhynchus cornutus* habitus of male, lateral aspect on glass.

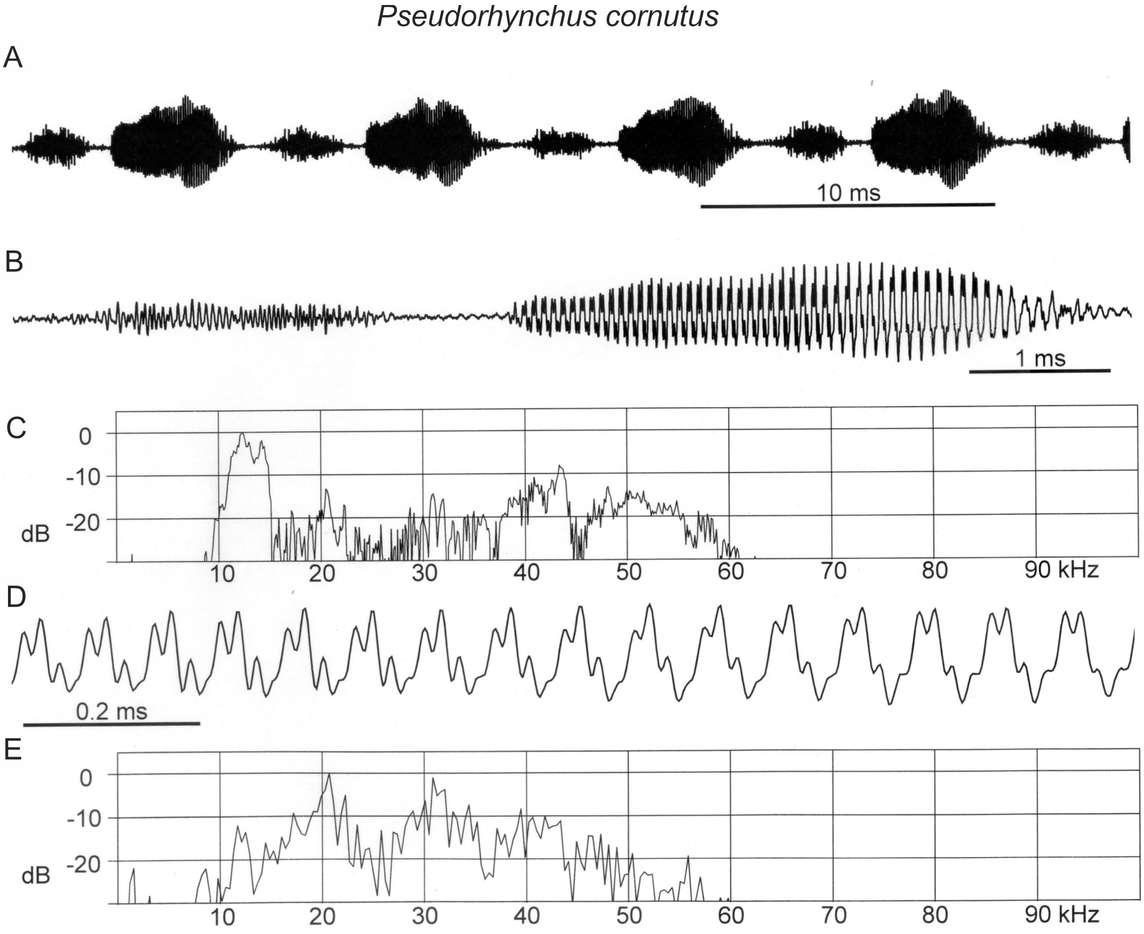


FIGURE 74. *P. cornutus* acoustic analysis A) 4 complete phonatomes (to-fro tegminal cycles), major (presumed closing) and minor (presumed opening) elements (hemisyllables) alternating; B) single phonatome at higher time resolution; C) Fast Fourier spectrum of time sample in B; human ear easily hears loudest spectral component a 12-15 kHz audio peak; lower intensity ultrasonics emitted up to beyond 50 kHz; D) train of characteristic waveforms, presumed associated with tooth events , sampled from the major emission of B; E) Fourier spectrum of the time sample in D.

Distribution & habitat. This species was described after 9 males from northern Australia and one male from E of Popondetta, Northern District, Papua. Apparently, the species is more widely distributed in New Guinea, as we have some more material before us from other parts of New Guinea: Anga Gorge, Southern Highlands District, Papua; Aseki, Morobe District & Kerowagi, Chimbu District, both NE New Guinea and from Mindiptanah along the Kau river, near Tanah Merah (Digul R.), SE West Irian.

Conocephalinae

***Conocephalus semivittatus* ssp.**
Female bluish morph
(Fig 75,76)

Stridulation. Transient stridulation may be the rule in this immensely speciose genus. The most resolved sound event is typically a pulse marked by a rapidly decaying complex wave train, a transient sound pulse that coincides with a file tooth scraper interaction. A series of regularly repeated rapid-decay pulses then comprise a major pulse train. A low intensity minor pulse train (opening of tegmina) precedes in which pulses are not necessarily clearly distinguished in time. The produced spectrum is broad band in the extreme in keeping with the highly transient pulses (impulses).

FIGURE 75. *Conocephalus semivittatus* (Walker, 1869) habitus of female colour morph.

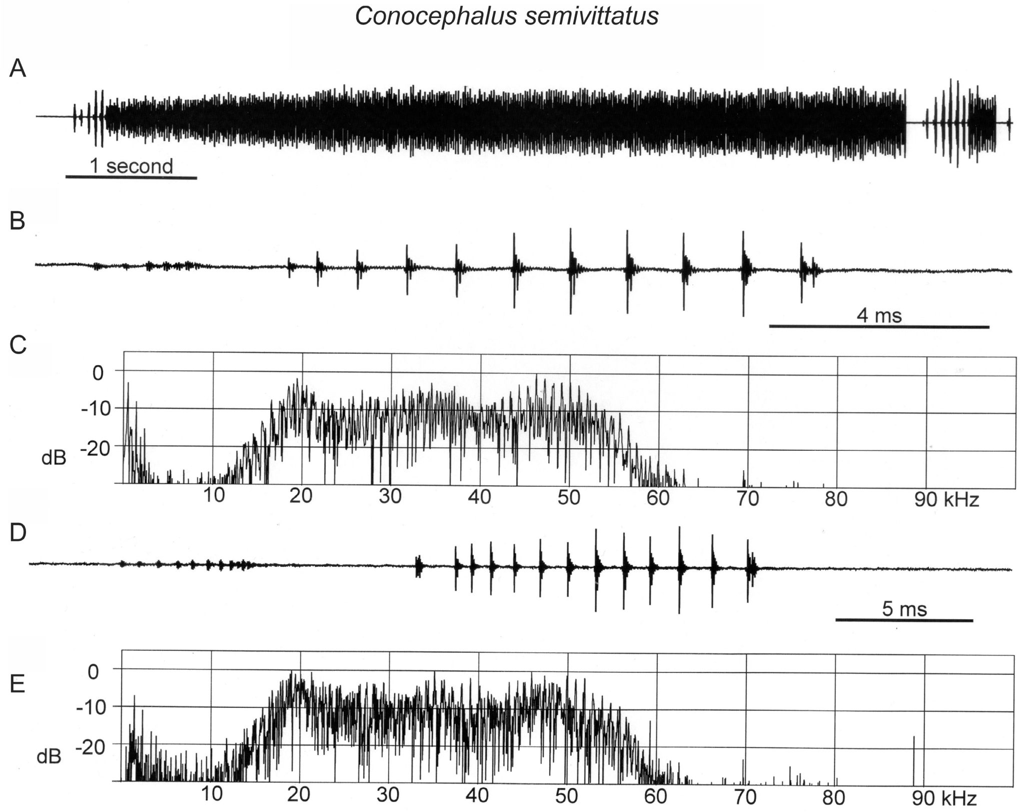


FIGURE 76. *Conocephalus semivittatus semivittatus* acoustic analysis, an example of transient stridulation: Low time-resolution song, a few ticks lead into a steady buzz lasting several seconds. B) One tick phonatome showing 11 transient pulses spaced in time forming a major train, preceded by a very faint file (minor) touch; C) spectrum of sound sample in B, a wide band of mostly ultrasonic frequencies ; D) buzz phonatome of 13 transient rapid-decay pulses in a major train; E) Fourier spectrum of the time sample in D. There is no apparent difference between these tick vs buzz spectra.

Listroscelidinae

Hexacentrus Serville, 1831

(Fig. 77)

Type-species: *Hexacentrus unicolor* Serville, 1831 (by monotypy).

More than 20 taxa are assigned to this genus. The systematic position of several of them is not clear, mainly by absence of reliable specific characters. It transpired however, that morphological particulars of the male stridulatory file offer uncommonly good means for identification. It might be expected that bioacoustics will do the same. We compared the files in *H. dorsatus*, *H. pusillus*, *H. australis* (all Redtenbacher 1891), *H. fuscipes* Matsumura & Shiraki 1908, *H. japonicus* Karny 1907, *H. karnyi* Griffini 1909, *H. borneensis* C. Willemse 1961 and a small yet undescribed species from eastern New Guinea with those in *H. unicolor* and *H. mundus*. All of them are quite characteristic and recognizable immediately.

Two males before us from the surroundings of Wau, Morobe District, NE New Guinea may easily be arranged under what hitherto has been understood to represent *H. mundus* (Walker, 1869).

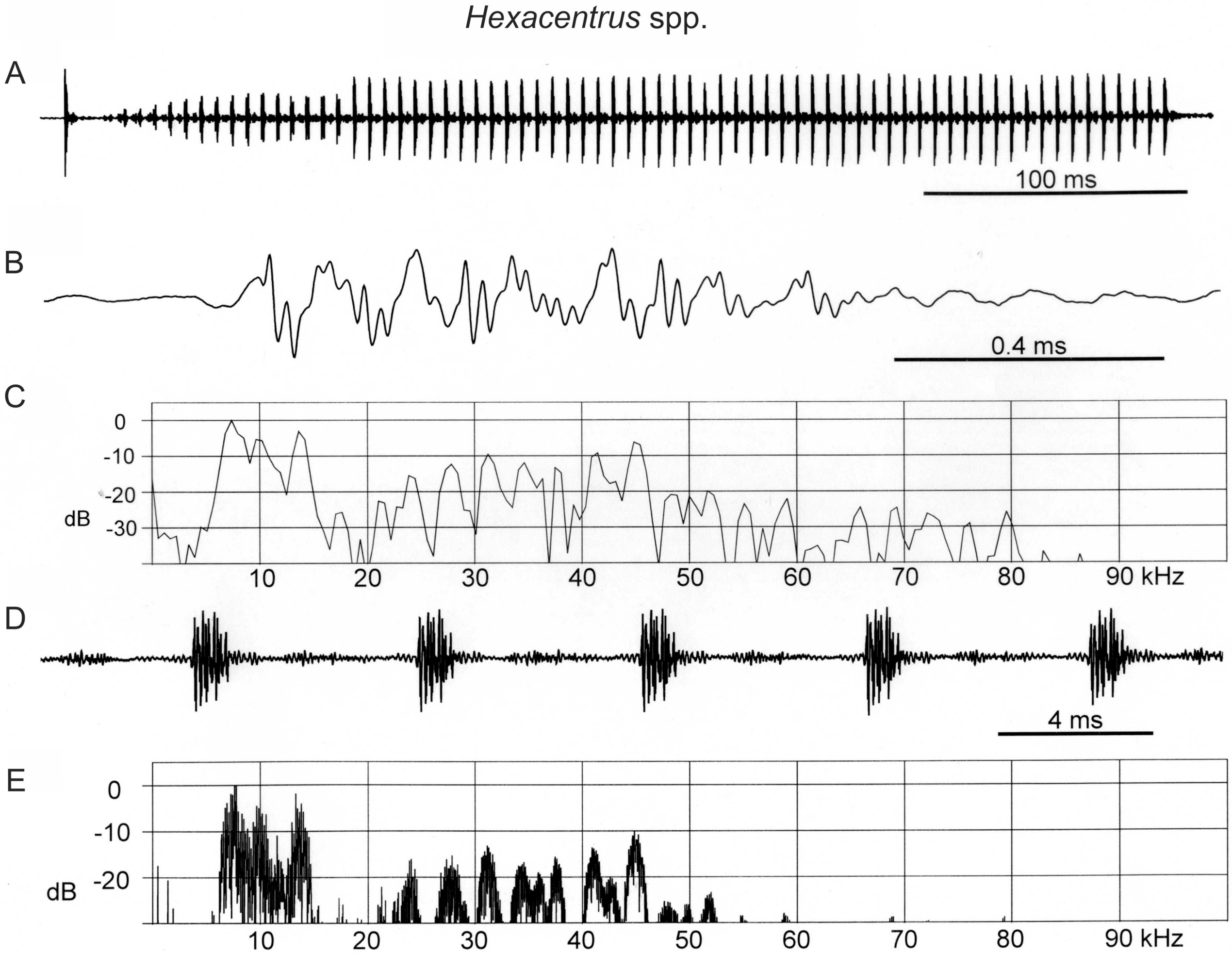


FIGURE 77. *Hexacentrus mundus* acoustic analysis: A) part of a calling bout, initiated by a single transient pulse, followed by high-rate repetition of multiple short sound bursts at a stable period; B) complex wavetrain of starting pulse; C) spectrum of this onset pulse; D) 5 sound bursts excerpted from sustained song in A, little or no indication in waveform of tooth events; E) spectrum of time sample in D, insect's most intense output in middle audio range.

Hexacentrus mundus auct. (= Walker 1869?)

Specimens studied. PNG, nr Wau, W.E.I., 30 vii & 4 viii 1981, G.K. Morris (2 males) (depository NBC Leiden, Specimens discovered missing 2024).

Systematics. This species, described from Ceram, the Moluccas, has been reported in many references from a range reaching from Japan, China and the Philippines to Borneo, Java, Sulawesi, the Moluccas, Timor and throughout New Guinea.

The Wau males have been compared with material at hand preliminarily arranged under *H. mundus*: from Java, from the islands of Obi, Halmahera and Key and the remainder from New Guinea. The stridulatory file of all these males comes near that of the type-species *H. unicolor* (figures and description of the latter in Heller 1986) but may be recognized immediately by the presence of one to three remarkably large teeth in the mid part of the file, which are lacking or scarcely indicated in *H. unicolor*. Among the mundus-like specimens it was found that the Java males have three, those from the Moluccas, especially from Obi one to two and the New Guinea males two of such large teeth. Besides there are additional differences in width, spacing and shape of the remaining teeth, especially apparent in the Javanese males. In the Wau males the two large central teeth are followed distally (i.e., towards the posterior margin of the elytron) by 4–5 stout ones and these again by 5–7 increasingly smaller and narrower spaced ones. The number of teeth between the central large ones and the base of the file is about 23, those near the large ones being widest of all teeth (0.25–0.3 mm) and most widely set (4 teeth per 0.25 mm). By lack of sufficient data, we abstain in any further analysis. It is clear, however, that revisionary work on the systematics of this group of species, based on their bioacoustics and stridulatory apparatus could be very useful.

Stridulation. The relatively massive species diagnostic files of *Hexacentrus* are sparsely toothed and twisted (Heller 1986, See his Fig. 1). The song of *H. mundus* also has a strangely loud percussive quality. Waveforms of sound bursts (Fig. 77D) show no time-distinct tooth-derived amplitude modulations. Perhaps its scraaper makes a single hammer-like impact, slipping off a single very enlarged file tooth to bang basad into a 90° file twist? In *Hexacentrus unicolor* with each cycle of movement to and fro, “only one pulse is created” (Heller 1986).

Phyllophorinae

Phyllophora Thunberg, 1815

Phyllophora spp.

(Figs 78–81)

Type-species: *Phyllophora speciosa* Thunberg, 1815 (by monotypy).

The systematics of this large genus of about 30 taxa is quite difficult. Characters appear often variable and unreliable. In addition, many taxa are badly known. The genus and probably most of the subfamily need revision.

Phyllophora sp.

Specimen studied. PNG, McAdam National Park, 28 viii 1981 G.K. Morris (1 male).

Systematics. The specimen comes near *Phyllophora lanceolata* (Brunner v. Watt., 1898) but could not be identified with certainty either from the literature (e.g., from Karny 1924b; de Jong 1946, 1947, 1972) nor from additional material before us.

Startle stridulation. Stridulation in this insect involves striations on the metacoxae (Fig. 80) that engage with the mesal edges of sternites projecting laterad from the midline. The generation of sound would be aimed at startling a naïve predator and only possible when the insect is restrained in the predator’s grasp while its lengthy hind limbs are free of their role in bearing body weight.

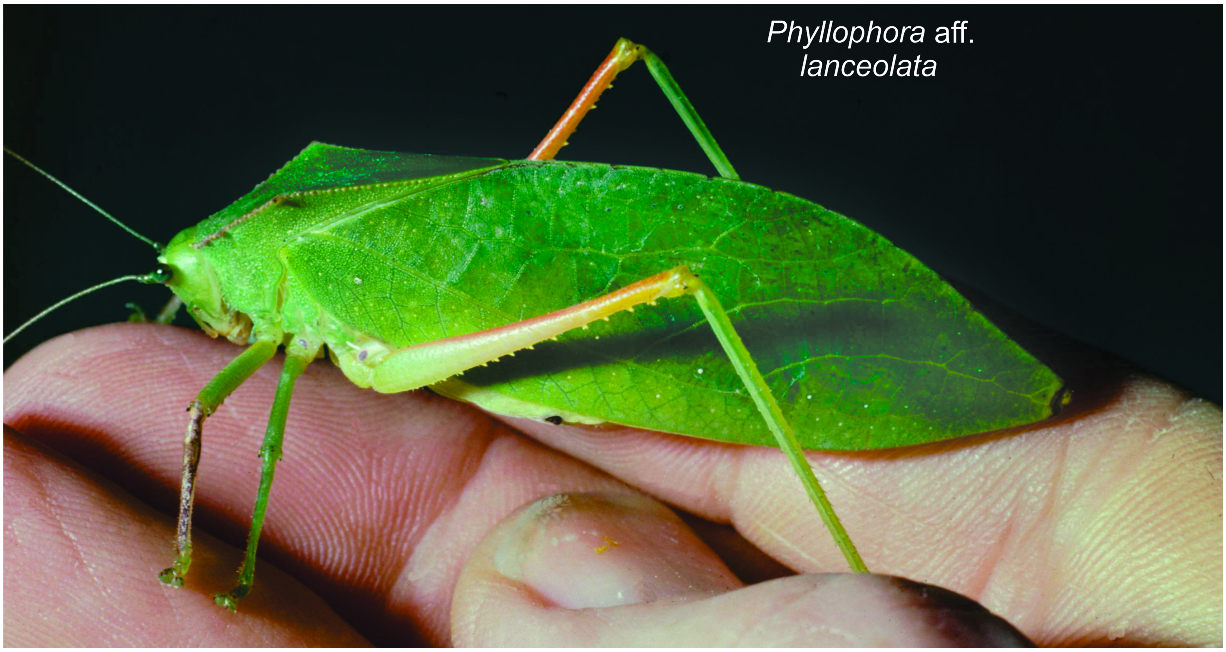


FIGURE 78. *Phyllophora* sp. Habitus of adult male; species without a tegminal strigin; orange legs contribute to defensive display.

FIGURE 79. Immature of *Phyllophora sp.*

FIGURE 80. Coxal strigin of *P. lanceolata*, striations visible on hind leg move against a weakly toothed metasternal flange.

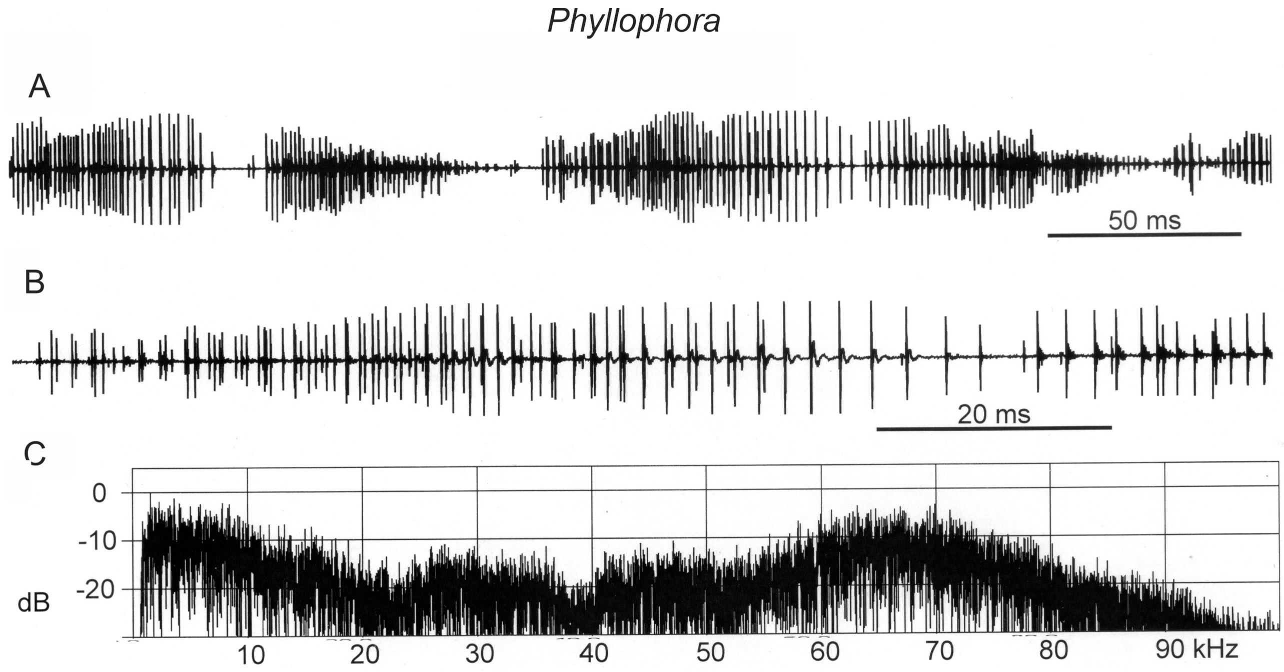


FIGURE 81. *Phyllophora* acoustic analysis: restrained by wings in hand, legs free to move, 19°C, QMC microphone-amplifier system. A, B) transient pulses of variable periods perhaps involving both right and left legs; C) maximally broad spectrum of time sample in B.

Discussion

‘Mirror’ tegmen morpholgy

In the two *Eumecopoda* species the mirror speculum (Figs 22, 28, 29, 82) is a plane ovoid sheet of very transparent cuticle, quite unlike a reflective surface. Its broad extent in two dimensions combines with extreme thinness and some appropriate degree of elasticity to give a shell/diaphragm that favours generation of the pressure and displacement forces associated with sound waves in air. The actual mirror thickness of these two *Eumecopoda* species is unknown, but in the katydid *Xiphelimum amplipennis* mirror thickness is a mere 2.4 microns (Morris *et al.* 2016). Tettigoniid ear tympana, likewise thin chitinous sheets that respond to the pressure and displacement of airbourne sounds, are <0.5 microns thick (pers. comm. F. Montealegre-Z.) The charging artifact seen in specular SEMs, arises from the close proximity of upper and lower (hence ‘doubled’) coatings of the ‘mirror’ diaphragm testifying thus to mirror’ thinness (Fig. 82 A,C).

The over mirror fold (OMF) (Gorochov 2020) (Figs 22, 28, 37C, 82) forms the roof of an air space—a semicavity—applied against the upper surface of the mirror. The ‘sides’ of this OMF space are closed in toward the trailing edge of the wing and broadly open toward its leading edge, its floor is the mirror speculum. As mentioned in the section on *R. rufa*, on the right side of the insect we measured an enhanced sound level of 7.7 dB, a bilateral asymmetry in the broadcast field perhaps attributable to the asymmetry of this OMFspace. The volume and shape of the subtegminal space into which the ventral aspect of the mirror oscillates, fluctuates with the tegminal open-close cycle. But for this OMF air space, as it rides to and fro upon the changing tilt of the scraper tegmen, volume and shape remain fixed, except to the degree of vibratory movement of the speculum itself.

On the anterior mirror rim, where the mirror shares a vein with the harp, is a short robust claw-shaped (unguiform) vein (CV), that tapers away into the plane of the mirror (Figs 22, 82). When the tegmen is viewed from below (ventrally) a branching truss can be seen to advantage (Fig. 82), The truss’ largest member, a broad somewhat flattened beam extends straight from the scraper to the vicinity of the CV (Fig. 82). The orientation and robustness of this beam is consistent with a function in conveying strong forces between the scraper and the CV.

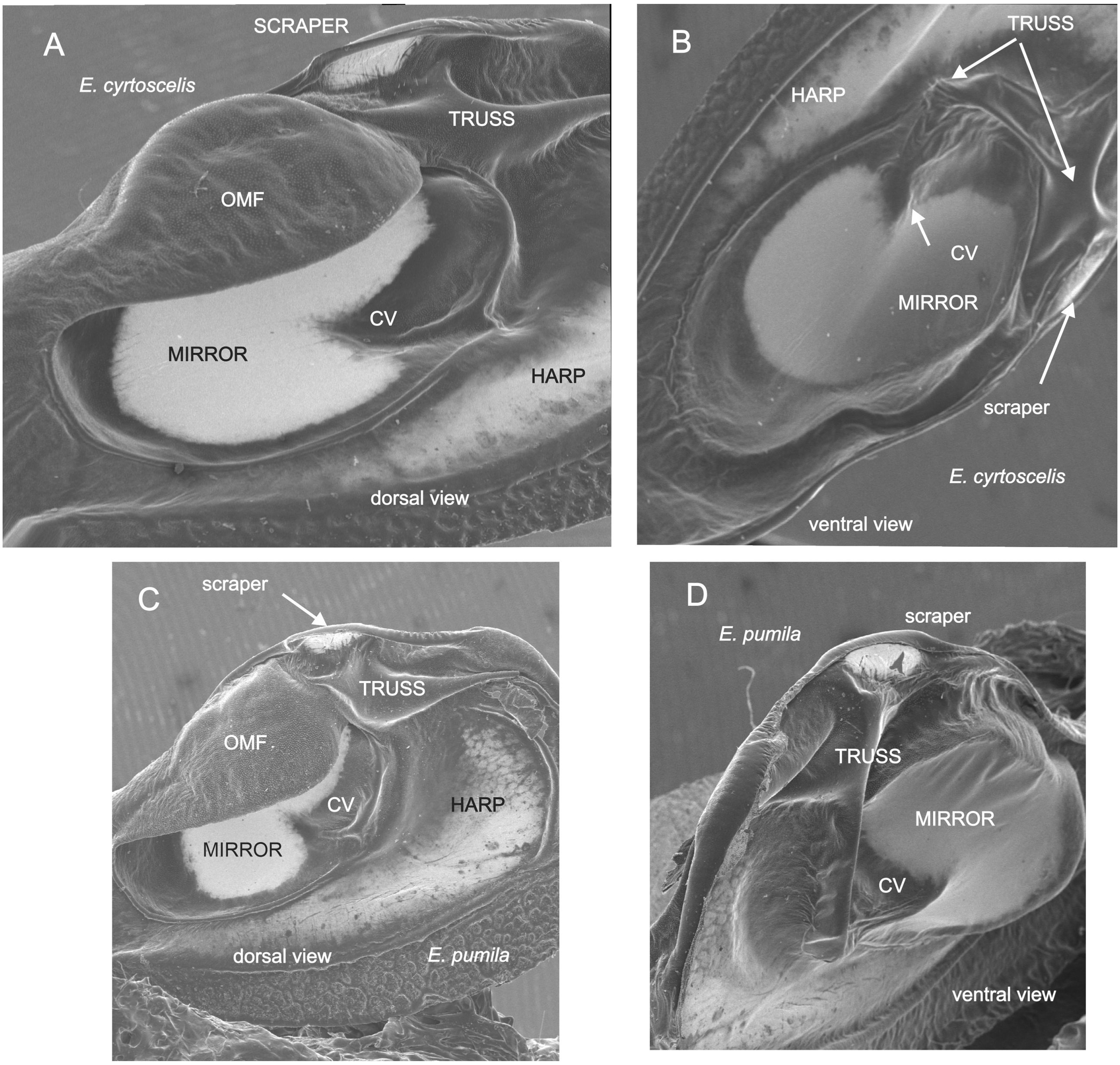


FIGURE 82. Right tegmen strigin comparison for the two *Eumecopoda* species. A) Laterodorsal aspect of *E. cyrtoscelis*; B) same SEM specimen seen from other side of the wing. C) laterodorsal aspect of *E. pumila*; D) same SEM specimen seen from other side of the wing.

Form and forces and the overmirror fold

The OMF cantilevers out above the mirror speculum (~1.6 mm above for *R. rufa* (n=1)) (Fig. 17, 37C), a puzzling structural oddity to occur in an organ for generating sound. It "protects the thin glossy membrane [mirror speculum] but leaves enough space for its vibrations" (Heller 2021). Yet this substantial structure, ventrally concave, relatively thick and stiff, must also significantly affect the near-field sound radiation of the dorsal side of the mirror. Any explanatory model of the mecopodine strigin must explain somehow the fold's loading of the mirror.

The overmirror fold is a ubiquitous diagnostic feature of Mecopodinae, visible in the many species figured by Gorochov (2020) and by Heller *et al.* (2021) (see especially the latter's Fig. 1 of *Mecopoda himalaya*). Among the mecopodine species in the present paper, the fold is most developed in the two *Eumecopoda* species, *E. cyrtoscelis* (Fig. 22) and *E. pumila* (Fig. 28). It is also prominent in *Rentziella rufa*, but in this species overhangs less than half the mirror (Fig. 37C). The fold is just present in *Charisoma* (Fig. 17) and *Segestidea* (Fig. 33): there it is a minor shaping of the posterior mirror rim. The remarks that follow apply to the two *Eumecopoda* species. Wing form is referenced as if the tegmina were extended in flight; thus, the leading edge is anterior and the trailing edge posterior (see labels Fig. 37C; basad indicates an approach to the wingbase, distad an approach to the wing tip).

On the basis that an organism's body parts will have evolved for the adaptive transfer of force, D'Arcy Thompson called the form of such structures 'diagrams of force'. "*The form… of any portion of matter…, and the changes of form which are apparent in its movements and in its growth, may in all cases alike be described as due to the action of force. In short, the form of an object is a 'diagram of forces', in this sense …that from it we can judge or deduce the forces that are acting or have acted upon it…* (D'Arcy Thompson 1961). Using morphology (thickenings, thinnings, beam shapes, size, orientation etc.) as indicators of force magnitude and direction, enables hypotheses of strigin mechanics. From body parts we can "judge or deduce" disparate strengths and directions of force vectors. Peculiarities of form of the mirror, harp, scraper, file teeth, veins and adjacent air cavities, such as the one created by the overmirror fold (OMF), hint at how the organ works. When the organ of interest as here, is acoustic, discovering its mechanics will also be guided by the wave form and spectra of the emitted sounds, i.e., a strigin 'diagram-of-force' hypothesis must necessarily be consistent with the sound 'forms' of time and frequency. With D'Arcy Thompson's encouragement we try to find a plausible 'diagram of forces' hypothesis for the working of the *Eumecopoda* spp. strigin and its overmirror fold.

Resonant stridulation in katydids that modulate frequency stepwise

As a "definitive" resonant stridulator the katydid *A. immunis* is believed to be generating its single-carrier sound pulses by matching slip rate to the natural resonance frequency of its mirror, a slip rate of ~8000 teeth/s for a sound output of ~8000 Hz. The phasing of the shear forces arising from each tooth-scraper event, like properly timed pushes of a child on a swing, should sustain the speculum's ongoing resonant oscillation at a best-amplitude. In a species such as *A. immunis,*which only employs one slip rate (for a given temperature) and where there is no overmirror cavity, this would be understood as making for signal efficiency. For the two *Eumecopoda* spp. things are more complicated because of the stepwise frequency modulation and the presence of the fixed-volume OMF semispace situated above the mirror. *E. cyrtoscelis* alternates two different slip rates of 3100 and 6700 teeth/s to achieve two single-note alternating sound frequencies of 3100 and 6700 Hz. *E. pumila* alternates slip rates of 4500 and 6900 to produce its two alternating sound frequencies of 4500 and 6900 Hz. How could the OMF space be tuned back and forth to create OMF chamber resonance at the two different slip rates? There are no intrinsic muscles to adjust cuticular parts of the insect wing, but of course the insect is changing scraper direction on the file with each tegminal cycle of open and close.

Diagram of forces push pull hypothesis

Moving basad on the file (closing), the scraper shears against a file tooth, creating a force that translocates along the major truss member (Figs 22, 23), arriving as a push upon the far side of the mirror rim near the curved vein (CV). This force transfer repeats with each tooth-scraper event until the file's basal block (BB, Fig.24) is reached. Moving back distad (opening) along the file, the scraper is now shearing in the opposite direction, creating a force in the opposite direction, one that again translocates via the scraper along the major truss member, but arriving now as a pull on the CV region. The tension in the mirror speculum or the shape of the vein lattice is altered, perhaps creating the necessary resonances to match the different slip rates?

Morphological oddities

Two other notable morphological oddities of the *Eumecopoda* spp. strigins are 1) the low, symmetric in profile, file teeth (Figs 24, 25, 27) and 2) a huge cigar-shaped blockage basad (BB of Fig. 24, BB Fig. 26) that must abruptly stall the advance of the scraper wing during closing.

Tettigoniid file teeth are often asymmetric in profile about the tooth cusp: file teeth "…lean toward the anal region of the file (i.e., opposite to the direction (anal to basal) of [wing closing] scraper motion" (Montealegre-Z 2012). Each tooth is buttressed on the aspect directed basad and so presents a steeper face to the advance of a wing-closing scraper. This asymmetry indicates a capacity to receive larger forces on wing closure than on wing opening and most Ensifera also produce the louder components of their sound signal on forewing closings (Montealgre-Z 2012). But for the two *Eumecopoda* spp. here the tooth profile is symmetrical about the tooth cusp (Figs 25, 27) which suggests the teeth are structured to accommodate scraper-shearing forces that are at least as strong on closing as on opening.

An eccentric tooth-damage experiment was conducted on a previously recorded male of *R. rufa*. The song of this species is a succession of well-separated transient pulses making a pulse train of smoothly incremental amplitude envelope (Fig. 43). The insect was restrained against a foam block without injury, using angled insect pins; viewed under a dissecting microscope, a few teeth were scratched away in the distal quarter of his file. In the time-domain record of this male's subsequent stridulation we observed an amplitude effect on the pulse train consistent with this train being emitted on the opening phase of the wing cycle, i.e., as the tegmina sheared apart. Perhaps in *Eumecopoda* spp. scraper direction has evolved for similar effectiveness in both directions, i.e., no directional bias during shearing arises from tooth shape.

This push-pull hypothesis though fails to explain the cuticular block. In both *Eumecopoda* species the file ends abruptly basad in a very large cuticular block (BB) presenting an obstacle to any further progress of the right tegmen against the left (Figs 24, 26). There is also another bar (DB) at the file's other (distal) end, but it is much smaller. The size of the BB implies a very substantial force of collision. Perhaps the BB could contribute elastically to scraper turnaround, rapid deceleration becoming acceleration in the reverse direction?

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Note added in proof

Specimens of two new species & one new subspecies, collected by Morris & Klimas and studied by Fer Willemse, have gone missing from Leiden. In the absence of Fer Willemse's originally studied types we include his descriptions but refrain from naming these taxa, indicating them rather as 'undescribed' and using the unorthodox nominal designations—'goggle eye', 'big blue', 'darth'.

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