

Research Article

Quality calls: phylogeny and biogeography of a new genus of neotropical katydid (Orthoptera: Tettigoniidae) with ultra pure-tone ultrasonics

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This paper describes *Artiotonus*, a new genus of tropical katydid from Colombia and Ecuador. These acoustic ensiferans are represented by three species with a geographic distribution generally restricted to the rainforest of the Bolivar geosyncline of northwestern South America (Pacific). A phylogenetic analysis based on 28 morphological and six behavioural characters produced a tree (*A. artius*, (*A. tinae*, *A. captivus*)) with a consistency index of 0.9. All species are defined by a few autapomorphic changes. The most reliable character for identification is the temporal pattern of the calling song, suggesting a recent genetic divergence. Biogeographic analysis indicates that such genetic divergence began with geographic isolation produced before the Holocene transgression. Species of this genus are remarkable in that the calling song of males exhibits a narrow spectrum with a high quality factor (37–42), unusual values for such ultrasonic signals. A broad discussion on the evolution of tonal calls and pulse trains is offered.

Key words: biogeography, calling song, Conocephalinae, high-*Q*, pure tone, ultrasound

Introduction

Insects represent the great majority of unknown animals (Wilson, 1999), and in the tropics many remain quite mysterious, with bizarre adaptations and unique traits. This is the case in the family Tettigoniidae (katydids), where many species are yet to be described. Among katydids males generate sounds by rubbing forewings together, a mechanism known as tegminal stridulation (Dumortier, 1963).

In Tettigoniidae wings are usually asymmetrical: the left has a transversely running vein (A1) supporting a tooth series – a file, while the right one has its anal margin modified as a sharply upturned edge (the scraper or plectrum). In many species the right tegmen has just a vestigial file, while the functional file is usually that of the left tegmen. During stridulation the scraper is swept along the tooth series, and vibrations produced by tooth impacts are transmitted to specialized wing-cell membranes, which radiate sound (Morris, 1999, 2008). Although katydids are known for using broadband (noisy) signals, in the past several years many

new species have been discovered with songs approaching pure tones: these more sinusoidal songs are far more common among katydids than expected (Montealegre-Z & Morris, 1999; Braun, 2002; Montealegre-Z, 2009).

Not only are many of these insects new to science, but they are adapted to very diverse specific environments. The acoustic displays of the males, in most cases used in the context of social communication, in part reflect these adaptations. For instance, a number of neotropical katydids (Suga, 1966; Morris *et al.*, 1994) make pure tone signals that are at extreme ultrasonic frequencies (>40 kHz); though these signals are high-*Q*, they are also produced in association with much shorter pulse durations than the common signals of other Ensiferans (Montealegre-Z, 2009); since the durations are shorter the *Q* values are compromised – that is, longer pulses reflect higher quality resonance systems (Morris *et al.*, 1994; Mason & Bailey, 1998; Montealegre-Z *et al.*, 2006).

During nearly 15 years (1995–2009) of working in several regions of the rainforests situated on the Bolivar geosyncline of Northwestern South America (Pacific coastal rainforest of ‘Chocó biogeográfico’) that extends

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northward through Colombia and Ecuador to Panama (Nygren, 1950), we occasionally encountered specimens of an unknown genus of katydid, presented as *Artiotonus* in this paper. The Departamento de Chocó is a province of Colombia, lying immediately north of Valle del Cauca in southern Colombia.

Here we describe three new species within this new genus of katydid; two have been studied previously by Montealegre-Z *et al.* (2006) (see table 1 of their paper). These three new species belong to the subfamily Conocephalinae, tribe Copiphorini. During our lab and fieldwork, as well as in publications, we have referred to these species as 'nr *Loboscelis*' in reference to their overall resemblance to the type species of the genus *Loboscelis*, *L. pilipes* Redtenbacher (1891). The taxonomic description given here is complemented by acoustic analyses, analysis of wing movements and a preliminary cladistic study.

Materials and methods

Specimens were taken at night from understorey vegetation from the following localities.

Bajo Anchicayá. This is situated on the extensive coastal plain lying between the western cordillera and the Pacific Ocean, within the Pacific portion of the Departamento del Valle del Cauca and within the municipality of Buenaventura (lat 3° 30' N, long 76° 50' W; 300–350 m elevation). It remains largely undisturbed tropical rainforest, reached via Simon Bolivar Road from Cali to the village of Buenaventura. Rainfall can exceed 7000 mm per year with peaks of precipitation March to May and October to November. Several small communities, referred to here as Bajo Anchicaya, are located along the Simon Bolivar Road: vereda Bellavista and the vereda El Danubio.

National Natural Park (PNN) Gorgona. PNN Gorgona is a Colombian island in the Southwest Pacific Ocean (lat. 2° 47' and 3° 6' N; long. 78° 6' and 78° 18' W). It has an area of 13.33 km² and encompasses the islands Gorgona and Gorgonilla. Elevation rises from sea level to 338 m; the average temperature is 26 °C, and the annual rainfall is 6891 mm. Ecologically it is tropical rain forest (with similar habitat as the mainland but changed climatic conditions). The island is separated from the continent by 35 km with maximum depths of 85 m. The nearest point on the mainland is found at 35 km, in Punta Reyes, where the town of Bazán is located, in the municipality of El Charco, Nariño.

Isla Gorgona was a former penal colony of Colombia at the onset of 'La Violencia' ('The Violence', a period of civil conflict in the Colombian countryside between supporters of the Liberal and Conservative Parties). The prison was commissioned in the 1950s and had a reputation as the 'Colombian Alcatraz'. Twenty-seven years ago a chance for an improved role re-emerged in Gorgona, following

a new state decision. A campaign by a handful of scientists, divers, environmentalists and human rights advocates, led to the closure of the prison and creation of the park (www.parquesnacionales.gov.co).

Tinalandia. A small private forest preserve in the province of Pichincha, southwest of Quito, 112 km along the road to Santo Domingo de los Colorados; 16 km southeast of Santo Domingo (lat. 0° 19' S, long. 79° 30' W; 600 m elevation). The vegetation is lowland rainforest, typical of the western slopes of the Andes, with faunal affinities extending into Colombia (e.g. Bajo Calima, see above). Additional information can be found at: www.tinalandia.com/html/about.html

Depositories

The material studied in this project was deposited in the following collections:

MEUV = Museo de Entomología de la Universidad del Valle, Cali, Colombia.

ICN = Instituto de Ciencias Naturales, Bogotá DC, Colombia.

MEUCE = Museo de Entomología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Phylogenetic analysis

Character states were polarized through outgroup comparison (Wiley, 1981; Nixon & Carpenter, 1993) using three species with varying systematic affinity to the genus *Artiotonus*. If ambiguous, the condition at the outgroup node was resolved in favour of the state in the sister group to *Artiotonus*. If the state was unknown in the sister group, then the outgroup state was resolved by reference to the other outgroups.

The genus *Loboscelis* Redtenbacher 1891 (Nickle & Naskrecki, 1999) and the species *Vestria punctata* (Redtenbacher, 1891) were chosen as outgroups because they share with *Artiotonus* some basic similarities involving the fastigium, and pronotal structure (see Appendix A, see supplementary material which is available on the Supplementary Content tab of the article's online page at <http://dx.doi.org/10.1080/14772000.2011.560209>). The genus *Copiphora* (Serville, 1831) was also included within the outgroup, because the fastigium shape, protruding eyes and optic lobes of most *Copiphora* species also share traits with *Artiotonus*. Additionally, song recordings of several species of *Copiphora* are available (Morris, 1980; Morris *et al.*, 1994; Naskrecki, 2000; Montealegre-Z & Morris, 2004; Montealegre-Z, 2005), which facilitates the polarization of acoustic characteristics. However, although *Vestria punctata* and *Loboscelis* might be related to *Artiotonus*, it is possible that they are not its sister groups (see Discussion). In our analysis, *Artiotonus* is phylogenetically more related to *Loboscelis* than to *Vestria* and *Copiphora* (see Results).

The relationship between genera across Conocephalinae (and also many other subfamilies) within the Tettigoniidae remains largely unknown, therefore the short phylogeny of *Artiotonus* presented in this paper might change if other species of the genus and related taxa are discovered. Here we describe a new genus of katydid, but give some phylogenetic basis in order to avoid the error of creating new taxa without regard for their phylogenetic relationships.

The inclusion of *Vestria punctata* and the exclusion of other *Vestria* spp., arises from evidence that taxa identified as *V. punctata* in Colombia (Montealegre-Z, 1997), Panama (Nickle, 1992), and Costa Rica (Naskrecki, 2000) are probably three different species, meriting creation of a new genus. This conclusion was also reached by Naskrecki (2000) and Nickle *et al.* (1996).

Cladistic analysis involves 34 characters (28 morphological, plus six taken from acoustic behaviour). Detailed descriptions of character states are in Appendix B (see supplementary material which is available on the Supplementary Content tab of the article's online page at <http://dx.doi.org/10.1080/14772000.2011.560209>). The character matrix (Appendix A, see supplementary material which is available online) was analysed using TNT, version 1.1 (Goloboff *et al.*, 2008). All characters were run unordered and unweighted, using the exhaustive search option. Characters for which the state was unknown (missing) were coded as '?'. Inapplicable characters were coded as missing. Phylogenetically uninformative characters (autapomorphies) were included because they are useful in diagnosing taxa.

Finally, the two measures of fit (consistency index, CI (Kluge & Farris, 1969) and retention index, RI (Farris, 1989)) were used in our study and are assumed here to serve as adequate statistics for calculating phylogenetic signal in the characters of interest and for describing the levels of homoplasy and synapomorphy, respectively. But the track of phylogenetic signal has also been reinforced using Bremer support values (Baker & DeSalle, 1997).

Recordings of sound and wing motion

Recordings of wing movements were made using high-speed video (HSV) (Redlake Motionscope PCI1000s, San Diego, CA, USA). This system was synchronized with a computer data acquisition board (National Instruments BNC-2110, Austin, TX, USA; 16 bit) using Midas software (version 2.0 Xcitex Inc., Cambridge, MA, USA) for simultaneous recording of sound production. Recordings were acquired at 1000 frames/s (f/s), and acoustic data sampled at rates of 200 or 300 kilosamples/s. Insects were free on a wood perch, the camera focused on the stridulatory field in dorsal view. Output of a microphone B&K 1/8" (4138), directed at a specimen for sound recording, was conveyed to a B&K Nexus amplifier (Type 2690). In some of the record-

ings, a motion detector (Hedwig, 2000) was also connected to the data acquisition board to augment wing-motion data. These recordings require a small piece of retro-reflective marker to be attached to one of the tegmina. Because this can affect sound (by wing loading), sound description is based on recordings obtained from natural animals.

The calling songs used in all these analyses were recorded in a sound-attenuating room at the University of Toronto (U of T) at Scarborough; the average temperature was 23.5 °C. Bruel & Kjaer microphones, clamped at about 10 cm distance from the dorsal aspect of the specimen, were used with a 2204 sound level meter. Sound levels obtained with the 2204 are relative to 20 μ Pa. The sound signals of *Artiotonus* spp. are so brief that the meter reading is a significant underestimate of their level; the readings given have been adjusted according to Bruel & Kjaer recommended allowances for short-duration signals.

The quality factor Q measures a resonant system's internal to external damping and also the rate at which such a system reaches maximum amplitude or decays (Prestwich & O'Sullivan, 2005). Q values were calculated using one of the methods suggested by Bennet-Clark (1999): Q , derived from the frequency spectrum of the vibrational response of the system, is defined to be the ratio of the frequency of the peak response divided by the spectral width at the two points above and below f_0 with amplitudes 0.707 times the peak value (Fletcher, 1992). Q values can be determined in such a variety of ways by different authors that the values might slightly change from method to method, and comparisons of Q values should be taken as only a rough index of system quality.

Results

Cladistic analysis

Characters and character states. Analysis of the dataset including all taxa resulted in a single most parsimonious tree of 39 steps (CI = 0.884 and RI = 0.762; Fig. 1). The monophyly of *Artiotonus* is supported by six synapomorphies (see genus description, also Fig. 1) and collapses with six additional steps. The characters that better describe *Artiotonus* are described in the diagnosis of the genus. In the single tree obtained, *Loboscelis* appears to be more related to *Artiotonus* than *V. punctata*. This relation is supported by four synapomorphies: acoustic, pronotal disk rugose (4), spiracle partially or completely exposed (6), membranous titillators (19) and upcurved ovipositor (20). Nodal support, as measured by the decay index (DI), is high for nodes B and C (Fig. 1).

Within *Artiotonus*, *A. tinae* and *A. captivus* form a solid clade (C in Fig. 1) supported by three synapomorphies: dorsal surface of cerci carinate [18(1)], lateral lobes of subgenital plate of female curved and projected laterally [23(2)],

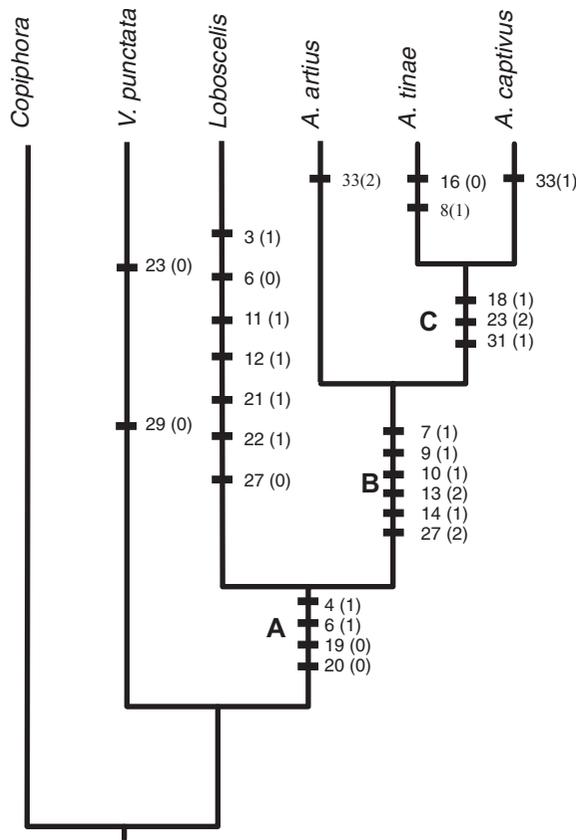


Fig. 1. Phylogeny of the genus *Artiotonus* (single most parsimonious tree) obtained with 28 morphological and six call characters. A, B and C indicate nodes. Numbers over individual branches show synapomorphies with character states in parentheses.

and during sound production, the wing-closing stroke made with pauses [31(1)]. This clade collapses with three additional steps. All three species are morphologically similar, and only a few autapomorphies (mostly acoustic characters) help to define each.

Artiotonus artius can be recognized by the asymmetry of the internal cercal tooth, and by the low rate of calling [33(3)]. *Artiotonus tinae* on the other hand, exhibits short tegmina [8(1)] as an autapomorphic trait. The elevated call repetition rate (>100 syllables/minute [33(1)], also common in *Copiphora*) is a useful character to distinguish this species from congeners. *Artiotonus captivus* is defined by only a single acoustic character: calls given at a rate of 15–20/min [33(2)], but because this species is endemic to PNN Gorgona (an island), its geographic distribution can be used to identify it.

Taxa descriptions

Artiotonus gen. nov.

TYPE SPECIES: *Artiotonus captivus* here designated.

ETYMOLOGY: the generic epithet is derived from a combination of latin *artius* (perfect) and *tonus* (pitch) in recog-

nition of the single pitch ‘perfect’, with perfect quality resonance observed in the spectra.

DIAGNOSIS: A quick diagnostic feature to recognize species of this genus is a pronotal marking, synapomorphic for the genus (Figs 2–7). The pronotal disk exhibits a narrow midline mark, broad on the metazona then tapering anteriorad on the prozona. This mark recalls the shape of a lab volumetric flask, or of the Eiffel Tower. Its external outline is white-cream internally brown-reddish. The marking does not include pronotal sulci, only the convex intervening areas (Figs 2–7). Stridulatory area of left wing dark: this patterning seems a continuation of the pronotal marking.

Other synapomorphic features that can help to distinguish this genus from *Loboscelis* are mirror frame of right wing pentagonal (Fig. 8), the stridulatory file shape (Figs 9–14) and the shape of male cerci (Fig. 8, see details below).

Description

HEAD: Fastigium long, acuminate, bearing dorsally two rows of small tubercles, ventrally with a conspicuous tooth separated from frontal fastigium by a gap. Eyes globose, strongly protruding. Subocular region with some irregular tubercles. **THORAX:** Pronotal zones clearly defined by deep sulci, metazona flat with posterior margin truncate (Figs 2–7). Humeral sinus conspicuous. Thoracic spiracle ovoid, only slightly covered by lateral lobes. Prosternum unarmed. Fore and mid femora armed with spines on both ventral margins, the posterior one bears shorter spines; all genicular lobes armed. **TEGMINA:** Tegmina elongate, covering abdomen, apically rounded or slightly acuminate. Functional stridulatory file sigmoid (Figs 10, 12, 14), intertooth distance gradually increases in the first 2/3 of file length (Figs 9–11). **MALE GENITALIA:** Cerci S-shaped, sharply acuminate (Fig. 8), with blunt internal tooth. Subgenital plate bicarinate, medially weakly emarginate, with long styles (Fig. 8). **FEMALE GENITALIA:** Subgenital plate of the female basally broad with a broad shallow v-shaped emargination between two triangular protuberant pseudostyli (Fig. 8).

Artiotonus artius sp. nov.

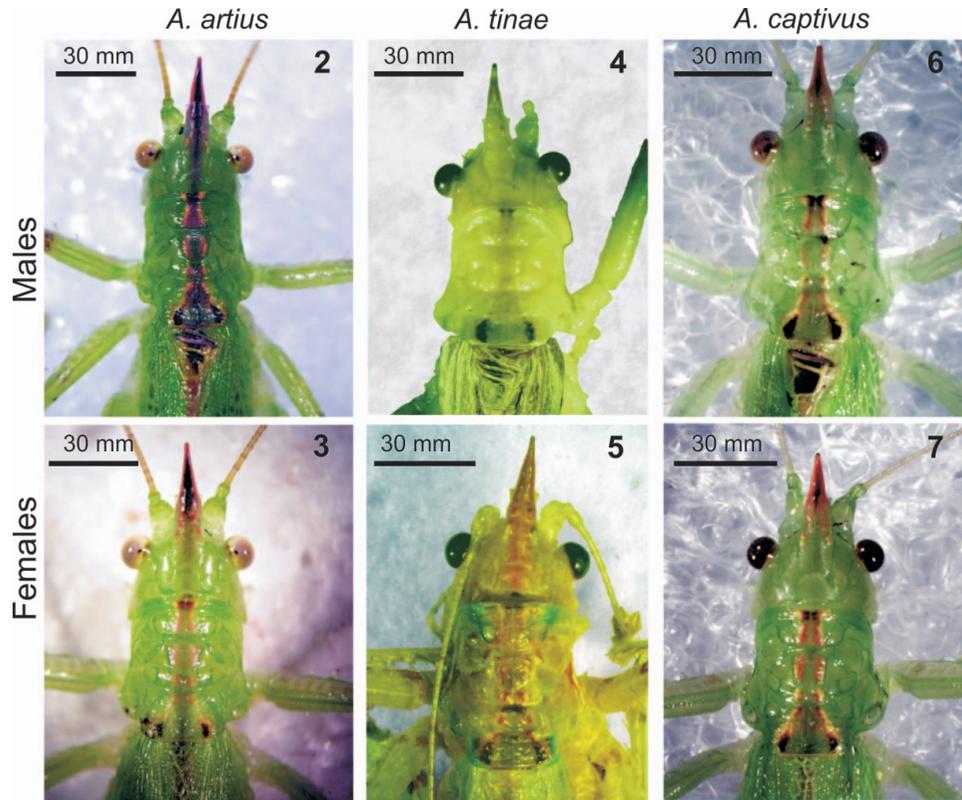
HOLOTYPE: 1 ♂ MEUV 23167, February 2010 (Fabio A. Sarria-S).

ALLOTYPE: 1 ♀ MEUV 23168, February 2010 (Fabio A. Sarria-S).

PARATYPES: 1 ♂ MEUV 20904, October 1995 (F. Montealegre-Z).

TYPE LOCALITY: COLOMBIA, Dept. Valle del Cauca, Dagua, Bajo Anchicaya, elevation 320 m.

ADDITIONAL MATERIAL: 1 ♂ ICN, Valle del Cauca, Buenaventura, Bajo Calima, 70 m. 15 May 1996 (G. K.



Figs 2–7. Head and thorax of *Artiotonus* spp. showing pronotal marks, one of the synapomorphic features of the genus. 2, 4, 6 males. 3, 5, 7 females.

Morris). 1♀MEUV 20905, Valle, Buenaventura (La Trojita), February 1997 (F. Montealegre-Z).

ETYMOLOGY: the specific epithet derives from the Latin word *artius* (perfect) in reference to the exceptionally sustained pulse and high- Q spectrum of this species. Among all known species of *Artiotonus*, this is the only one that uses a single sustained pulse per wing cycle; the other two species employ trains of very sinusoidal pulses in each cycle of wing movement.

DIAGNOSIS: This species may be recognized by the genitalia of males and by calling song. The male cercus bears an internal asymmetric tooth which projects dorsolaterally; the surface of this tooth is smooth. In the other two species this tooth is symmetrical, projects contralaterally (i.e. in the direction of the opposite side) and has a dorsal carina. The call of this species occurs as a smoothly uniform single sustained pulse lasting almost 4 ms, at a carrier frequency of 40 kHz (± 0.4); in the other two species each call is given as a train of shorter pulses, but carrier frequencies are within the range (37–45 kHz).

Description

HEAD: fastigium elongate (Figs 2–3, Table 1). Subocular region with three rounded granules. **TEGMINA:** tegmina

pale green, with some scattered spotting, extending well beyond terminalia. Female and male similar in coloration. Tegminal apices rounded. Stridulatory file of 1.4 ± 0.02 mm in length, holding 163–170 teeth (tooth density = 111–120 teeth/mm) (Figs 9, 10, 15). **MALE GENITALIA:** subgenital plate basally broad, gradually narrowing, with medial round emargination, bearing elongate styles (Fig. 8). Tenth tergite bilobular, medially broadly incised. **FEMALE GENITALIA:** subgenital plate with internal margin of pseudostyli, straight (Fig. 8).

DISTRIBUTION: Southwest part of the Pacific lowlands of Colombia in Valle del Cauca. Specimens of this species have been collected from different rural localities belonging to the municipality of Buenaventura (Fig. 16), but its distribution probably extends to the greater part of the Pacific coast rainforest in Colombia.

SONG DESCRIPTION: Analysis based on recordings of seven males. At 24 °C, the song of this species is an unbroken wave train (a quite short very sinusoidal pulse) of 3.78 ± 0.14 ms duration ($n = 7$), produced by a single continuous closing stroke (Figs 17a–d). At 23.5 °C the calls are given at a rate of 7.6 ± 0.21 per minute (range 4–9 calls/min, $n = 7$, seven sound recordings of 2 minutes each were used for analysis). This low call rate equates to some 0.10–0.15 calls/s. Calls are all given in slow sequence

Table 1. Measurements (in mm) of some morphological structures of *Artiotonus* species. F = fore, M = mid, H = hind, S = subgenital.

	<i>Artiotonus artius</i>						<i>Artiotonus tinae</i>						<i>Artiotonus captivus</i>					
	Male (n = 7)			Female (n = 4)			Male (n = 7)			Female n = 1			Male (n = 9)			Female (n = 6)		
	Mean	Range		Mean	Range		Mean	Range		Mean	Range		Mean	Range		Mean	Range	
Body	39.44	35–43.2		43.70	43.65–43.75		27.33	27–27.7		29.81	27–27.7		35.27	33–37.4		41.05	41.12–41.65	
Fastigium	2.71	2.13–3.38		2.15	1.76–2.54		1.93	1.91–1.94		2.00	1.91–1.94		2.16	2.4–2.74		3.18	3.07–3.44	
Pronotum	5.29	5–5.46		5.53	5.38–5.68		5.25	5.2–5.3		5.44	5.2–5.3		5.45	5.2–5.71		5.44	5.33–5.52	
Tegmen	30.24	27.4–33.4		33.29	32.37–34.22		17.99	17.3–18.7		20.16	17.3–18.7		26.72	26.25–27.1		30.44	30–31	
F-femur	7.22	7.08–7.4		7.19	7.15–7.24		6.12	6.1–6.2		6.70	6.1–6.2		6.55	6.25–6.78		7.07	6.54–7.31	
M-femur	6.99	6.21–7.6		7.35	7.31–7.38		6.25	6.0–6.5		6.41	6.0–6.5		6.96	6.46–7.44		7.31	7.16–7.35	
H-femur	16.71	15.09–17.6		18.28	18.25–18.31		15.02	14.8–15.2		16.53	14.8–15.2		16.40	15.75–16.9		18.39	18.28–18.76	
F-tibia	8.44	7.48–9.10		9.09	8.68–9.5		7.93	7.8–8.1		8.87	7.8–8.1		8.79	8.56–9		9.24	8.58–9.71	
M-tibia	7.35	7.15–7.72		8.56	8.42–8.71		7.32	7.7–7.3		7.53	7.7–7.3		7.76	7.71–7.82		8.58	8.47–8.61	
H-tibia	17.94	16.66–17.77		19.80	19.28–20.33		16.19	15.9–16.5		17.81	15.9–16.5		17.35	17.32–17.38		19.39	19.6–19.98	
S-plate	2.00	0.9–2.6		1.81	1.79–1.83		2.19	2.1–2.3		1.46	2.1–2.3		2.59	2.37–2.72		1.35	1.03–1.9	
Cercus	1.81	2.6–2.8		2.26	2.22–2.30		2.08	2.07–2.09		1.79	2.07–2.09		2.37	2.34–2.4		1.95	1.24–2.20	
Ovipositor	0.00	NA		11.95	11.48–12.43		NA	NA		10.49	NA		NA	NA		12.22	12.00–12.76	
Eye diameter	1.27	1.28–1.29		1.32	1.28–1.35		1.21	1.20–1.22		1.28	1.20–1.22		1.18	1.15–1.22		1.19	1.13–1.22	

distributed over 30 s, insects then pause for another 30 s and begin calling again (Fig. 17a). The mean sound level of the call of seven specimens was 92.70 ± 0.71 dB (SPL meter operating in fast impulse mode) as recorded at 10 cm with the microphone directed at the dorsal field of the tegmina. In one specimen the level was measured with the SPL meter operating in impulse hold mode giving an average level of 101.82 ± 0.10 dB (SPL). The spectrum peaks very narrowly at 40.6 ± 0.21 kHz ($n = 7$, range 40.3–40.8 kHz; Fig. 17e). Even at 30 dB below peak maximum no harmonic components of the fundamental frequency are apparent. This is among the most pure-tone of tettigoniid songs we have ever recorded (Table 2). There is only the single pulse with each cycle of wing movement; emission never occurs as a train of shorter pulses; the envelope of the pulse rises and falls over the ~ 4 ms symmetrically in time. The call's remarkable tonality is reflected in a very high- Q value, calculated from sound pulses to be 42.6 ± 1.3 ($n = 7$). In the lab, males interacted acoustically alternating calls, and the song of one evoked an acoustic response in others. But a male could be initiated in his calling by the sound (rich in ultrasonics) of a human back-sucking saliva through the teeth.

Artiotonus tinae sp. nov.

HOLOTYPE: 1 ♂ MEUCE, 16 July 2003 (F. Montealegre-Z & G. K. Morris).

ALLOTYPE: 1 ♀ MEUCE, 16 July 1986 (G. K. Morris).

PARATYPE: 1 ♂ ICN, 16 July 2003 (F. Montealegre-Z & G. K. Morris).

TYPE LOCALITY: ECUADOR, Prov. Esmeraldas, Natural Reserve Tinalandia. Most males collected and recorded (5 of 7) were destroyed during physiological experiments and therefore were not used as type material.

ETYMOLOGY: the specific epithet *tinae* refers to the name of the founder and original owner of the natural reserve *Tinalandia*: Mrs Tina Platonoff. Without her intervention this habitat and hence this species in Ecuador might have been lost.

DIAGNOSIS: *Artiotonus tinae* may be recognized by body size, tegminal shape, male genitalia and calling song. Its average body size is smaller than that of the other two congeners (Table 1). Tegmina acuminate, shorter than those of the other two congeners (Table 1). The male cerci bear an internal tooth which projects contralaterally; the surface of this tooth is carinate (Fig. 8). The call of this species is given at an elevated rate (in relation to the other two species, nearly 126 syllables/min), each syllable consisting of pulse trains (usually 3–5 pulses/train) at 36.6–38.4 kHz (Fig. 18a, b).

Description

HEAD: Fastigium shorter than that of the other two species (Figs 4–5). **TEGMINA:** Tegmina green pale, with some

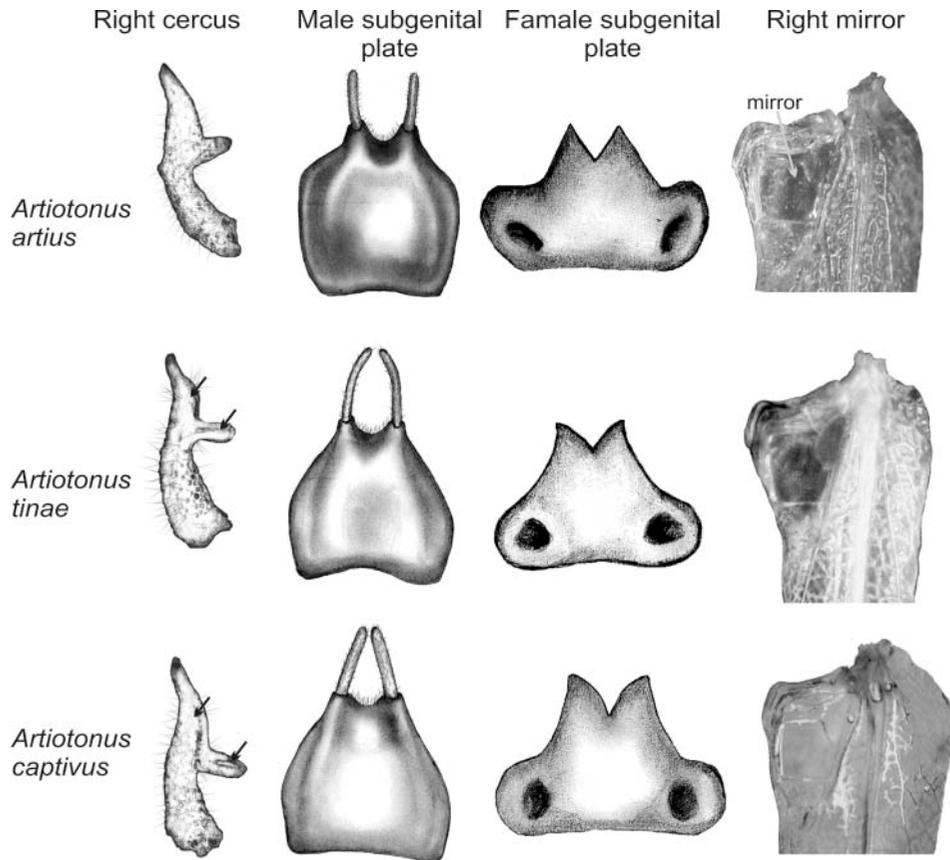
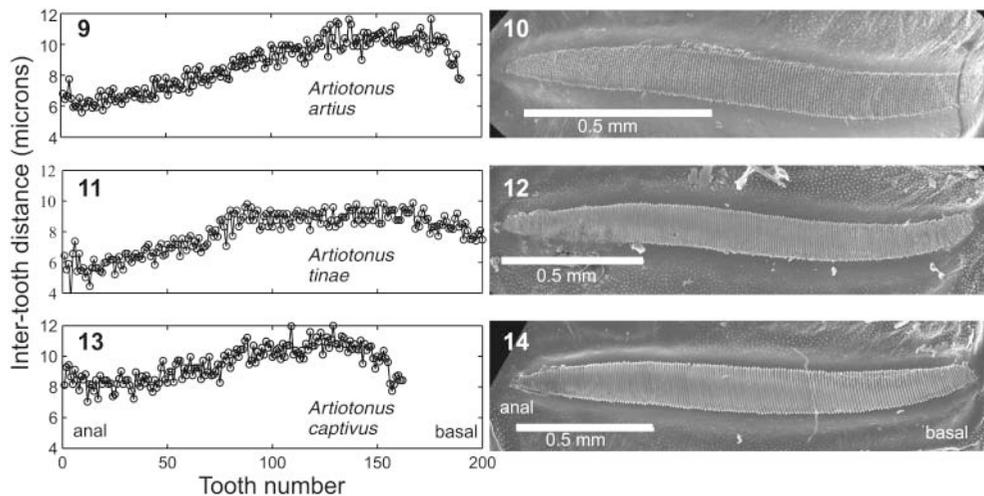


Fig. 8. Relevant morphological characters for identification of *Artiotonus* spp. Black arrows show carinae of cerci.

scattered spotting, barely extending beyond terminalia. Tegminal apices gradually tapering. Female and male similar in coloration and general shape. Stridulatory file (Figs 11, 12, 15) larger than in the other two species (1.7

± 0.05 mm, $n = 7$) comprised of 210–220 teeth (density 123–128 teeth/mm). MALE GENITALIA: subgenital plate basally broad, gradually narrowing, with medial round emargination, bearing elongate styles that converge



Figs 9–14. The stridulatory file of *Artiotonus* spp. 9, 11, 13, Intertooth distance distribution. 10, 12, 14, SEM pictures of the files of the respective species. 9–10, *A. artius*; 11–12, *A. tinae*; 13–14, *A. captivus*.

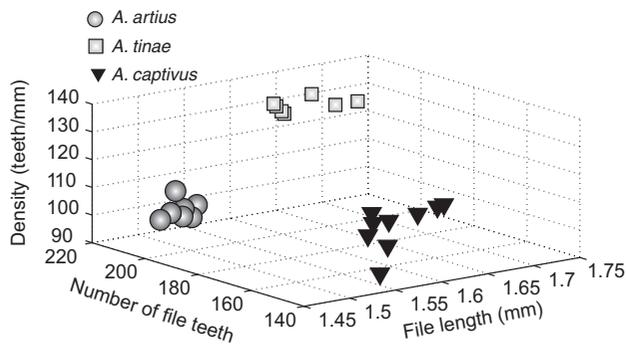


Fig. 15. Three-dimensional representation of three of the variables that dictate the morphology of the stridulatory file in *Artiotonus* spp. Symbols represent species.

medially (Fig. 8). Tenth tergite bilobular, medially broadly incised. FEMALE GENITALIA: Subgenital plate with internal margin of pseudostyli, semicurved, diverging laterally (Fig. 8).

DISTRIBUTION: Known only from type locality (Fig. 15), but probably its distribution extends to other regions of Esmeraldas and to the south part of the Bolivar geosynclines in Colombia.

SONG DESCRIPTION: Analysis based on seven males recorded. The song of *A. tinae* is a pulse train (8.12 ± 0.52 ms, $n = 7$), with 3 to 5 pulses increasing slightly in intensity, these resulting from a discontinuous closing stroke (i.e. both wing and scraper pause during closing) (Figs 18b, 20b). This infrastructure of course has an effect on the central tendency of the spectral peak, reducing (in relation to that of *A. artius*) the Q value of song resonance to 37.9 ± 4.1 ($n = 7$). At 23.5°C , calls are given at a rate of 2.1 per second ($n = 7$, for every specimen a 1-minute song recording was used to determine call rate). Males of this species call continuously for a few minutes (usually 3–6), and calls occur at regular intervals (0.50–0.52 s, Fig. 18a). This pulse rate is high compared with that used by the other two species of the genus, and is one of the critical call parameters to distinguish this species from *A. captivus*. Call intensity was 97.5 ± 0.86 dB (SPL meter operating in fast impulse mode) measured with the microphone directed from 10 cm at the dorsal field of the tegmina ($n = 7$). The spectrum shows only a single frequency peak at 37.82 ± 0.82 kHz ($n = 7$, range 36.6–38.4; Fig. 18e). No harmonic components were found as far up the spectrum as 150 kHz.

As described for *A. artius*, in the laboratory males interacted acoustically and also alternate calls: the song of one evoking an acoustic response from others. Singing males of *A. tinae* were put together in a cage ($30 \times 20 \times 20$ cm) with females of *A. captivus* and were monitored for 9 consecutive days using a camcorder. The females of *A. captivus* were not receptive to those males. The same *A. captivus* females were quickly attracted (first night) only to conspecific males

placed in the same cage. Two females of *A. tinae* and four males of *A. captivus* were also monitored in a similar arena for 7 days, but no compatibility was observed. More data of mating behaviour will help to corroborate that the call is indeed an effective prezygotic isolating barrier between these species.

Artiotonus captivus sp. nov.

HOLOTYPE: 1 ♂ MEUV 23165, 25 Nov. 2009 (Fabio A. Sarria-S).

ALLOTYPE: 1 ♀ MEUV 23166, 25 Nov. 2009 (Fabio A. Sarria-S) (MEUV).

PARATYPES: 1 ♂, 1 ♀ MEUV, 19 Nov. 2009 (Fabio A. Sarria-S). 1 ♂, 1 ♀ MEUV, 25 Nov. 2009 (Fabio A. Sarria-S).

TYPE LOCALITY: COLOMBIA, Dept. Cauca, PNN Island of Gorgona (see area description).

ETYMOLOGY: the specific epithet *captivus* is derived from Latin, *captivus* meaning ‘prisoner’, and refers to the species’ endemism and to the history of PNN Gorgona as a prison.

DIAGNOSIS: *Artiotonus captivus* can be recognized by the genitalia of males and by their calling song. The male cercus bears an internal tooth which projects contralaterally, the surface of this tooth is carinate. The dorsal part of the cercus is also carinate between the internal tooth and the region where the ventral curvature of the tip begins (Fig. 8). The call of this species is given in pulse trains (usually 6 to 8 short discrete pulses) at nearly 43 kHz (Fig. 19a–c).

Description

HEAD: Subocular region with three rounded granules. TEGMINA: Tegmina green pale, with some scattered brown-reddish spots, extending well beyond terminalia. Tegminal apices rounded. Male and female similar in coloration and general shape. Stridulatory file short (1.60 ± 0.05 mm, $n = 7$) with 166–170 teeth (tooth density = 94–112 teeth/mm) (Figs 13–14, 15). MALE GENITALIA: subgenital plate basally broad, gradually narrowing, with medial rounded emargination, bearing elongate styles that converge medially (Fig. 8). Tenth tergite bilobular, medially broadly incised. FEMALE GENITALIA: subgenital plate with internal margin of pseudostyli curved, diverging laterally (Fig. 8). See Table 1 for measurements.

DISTRIBUTION: This species is endemic to the PNN Gorgona in Colombia (Fig. 16) and is undocumented for other locations.

SONG DESCRIPTION: Analysis based on nine males recorded. Males of this species produce a continuous closing stroke with periodic pauses, which generates a train of 7–12 sinusoidal ultrasonic pulses, incrementing in peak amplitude, lasting 12.8 ± 1.7 ms ($n = 9$) (Figs 19b–d, 20c). This pulse infrastructure has an effect on spectral

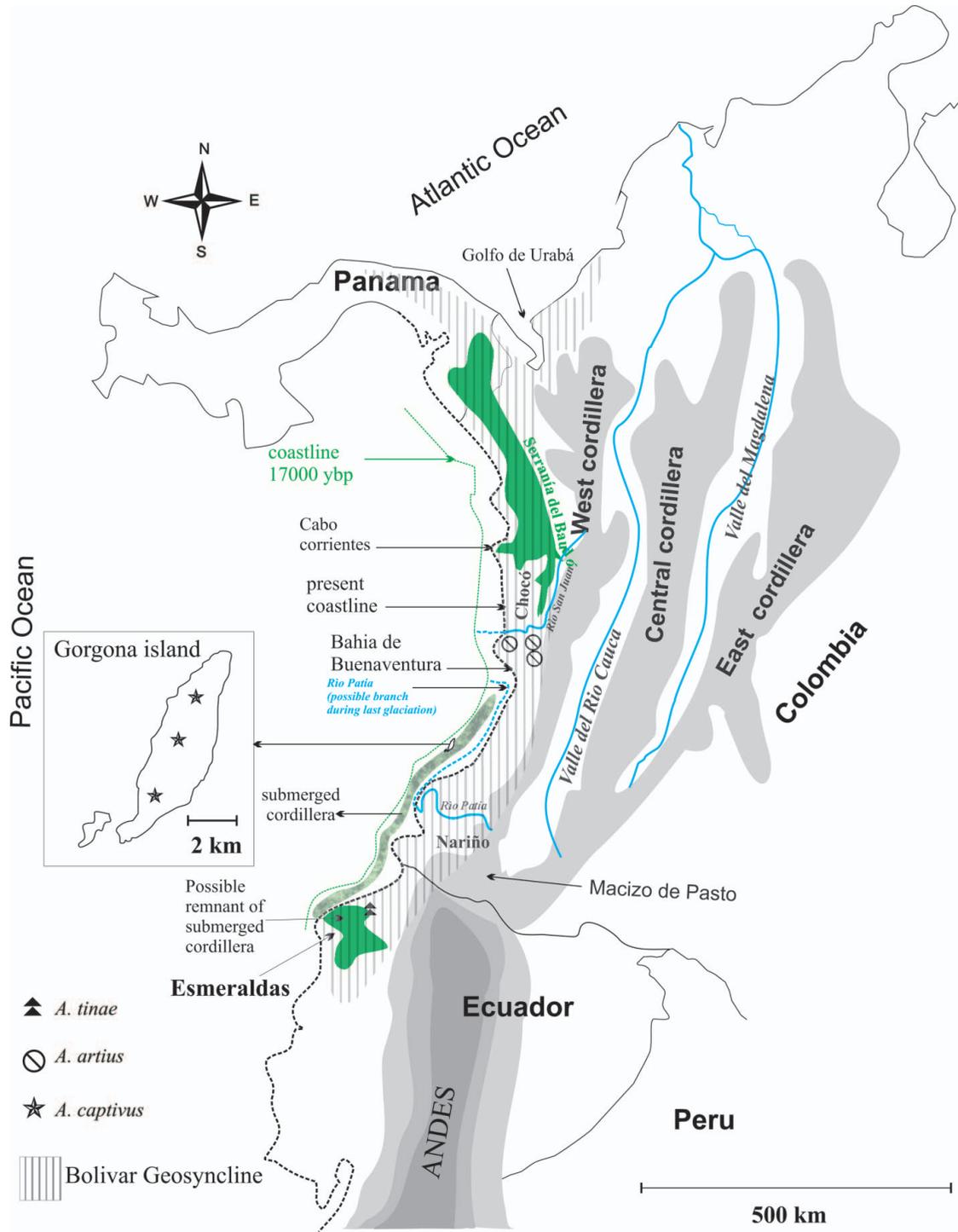


Fig. 16. Geographic distribution of *Artiotonus* spp. in Colombia and Ecuador. The map illustrates the coastline encompassing Gorgona Island during the last glaciation, some 17 000 yBP (green dashed line). The coast was extended more than 30 km from the present coastline (black dashed line) due to a lowering of nearly 120 m in sea level. The Andes and its trifurcation as the present three major cordilleras in Colombia are shown in grey. The Serranía del Baudó was probably part of another cordillera running along the coastal line, which was submerged at the end of the last glaciation. The mountains found in Esmeraldas (Ecuador) are probably remnants of this cordillera. Shaded striped area = Bolivar geosyncline.

Table 2. Some Tettigoniidae species with low and high- Q signals. Species with sonic (1–20 kHz), moderately ultrasonic (20–40 kHz), and extreme ultrasonics (>40 kHz) are included. Note that Q is usually low in those species with extreme ultrasonics. CF = carrier frequency, SD = standard deviation. Col = Colombia, Ec = Ecuador. Pseu = Pseudophyllinae, Cono = Conocephalinae, Mec = Meconematinae, Listr = Listrosclidinae.

Species	Subfamily	CF kHz	SD	Q -value	SD	N	References
<i>Typophyllum mortuifolium</i> (Ec & Col)	Pseu	9.4	0.3	95	11.7	3	Morris <i>et al.</i> (1989, unpublished)
<i>Panacanthus cuspidatus</i> (Ec)	Cono	10.9	0.3	16.0	2.1	2	Montealegre-Z & Morris (2004)
<i>Championica walkeri</i> (Ec/Col)	Pseu	13.3	0.2	49.0	6.4	5	Morris <i>et al.</i> (1989)
<i>Typophyllum bolivarv</i> (Ec)	Pseu	14.0	0.0	39.2	—	1	Morris <i>et al.</i> (1989)
<i>Ischnomela</i> sp. (Col)	Pseu	15.1	0.0	50.0	9.1	6	Unpublished
<i>Trichotettix pilosula</i> (Col)	Pseu	16.9	0.6	17.2	1.4	2	Montealegre-Z & Morris (1999)
<i>Typophyllum</i> sp. 1 (Ec)	Pseu	18.4	0.5	36.3	—	1	Braun (2002)
<i>Typophyllum egregium</i> (Ec)	Pseu	19.2	0.9	18.3	—	1	Braun (2002)
<i>Typophyllum zingara</i> (Col)	Pseu	19.7	0.0	45.0	2.3	1	Montealegre-Z & Morris (1999)
<i>Typophyllum nr. trapeziforme</i> (Ec)	Pseu	20.5	0.0	20.2	—	1	Braun (2002)
<i>Copiphora gracilis</i> (Ec)	Cono	20.6	0.7	29.0	2.3	2	Unpublished data
<i>Typophyllum</i> sp. 205 (Col)	Pseu	20.6	0.0	47.0	9.6	2	Unpublished data
<i>Diacanthodis granosa</i> (Col)	Pseu	21.4	0.0	25.0	0.7	1	Unpublished data
<i>Eubliastes aethiops</i> (Col)	Pseu	21.6	0.8	8.5	1.2	7	Unpublished data
<i>Docidocercus gausodontus</i> (Col)	Pseu	22.5	0.0	22.9	2.5	7	Montealegre-Z & Morris (1999)
<i>Docidocercus gigliotosi</i> (Panama)	Pseu	23.0	0.0	24.7	0.3	3	Morris <i>et al.</i> (1994)
<i>Typophyllum trapeziforme</i> (Ec)	Pseu	23.2	0.0	54.3	—	1	Morris <i>et al.</i> (1989)
<i>Docidocercus chlorops</i> (Ec)	Pseu	24.0	0.0	25.3	1.1	1	Morris <i>et al.</i> (1989)
<i>Daedalus</i> sp. (Col)	Cono	33.0	3.1	10.1	0.8	3	Unpublished data
<i>Artiotonus tinae</i>	Cono	36.0	0.0	37.9	4.1	2	This paper
<i>Uchuca amacayaca</i> (Col)	Cono	36.6	0.0	18.2	1.1	2	Montealegre-Z & Morris (2003)
<i>Artiotonus artius</i>	Cono	40.7	0.1	42.6	1.3	2	This paper
<i>Uchuca halticos</i> (Ec)	Cono	42.3	0.0	33.4	3.3	7	Montealegre-Z & Morris (2003)
<i>Artiotonus captivus</i>	Cono	43.1	1.6	39.3	1.6	9	This paper
<i>Phlugis</i> sp. 2 (Ec)	Mec	47.6	0.0	14.8	—	1	Unpublished data
<i>Eschatoceras</i> sp. (sp. 0242, Col)	Cono	64.0	0.0	27.0	—	1	Unpublished data
<i>Haenschiella</i> sp. 1. (Ec)	Pseu	66.0	0.0	3.3	—	1	Morris <i>et al.</i> (1994)
<i>Drepanoxiphus angustelaminatus</i>	Pseu	73.0	0.0	7.6	—	1	Morris <i>et al.</i> (1994)
<i>Arachnoscelis arachnoides</i>	Listr	74.5	3.4	6.1	4.5	5	Unpublished data
<i>Myopophyllum speciosum</i> (Ec)	Pseu	83.3	4.8	8.3	2.8	4	Morris <i>et al.</i> (1994)
<i>Haenschiella</i> sp. 2. (Ec)	Pseu	105.5	1.7	8.7	0.7	1	Morris <i>et al.</i> (1994)
<i>Arachnoscelis</i> sp. (Col. Mainland)	Listr	129.0	5.5	14.8	3.5	2	Montealegre-Z <i>et al.</i> (2006)
<i>Arachnoscelis</i> sp. (Col. Gorgona)	Listr	148.0	0.0	17.1	2.2	6	Unpublished data

sharpness, gently reducing (in comparison with that of *A. artius*) its Q value to 39.3 ± 1.6 ($n = 9$). Sound level was 90.56 ± 1.42 dB (SPL meter operating in fast impulse mode) as recorded at 9 cm with the microphone directed at the dorsal field of the tegmina ($n = 9$). The spectrum peaks at a single frequency 43.1 ± 1.6 kHz (23.5°C , $n = 9$, range 41.2–44.7.0 kHz; Fig. 19e). No harmonics are seen within 30 dB of the carrier peak. At 23.5°C , calls are given at a rate of 14.44 ± 2.13 calls/min (= 0.24 calls/s). Within intervals of one minute, call timings were more or less random for all animals recorded, i.e. no particular call organization was observed (Fig. 19a).

Males interact acoustically with alternating calls, and the song of one male evokes an acoustic response from other males. Females are easily attracted to calling males and obtaining offspring is relatively easy. In the laboratory, we randomly observed for nearly 2 months (monitoring with a camcorder overnight) five females all responding to the call of seven different conspecific males. Four of these females

were promiscuous and copulated with various males on different days.

Discussion

With only three species, our phylogenetic analysis of the genus *Artiotonus* is necessarily brief, producing only a single most parsimonious tree. But even the most minimal of phylogenetic analyses can raise many new questions (though see Kumala *et al.*, 2005).

Of the three *Artiotonus* species, excepting only the structure of the stridulatory file (Figs 9–15), no species has undergone extensive morphological and/or behavioural divergence. These three are differentiated by a few morphological traits, but mostly by stereotypic song characters, especially the temporal structure of the call (Fig. 21). A few autapomorphies of morphological and acoustic characters define each species. *Artiotonus artius* is distinguished by the internal asymmetric tooth on its cercus (Fig. 8), and

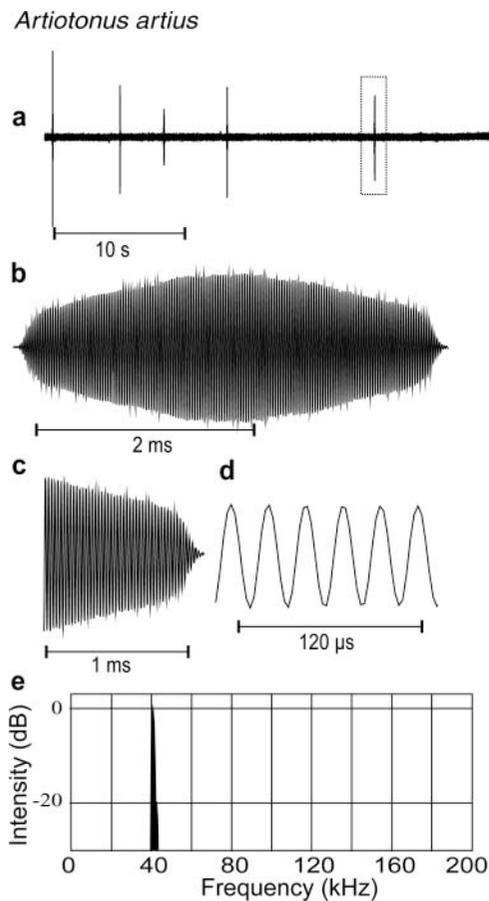


Fig. 17. Calling song features of *Artiotonus artius*. **a.** Temporal component of the song displayed in 35 s. **b.** A single call made during a closing stroke of the wings (rectangle in **a**, see also Fig. 20). **c.** Last segment of the call at high resolution. **d.** High resolution of the pure tone wave form taken from **c**. **e.** Power spectrum of the call in **b**.

a low call rate [33(2)]. *Artiotonus tinae* possesses smaller body size (this trait not being included in the analysis) and short acuminate tegmina [8(1)]. *Artiotonus captivus* can be identified only by call rate [32(1)].

In our analysis, call rate [33(1)] is homoplastic between *Copiphora* and *A. tinae*, but this character might be difficult to evaluate since call repetition rate evolved many times in tettigoniids (Heller, 1988, 2006). Better polarization and coding might result if some other relevant acoustic patterns were combined with this character (e.g. call rate with carrier frequency or some other related feature of the call). In this way, the elevated call rate observed in *A. tinae* might become inapplicable to *Copiphora*, thus becoming autapomorphic for *A. tinae*.

Biogeography

Artiotonus spp. inhabit strategic zones of the Bolivar geosyncline in Colombia and Ecuador that have undergone

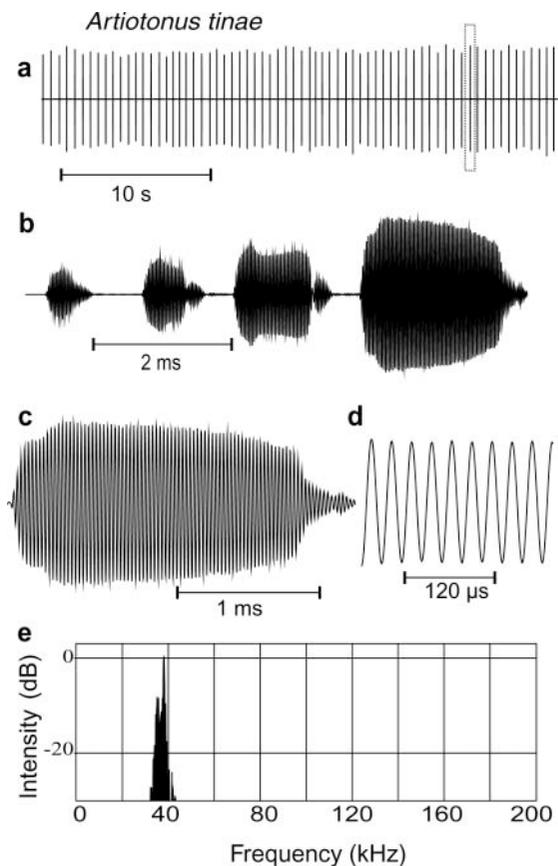


Fig. 18. Calling song features of *Artiotonus tinae*. **a.** Temporal component of the song displayed in 35 s. **b.** A single call made during a closing stroke of the wings (rectangle in **a**, see also Fig. 20). **c.** Last segment of the call at high resolution. **d.** High resolution of the pure tone wave form taken from **c**. **e.** Power spectrum of the calls in **b**.

dramatic changes (Fig. 16). Most geological and biogeographic studies of the zone suggest that Gorgona is, from all points of view, a continental 'small island' (Gansser, 1950), and that some 17 000 yr BP this island was connected to the continent as part of a chain of mountains skirting the Pacific coast of Colombia and Ecuador (Fig. 16) (Pregill & Olson, 1981; Alberico, 1986). During the Pleistocene, in times of low temperatures, large glaciers covered the peaks of high mountains in the tropics; this produced a considerable decrease in the sea level. During the last glaciation, 17 000 yr BP, sea level decreased by some 120 m (Pregill & Olson, 1981). Withdrawal of the sea was enough to connect Gorgona with the rest of the continent.

Gorgona, as an integral part of a continuous 'green carpet' from the Choco southward to the Ecuadorian coast, would facilitate dispersion of species in this area. But, geological studies suggest this connection did not occur directly between Gorgona and the Colombian coast opposite the island (i.e. the Serrania del Baudo and the part of Valle del Cauca's coast near the Buenaventura area, Fig. 16) (Ayala *et al.*, 1979; Alberico, 1986).

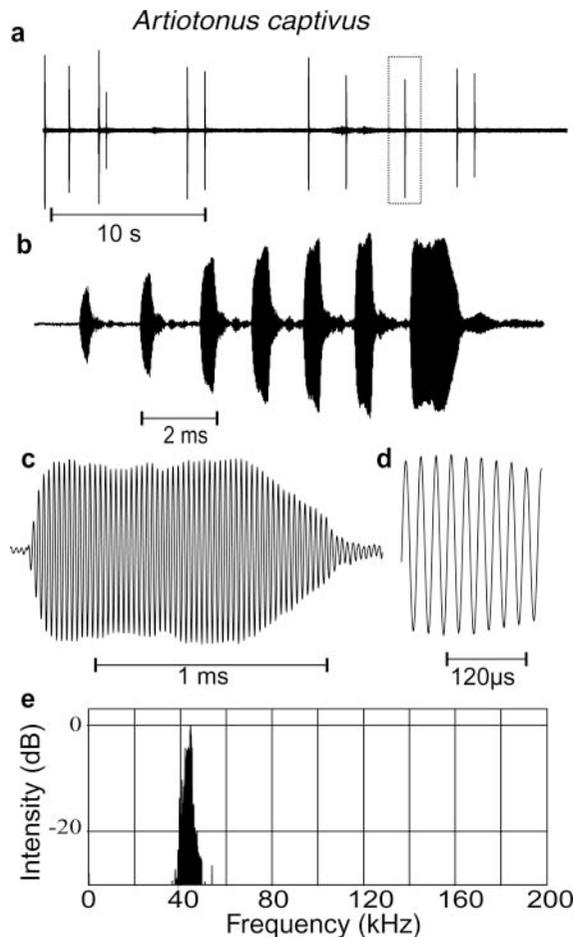


Fig. 19. Calling song features of *Artiotonus captivus*. **a.** Temporal component of the song displayed in 35 s. **b.** A single call made during a closing stroke of the wings (rectangle in **a**, see also Fig. 20). **c.** Last segment of the call at high resolution. **d.** High resolution of the pure tone wave form. Power spectrum of the calls in **b**.

One theory (Alberico, 1986) suggests that a narrow valley occurred between the vanished coastal cordillera and the present-day west cordillera, and that of course this valley was drained by a river system (Fig. 16). This vanished system was probably a larger portion of the Patía river drainage (which, at present, outfalls on the Pacific Ocean at Departamento de Nariño). In Alberico's model this lost river ends near Bahía de Buenaventura, on the coastline of 17 000 yr BP (Fig. 16), creating a biological barrier between Gorgona (and the surrounding exposed land), and the area south to Serranía del Baudó, but allowing species between Esmeraldas and Gorgona to interact by a direct corridor (Fig. 16).

The two present disjunctive areas (Esmeraldas and Gorgona) were connected by a prevailing emerging corridor. During the Holocene transgression most of this coastal corridor was immersed, leaving only the highest peaks of the mountains (such as Gorgona and those in the Esmeraldas

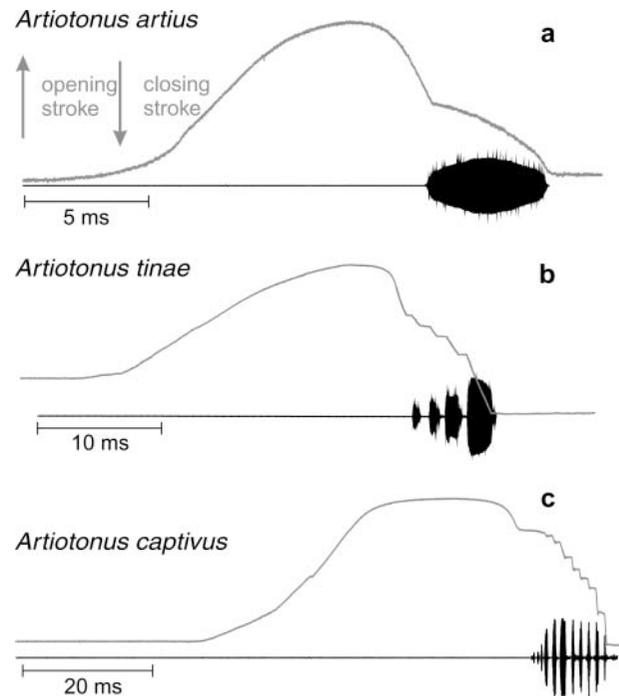


Fig. 20. Song production (calls in black trace) and associated motor pattern (grey trace) in *Artiotonus* spp. Arrows indicate the direction of opening and closing wing strokes during sound production.

area) exposed. This flooding also caused the Patía River to lose its north curvature or branch and end earlier at the coast in Nariño (Fig. 16). But this river branch might not have been a strong barrier against insects such as *Artiotonus*' ancestors, insects able to perform some modest-distance flights (see below).

Collected data favour an allopatric origin of *A. tinae* and *A. captivus* in Gorgona and Esmeraldas. Congeners of other katydid species (mostly flightless), and of other organisms (Alberico, 1986), also occur in both regions (see Tables 3 and 4; for Table 4, see supplementary material which is available on the Supplementary Content tab of the article's online page at <http://dx.doi.org/10.1080/14772000.2011.560209>). Interestingly, in some cases the same (putative) species are found in both localities, but with distinctive features marking them as perhaps intraspecific variations at the population level (Tables 3 and 4).

The morphological similarity of the three species, taken with the fact that they can be separated reliably only by song features, suggests relatively recent speciation. Here we explore three scenarios (two speciation scenarios: points 2 and 3 below) in *Artiotonus* spp., especially as they might have occurred between the two most cryptic species *A. tinae* and *A. captivus*.

Scenario 1. The two populations (known as *A. tinae* and *A. captivus*) in their present forms are not biospecies, but

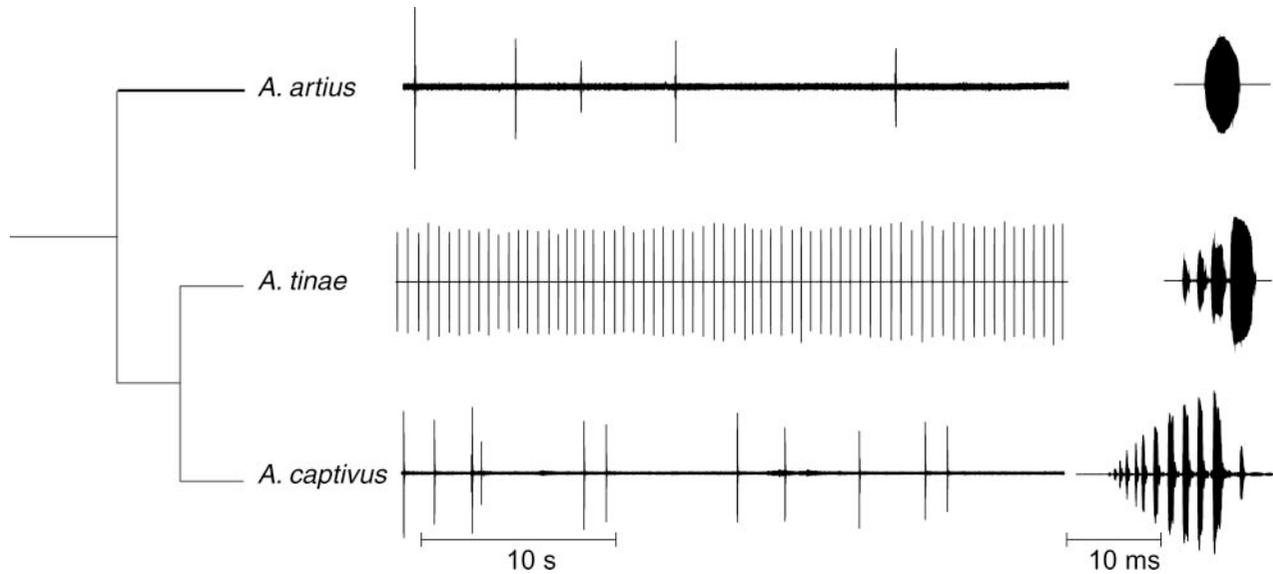


Fig. 21. Evolutionary path of the temporal component of the calling song in the genus *Artiotonus*. The production of longer pulse trains seems to have been an evolutionary tendency in this genus.

represent only a case of intraspecific variation at the level of populations.

Scenario 2. *Artiotonus captivus* and *A. tinae* may have been the result of a recent speciation process that began with the Holocene transgression some 11 500 yr BP. One plausible hypothesis is that the range of the ancestral species was comprised of the two presently disjunctive areas (Esmeraldas and Gorgona) and the prevailing connecting corridor. This hypothesis implies a fast speciation process of nearly 50 species per million years.

Scenario 3. Divergence between the two forms began prior to contact, i.e. the two forms (*A. tinae* and *A. captivus*)

are older; their isolation happened during one of the earlier glaciations. Speciation may have been driven by ecological factors, for example, if the two isolated populations evolved traits that allowed them to exploit different resources in their new environments.

Alternatively scenario 1 can be discarded, as we have shown here that there are remarkable differences in pulse rate pattern of the calls of *A. tinae* and *A. captivus* (Fig. 21), a secondary sexual trait widely used in ensiferan mate attraction. [Subtle differences in pulse rate are critical in speciation of other acoustic Ensifera inhabiting island ecosystems (e.g. Mendelson & Shaw, 2002, 2005).] The two forms

Table 3. List of species allopatrically distributed in the three geographic regions studied in the present paper. *, Canopy dwellers, possibly able to perform long flights; †, endemic species. OSF = Orthoptera Species File (<http://orthoptera.speciesfile.org/>).

Genus	Geographic location in Ecuador and Colombia			References
	Esmeraldas	PNN Gorgona	nearby Buenaventura	
nr. <i>Arachnoscelis</i>	nr. <i>Ara.</i> sp. 1	nr. <i>Ara.</i> sp. 2 †	nr. <i>Ara.</i> sp. 3	Montealegre-Z <i>et al.</i> (2006, this paper)
<i>Artiotonus</i>	<i>A. tinae</i>	<i>A. captivus</i> †	<i>A. artius</i>	This paper
<i>Panacanthus</i>	<i>P. varius</i>	<i>P. varius</i> (subsp.)	<i>P. intensus</i> , <i>P. lacrimans</i>	Montealegre-Z & Morris (2004)
<i>Copiphora</i>	<i>C. brevicauda brevicauda</i>	<i>Copiphora gorgonensis</i> †	<i>C. brevicauda brevicauda</i> , <i>C. brevirostris</i>	OSF, Montealegre-Z & Postles (2010)
<i>Ischnomela</i>	<i>Ischnomela</i> sp.	<i>I. gracilis gracilis</i>	<i>I. gracillima</i>	Montealegre-Z (1997)
<i>Championica</i>	<i>Ch. walkeri</i>	<i>Ch. Walkeri</i> (subsp.)	<i>Championica</i> spp.	Montealegre-Z & Morris (1999)
<i>Eubliastes</i>	<i>Eu. festae</i>	<i>Eu. Aethiops</i> (subsp.)	<i>Eu. Aethiops</i>	Montealegre-Z <i>et al.</i> (2006)
<i>Triencentrus</i>	<i>Tr. atosignatus</i>	<i>Triencentrus</i> sp. †	<i>Triencentrus</i> sp. 2	Montealegre-Z & Morris (1999)
<i>Docidocercus</i>	<i>D. chlorops</i>	<i>D. chlorops</i> (subsp.)	<i>D. gausodontus</i>	Montealegre-Z & Morris (1999)
<i>Xestoptera</i> *	?	<i>Xestoptera</i> sp.	<i>X. cincta</i>	Montealegre-Z (1997)
nov. gen. A	nov. gen. A sp.1	nov. gen. A sp. 2	nov. gen. A sp. 3	Unpublished data
nr. <i>Uchuca</i>	nr. <i>Uchuca</i> sp.1	nr. <i>Uchuca</i> sp. 2	?	Unpublished data

(*A. tinae* and *A. captivus*) also differ in the structure of their files and in the neuro-muscular mechanism controlling stridulatory patterns (Figs 15, 20). Some empirical observations of sex compatibility between individuals (males and females) of both groups also imply that the calling song is a barrier to reduce inter-breeding. These differences are adequate to suggest that both forms are indeed two biospecies.

Considering alternatives 2 and 3, it is known that cryptic species of other arthropods have been observed and studied in more complex island ecosystems. Mendelson & Shaw (2005) showed a high speciation rate, 4.17 species per million years, in a monophyletic clade of the cricket genus *Laupala* from Hawaii Island – a high speciation rate, compared with the average estimated rate of arthropod speciation (0.16 per million years; Coyne & Orr, 2004). Closely related species of *Laupala* are morphologically cryptic, have no ecologically distinguishable features, and are distinguishable only in the pulse rate of their male courtship song (Parsons & Shaw, 2001; Mendelson *et al.*, 2004; Mendelson & Shaw, 2005). Mendelson & Shaw (2005) suggested that the forces responsible for such a high speciation rate in *Laupala* are those that cause the evolutionary divergence of secondary sexual traits (calling song in this case). Other mechanisms of speciation (e.g. ecological speciation) were said unlikely to explain speciation in this group, because ecological traits adapted to novel environments do not distinguish *Laupala* spp.

The available evidence so far suggests that the evolution of the present forms of *A. captivus* and *A. tinae* did not occur during isolation by the last glacier (i.e. a fast rate of speciation). These two species both inhabit different ecosystems, an island and a forest patch on the continent, respectively. There are a few species and subspecies of katydid and other organisms (including vertebrates) endemic to the island of Gorgona with congeners in the Esmeraldas region (Alberico, 1986; see also Table 4, see supplementary material, which is available on the Supplementary Content tab of the article's online page at <http://dx.doi.org/10.1080/14772000.2011.560209>), which suggests that reproductive isolation between the two populations started to build in allopatry, probably before the last ice age. Species colonization (migration from the continent to the island) is unlikely to have occurred, because the chance that these species (and those of other invertebrates and vertebrates documented by Alberico, 1986), have used similar means of dispersion to 'colonize' Gorgona is very small. Their presence in Gorgona is not mere coincidence, and allopatry is the best model to explain it. Below, we suggest a model of speciation that the *Artiotonus* spp. might have followed.

The present distribution of *Artiotonus* spp. could be explained by migration of individuals of the ancestral species across Alberico's (1986) Patia River branch from the Buenaventura region to the fourth cordillera. Travelling a few metres on fresh water between riversides seems to be more

plausible than dispersing on the sea for a terrestrial insect. Accepting this hypothesis, the ancestral species was divided into two populations, each distributed on both sides of the river: one on the Buenaventura side of the Patia River branch (north side), and the other on the connecting land side of the river (south side). The population isolated on the south side might have produced the ancestor of *A. tinae* and *A. captivus* after complete seclusion from the original population (i.e. no connection through the river) and a possible fragmentation of the new area of distribution on the south side of the river. The area of distribution of this population might have been fragmented by some geological event prior to the last glaciation, permanently isolating two large groups of the south population. The two populations might have accumulated adaptations to unique aspects of their new environments. A possible secondary contact during the maximum of the last ice age could have occurred, premating isolation being then completed by reinforcement after sympatry (Schluter, 2001). The original population on the north part of the river might have eventually evolved to what we know as *A. artius*. The current distribution of animal species in both localities (Tables 3 and 4), and the fact that *A. captivus* and *A. tinae* are relatively similar morphologically with a few differences in their acoustic behaviour, fits within this allopatric model.

The biogeography of *A. captivus* and *A. tinae* might become better understood if other species of animals endemic to Gorgona are studied with a similar perspective, for instance, the blue lizard *Anolis gorgonae* and its sister species *A. chloris* (widely distributed in the Bolivar geosyncline). Unfortunately, little work has been done on these species and almost nothing is known about their speciation and biogeography (Losos, 2009; J. Losos, 2010, pers. comm.). Hence the perspectives presented above should remain as speculative, based on the available evidence.

Evolution of sound and wing motion patterns

Sexual signals such as the calling songs used by many Ensifera may be both selected as species-specific identifiers and subject to sexual selection (Gwynne, 1982, 2001; Ryan, 1988; Ryan & Keddy-Hector, 1992; Mendelson & Shaw, 2005). In such a process, it is expected that sexual signals are more distinct in sympatry than in allopatry, i.e. in sympatry character displacement should be common to reinforce species differences (Fitzpatrick & Gray, 2001; Izzo & Gray, 2004; Gray, 2005). In some groups of tettigoniids, differences in song or morphology between isolated allopatric populations of members of a single clade are typically smaller than differences between widespread sympatric species (Heller *et al.*, 2006). Contrary to what Heller (1988, 2006) observed in the genus *Parnassiana* (in which all species underwent allopatric speciation, and the sound

is not useful for species differentiation), in *Artiotonus* one of the most useful characters for species recognition is the temporal component of the call. Only minor morphological differences occur among species.

In *Artiotonus* spp. differentiation in calling song pattern probably began during the allopatric phase prior to the last glaciation. Biotic and abiotic elements of habitat (e.g. climate, resources and physical structure) as well as interactions with other species (e.g. resource competition, predation and various forms of interspecific interference), might have affected the mechanism of sound signalling, which could lead to the divergence observed (Schluter, 2001). Our analysis suggests that the call evolved from very regular, relatively long-duration (sustained) pulses (such as those used by *A. artius*), to shorter pulses grouped into longer pulse trains such as those used by *A. tinae* and *A. captivus* (Fig. 21). Both these latter species produce a discontinuous closing stroke, which ends in pulse trains of different duration in each species. Song structure went from a simple single-pulse wave to trains of pulses. Amplitude modulation became more complex with the addition of silences between several shorter wave trains in succession. The general motor stridulation pattern suggests that the ancestral wing motion could have been similar to that currently used by males of *A. artius*. This pattern diverged to incorporate discrete pulses in the calls of isolated populations. Discrete pulses make the call last longer, as observed in *A. tinae* and *A. captivus*. Between these two species, *A. tinae* exhibits the shortest call, while in *A. captivus* the syllables last longer. Therefore both species might have evolved different mechanisms to increase the chance of attracting distant females: in *A. tinae* an incremented duty cycle was selected, while in *A. captivus* selection favoured lengthening the duration of the syllable (see Fig. 21). The low duty cycle observed in *A. captivus* might be symplesiomorphic with that of the ancestor.

Evolving a sound signal that is a pulse train can be considered as incorporating silent intervals into the syllable, thus producing longer syllables. In Tettigoniidae, syllable duration is positively correlated with stridulatory file length (Montealegre-Z, 2009), therefore the stridulatory files and tooth organization can be morphological markers of selection for longer syllables. In fact, the structure of the stridulatory file (file length, tooth number and tooth density) is the only reliable morphological character that has diverged in the three *Artiotonus* spp. (Fig. 15). In *Artiotonus*, the observed changes in pulse duration and envelope are smoothly associated with discrete increments in file length. *Artiotonus artius* produces a very short syllable and the file is the shortest of all species (1.4 mm). In the other two species the files are a bit larger (*A. tinae* = 1.7 mm and *A. captivus* = 1.6 mm), and both produce longer syllables. For small delicate insects (as *Artiotonus* spp.) with short stridulatory files, even a small change in file length of 0.1–0.2 mm

might represent considerable alteration of the syllable duration.

The distribution and spacing of teeth in all species of *Artiotonus* follows the pattern of files adapted for producing pure tones: inter-tooth spacing gradually increases from the anal to the basal file ends (Bennet-Clark, 2003; Montealegre-Z, 2005; Montealegre-Z & Mason, 2005; Prestwich & O'Sullivan, 2005). This type of file is usually designed for continuous scraper sweeps (e.g. the file of *A. artius*). Files adapted for a discontinuous closing stroke as those of *A. tinae* and *A. captivus* are usually different. Tooth spacing in katydid species using pulse trains is more erratic or at least does not follow a systematically increasing pattern (Montealegre-Z, 2005; Montealegre-Z *et al.*, 2006). This tendency can be easily observed in the genus *Panacanthus* (Montealegre-Z & Morris, 2004; Montealegre-Z & Mason, 2005). In *A. tinae* and *A. captivus* the tooth spacing increases along the file, but in a more erratic way than in the file of *A. artius*. The files of these two species might still preserve the typical feature for continuous scraper movement, while the production of discrete pulses results from a change in the neuromuscular mechanism to close the wings.

The incorporation of silent intervals (i.e. conversion into pulse trains) might have been selected as an alternative for lengthening the effective duration of the signal. As mentioned above, file length is highly correlated with pulse duration, and intertooth distance and the speed of the closing stroke affects the frequency of the call (Montealegre-Z *et al.*, 2006; Montealegre-Z, 2009). Thus a fast closing stroke in a short file usually ends in a pulse of short duration (e.g. *A. artius*; Figs 17a, b, 18a). The female sensory system probably cannot encode pulse durations in the range 1–3 ms (Rossler & Schul, 1993). The incorporation of regular scraper pauses during the closing stroke therefore increases the duration of the syllable, as observed in the *A. tinae* and *A. captivus* (Fig. 17b, c).

An emerging question: why not go to groupings of the longer pulse in time, i.e. coarser amplitude modulation? It might be more physiologically demanding to use an elevated rate of syllables (as that of *Neoconocephalus*) (Josephson & Halverson, 1971; Deily & Schul, 2004) in small insects as *Artiotonus* spp. Similar call features (low duty cycle and the purity of ultrasonic calls) have also been observed in the Australian genus *Kawanaphila*. Males of *K. yarraga* produce a short train of four brief (<0.5 ms) sinusoidal pulses at about 40 kHz; likewise in *Artiotonus* spp., several males interact singing in synchrony (Mason & Bailey, 1998).

The fact that *Artiotonus* spp. exhibit both types of syllable (continuous and pulse trains), and that all three species (known so far) exhibit a remarkable drastic reduction of pulse rates in the high ultrasonic range, makes this genus a suitable model for the study of sexual selection, signal evolution and neurophysiology.

Except for the faster syllable rate adopted by *A. tinae*, the similarity in the call between *A. tinae* and *A. captivus* and the similarity in the stridulatory file tooth spacing (in spite of different temporal patterns) support an allopatric speciation process in this genus. If the calling song of *Artiotonus* has followed a similar path to that of *Panacanthus* (i.e. evolved from a pure-tone sustained pattern; Fig. 20), the similarity in the distribution of file teeth with increasing spacing suggests a recent divergence of gene flow in these species after geographic separation. The stridulatory file of *A. tinae* and *A. captivus* might be experiencing transitional change to adapt tooth spacing and tooth distribution to the production of pulse trains (discontinuous closing strokes). For instance, the song syllables produced by *A. captivus* are longer than those of *A. tinae*, incorporating more discrete pulses and more silent intervals. But curiously tooth density in *A. captivus* has been reduced (106 teeth/mm) at the expense of increasing inter-tooth distances (see Figs 9–10, 15) in relation to the other species.

It seems that at low frequencies, or at moderate ultrasonic calls, the sound purity can be more accurately controlled than at extreme frequencies (Morris *et al.*, 1994; Montealegre-Z *et al.*, 2006). Most katydid species known to use extreme pure-tone ultrasounds tend to have relatively low Q values (Table 2) and this seems to be linked to the mechanism of stridulation used by species singing above 40 kHz. With a few exceptions, there is a consistent tendency to produce pulse-train calls in species communicating at extreme ultrasounds (Morris *et al.*, 1994; Montealegre-Z *et al.*, 2006). At very high frequencies there are limitations of minimum tooth spacing and maximum wing closing stroke to maintain the necessary tooth impact rates, so these species have to use short bursts of elastic energy (Montealegre-Z *et al.*, 2006).

Adaptiveness of an ultrasonic high Q

All the species in this genus and in particular *A. artius*, with its single sustained pulse per syllable, are unusual in producing an ultrasonic note of extreme purity. Its Q value of 42.6 is remarkably larger than the Q calculated for 12 other katydids that use extreme ultrasonic (i.e. >40 kHz) and tonal calls (Table 2). The carrier frequencies of all three species fall within 7 kHz of each other. These excessively narrow-peaked carriers all lie between 36 and 42 kHz. Mirror dimension is correlated with carrier frequency (Morris & Pipher, 1967; Bailey, 1970; Sales & Pye, 1974; Montealegre-Z, 2009), but since carrier frequency does not change dramatically within species of *Artiotonus*, no structural change would be expected in mirror morphology or dimension, which is the case here. Thus, changes in file morphology and perhaps more importantly, the neuromuscular components of the closing stroke (Fig. 20) might form the basis for song differentiation and speciation in this genus. This effect has been well documented in species with high

pulse rates. For instance, in two sister species of the genus *Neoconocephalus* a delay in the closing stroke of the wings in one of them transformed a single pulse rate into a double-pulse rhythm and could have led to the divergence of both species (Deily & Schul, 2004).

What might be the adaptive basis of these high- Q signals? Three possibilities are suggested. (1) It is an effect, a non-adaptive product of selection acting upon other features. (2) It is the product of natural selection for phase-based unilateral localization. (3) It is a secondary sexual character (analogous for example to the plumage of many male birds) resulting from the sexual selection brought about by females that benefit by preferring a higher Q .

High- Q (narrowly tuned) peaks in the low audio range are a localization adaptation for field crickets: the ability of a cricket female to determine the direction of sound arriving from a conspecific male relies on this high- Q peak, a pressure difference receiver system that is based upon achieving critical phase relationships of narrowly tuned waves (Michelsen *et al.*, 1994; Michelsen, 1998). These differences in sound arrival, front and rear to an eardrum of one side, could translate into differences in ear neural activity that change with the insect's changing orientation to the sound source. Sound from a singing katydid male goes to the front of the female's eardrums of one body side and also via the ipsilateral acoustic spiracle down the leg trachea to the eardrums' rear (reaching the rear in a different phase). This phase will change as the insect changes the direction in which it faces and path-length changes. The proportion of path length change needed to effect a significant phase shift is less for shorter (40 kHz) wavelengths than for 5 kHz (crickets) wavelengths. Phase-mediated localization is still a hypothesis to consider for the unilateral pressure gradient katydid ear. Perhaps other things are involved in localization such as body diffraction, which is greater for short wavelengths (with small body dimensions). This could favour high frequencies in small animals; the other changes are adaptations to produce high ultrasound efficiently. But if phase changes with orientation, and plays a role in localization unilaterally, then keeping a stable single-frequency wave (Figs 17d, 18d, 19d) to achieve a better phase differences makes localization function a possible adaptive basis of *Artiotonus*' high Q .

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