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On the bioacoustics of the Iberian Ephippigerini (Orthoptera, Tettigoniidae, Bradyporinae)

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The bioacoustics of 24 taxa of the Ephippigerini (Tettigoniidae, Bradyporinae) from the Iberian Peninsula is described and illustrated. The special communication of the genus *Platystolus* Bolívar, 1878, which consists of three parts (the male initial song, female response and male confirmatory response), was found to be present in seven additional species of the Ephippigerini: *Albarracinia zapaterii* (Bolívar, 1877), *Callicrania plaxicauda* Barat, 2007, *Lluciapomaresius nobrei* (Bolívar, 1898), *L. ortegai* (Pantel, 1896), *L. panteli* (Navàs, 1899), *L. stalii* (Bolívar, 1877) and *Parasteropleurus perezii* (Bolívar, 1877). Furthermore this behavioral characteristic was deduced for *Uromenus maroccanus* (de Saussure, 1898) from the existence of the male «spontaneous confirmatory response», which constitutes an accessory shortened and usually modified echeme, appended to the initial song without a preceding female response. The benefits of the special duetting of the Ephippigerini with the use of confirmatory responses are discussed; conclusions are drawn on its evolution and secondary reduction in different lines.

Keywords: Tettigoniidae, Ephippigerini, bioacoustics, communication, evolution

INTRODUCTION

The Ephippigerini constitute a group of the Tettigoniidae, which is represented especially on the Iberian Peninsula with a considerable large number of species. However, our knowledge of the actual taxon-validity, the geographic range and the ecological-biological peculiarities of many species is rather incomplete. In recent times mainly the efforts of Peinado (1990a, b, 1992), Peinado & Mateos (1985) and Barat (2004, 2007, 2012, 2013) revealed many taxonomic alterations, the discovery of new taxa (e.g. Fig. 2a) and the retrieval of species which had got lost (e.g. Fig. 12a). The re-evaluation of characters resulted in a preliminary revision of the whole group and in improved identification-keys (Barat 2007, 2012).

Since 1981 we have undertaken several excursions through Spain and Portugal, mainly for gathering bioacoustic data of representatives of special genera of the Ephippigerini and Bradyporini: *Platystolus* *Platystolus* Bolívar, 1878, *Platystolus Neocallicrania* Pfau, 1996 (*Callicrania* Bolívar, 1898, *Platystolus* Bolívar, 1878, *Neocallicrania* Pfau, 1996 and *Synephippius* Navàs, 1905 in Barat 2012) and *Pycnogaster* Graells, 1851; the results are summarized in different publications (Schroeter & Pfau 1987; Pfau & Schroeter 1988a, b; Pfau 1988, 1996; Pfau & Pfau 1995; Pfau *et al.* 2014).

The science progresses in the meantime, as mentioned above, inspired us to review the whole material of our excursions (specimens, audio tapes and diaries) for the presence of «bycatches» of additional Ephippigerini and sound registrations. Since previous investigations already pointed to a more extended existence of the

special duetting of the Ehippigerini (Pfau & Schroeter 1988a, Pfau 1996), particular attention was paid to the presence of «antiphonies» between males and females. In addition to the bioacoustic findings, interesting observations, which have been noted in our diaries, are included. The (preliminary) taxonomic revision of Barat (2012) was used as a basis in the present paper.

MATERIAL AND METHODS

In general, the collected animals were kept in small cages of metal grid (11x11x13 cm and 8.5x9x10 cm), which showed only small echo effects of the recorded sounds. The cages were placed in a cooling box during travelling and hot weather and positioned in the shade for at least half an hour before a sound recording began. Thus it was tried to match the temperature of the animal's body during singing to the temperature of the shaded place. «?°C» in the Figures normally means that the recording was taken in the field without temperature measurement. During the night-surveys (recently with automatic recording) the temperature was measured as often as possible and interpolated if necessary. The animals were fed twice a day, preferentially with delicate herbs, and lived obviously rather well and active for weeks or months.

The identification of the species of the Ehippigerini requires some experience, due to several characters, which are difficult to assess, and also due to uncertainties and errors in some identification keys (e.g. Harz 1969). In cases of doubt, keys and figures of Peinado (1990a) and Barat (2012) have been used. The animals were liquid-preserved (70 % alcohol), which has the advantage that structures, which are difficult to access (e.g. male titillators, female caudal subgenital plates), can be examined with greater ease.

Various tape recorders (UHER 4000 Report, SONY TCD-D7, SHARP MD-MT877H, TASCAM DR-100, TASCAM DR-40) and microphones (SENNHEISER ME 80, VIVANCO EM216, RODE NTG-2) have been used. In recent times a special digital SongFinder (Nature Sound Electronics, Inc.) was utilized, to compensate for the observer's high frequency hearing loss.

All tape-recorded sounds were digitalized (accumulating to more than 6000 files) and investigated as time-amplitude diagrams (oscillograms) with the help of bioacoustic software, BatSound (Pettersson Elektronik AB) and WavePad Sound Editor (NCH Software).

In this study a cluster of syllables with the appearance of belonging together was specified as an echeme or (in the case of a male's first echeme during the course of a duet) as an initial song. The components of the echemes, the syllables, are the sounds, which are produced by the rubbing of special structures (generally plectrum and file) of the brachypterous fore wings (tegmina) against one another during the opening and closing movements. The result of an outward movement (opening) is the opening hemisyllable (Op-HS), which is however sometimes very low or missing; the result of the inward movement on the other hand is the closing hemisyllable (Cl-HS). The sound effect of each impact of the plectrum with a denticle of the file, the impulse, constitutes the shortest subunit of a hemisyllable. However, different accessory structures of the tegmina (cf. Pfau & Schroeter 1988a) and also echoes are sometimes involved, resulting in «polyphonic» sounds. For this reason we used the term «pulse» for every very short sound event (just as Heller 1988 did;

l.c. p. 9f.), which could in reality constitute an impulse, i.e. stem from an impact of the plectrum with a single denticle of the file.

It is essential to know whether the sound is produced during the opening or the closing movement of the tegmina, but in most cases the wing movements are too rapid or insignificant for a direct observation. The fundamental parallel registration of the movements of the tegmina by an opto-electronic device (Helvesen & Elsner 1977; Heller 1984, 1988) had therefore provided essential further insights; accordingly the results of Heller (1988) were used in this study for interpretations, whenever possible.

Increase and decrease of sound intensity and changes of frequencies inside the syllables are often rather variable characters in different specimens of the same species, in different echemes of the same animal or even in different syllables in the course of an echeme. In general details of this kind are not mentioned.

Some parameters of the echemes (duration, syllable number, echeme-echeme pause and maximal hemisyllable duration) are juxtaposed in tabular form (Appendix 1). For the different locations of the collected specimens and the origin of bio-acoustic and morphological figures see there too.

Abbreviations:

- I initial song of the male.
- Op-HS opening-hemisyllable; sound produced by the opening movement of the tegmina; ↑ in the figures.
- Cl-HS closing-hemisyllable; sound produced by the closing movement of the tegmina; ↓ in the figures.
- R female response to an initial song.
- CR male confirmatory response to a female response.
- sCR male spontaneous confirmatory response.

RESULTS

1 *Albarracinia zapaterii* (Bolívar, 1877)

Undisturbed males of this species sang very long series of echemes, in which the echeme-pauses were approximately of equal length (Fig. 1a).

Each echeme began with a first part, which consisted of gradually prolonged crescendoing syllables (Fig. 1b); this part corresponds to part I of echemes of the genus *Platystolus* (Pfau 1996). A second part – corresponding to part II of *Platystolus*-echemes – contained 1 (Fig. 1b) – 3, rarely 4–5, particularly long and loud syllables, in which (in contrast to part I) the Cl-HS dominated in length. Sometimes, however, the part II-syllables were lower, shortened or totally suppressed (Fig. 1c); these songs were mainly produced in the sun, i.e. at higher temperatures.

In an outdoor recording at night (Fig. 1d) it was remarkable that further prolonged syllables (one Cl-HS + one long complete syllable in Fig. 1d) sometimes followed the echeme – in certain respects constituting a part II of a further echeme without preceding crescendoing part I-syllables. The closer analysis showed that immediately after the first (the complete) male echeme a very low syllable had been emitted somewhere in the field. This very low signal was amplified in Fig. 1d; it was interpreted as a response of a female (R1 ♀). The following loud prolonged syl-

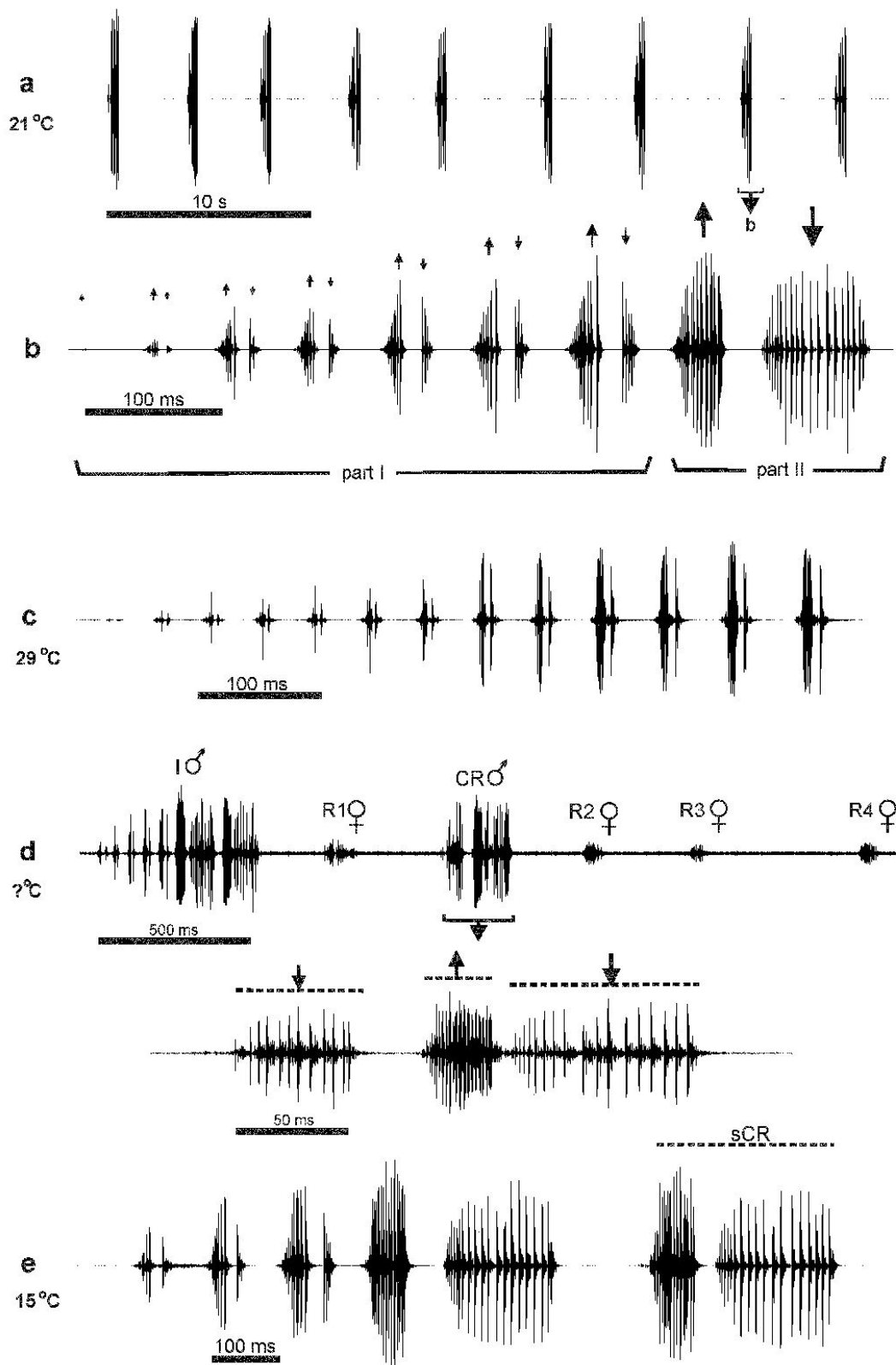


Fig. 1. *Albarracinia zapaterii*.

lables of the male represented accordingly a «confirmatory response» (CR♂; Pfau & Schroeter 1988a, Pfau 1996: «Rückantwort»). The confirmatory response for its part induced three further low syllables, apparently again responses of the same far away positioned female (R2♀ - R4♀). Analogous to some species of *Platystolus*



Fig. 2a. *Callicrania plaxicauda*, female.

(Pfau 1996) the male duet-inducing first echemes are designated as initial songs (I♂ in Fig. 1d).

Considering the ability of *A. zapaterii* to produce complex duets between males and females, certain male initial songs, in which the last of the long part II-syllables was produced after a prolonged intermission (Fig. 1e), could be explained as follows: It is suspected that highly motivated males sometimes add a «spontaneous confirmatory response» (sCR) directly to the initial song, without the presence of female responses (just as in *Platystolus*, where the spontaneous confirmatory response is widespread; cf. Pfau 1996).

The length-ratio of part I to part II of the initial song of *A. zapaterii* was variable. For instance, a very short part I could be followed by a part II, which consisted of three long syllables. Extremely shortened echemes, which sometimes contained only one part I- and one part II-syllable, may represent complete (but strongly shortened) initial songs, but they can as well be interpreted as spontaneous confirmatory responses, similar to the sCR described above.

The two-part appearance of the initial songs of *A. zapaterii* is very similar to that of echemes of certain species of *Platystolus* (Pfau 1996; = *Callicrania*, *Platystolus*, *Neocallicrania* and *Synephippius* according to Barat 2012). However, the initial songs of *A. zapaterii* are much shorter at the same temperature (the echemes of e.g. *Platystolus ramburii*, a species with relatively short two-part echemes, were about three times longer). The song-structure of *A. zapaterii* was also very similar to that of some species of *Lluciapomaresius*: compared with *L. stalii* (type A, see below) the syllable-frequency of the echemes of *A. zapaterii* was, however, comparatively low, approximately 2/3 at the same temperature.

2 *Callicrania plaxicauda* Barat, 2007 (Fig. 2a)

The echemes of *C. plaxicauda* showed, in a fairly typical part I, a number of syllables, which increased successively in volume and length (Fig. 2b). The Op-HS

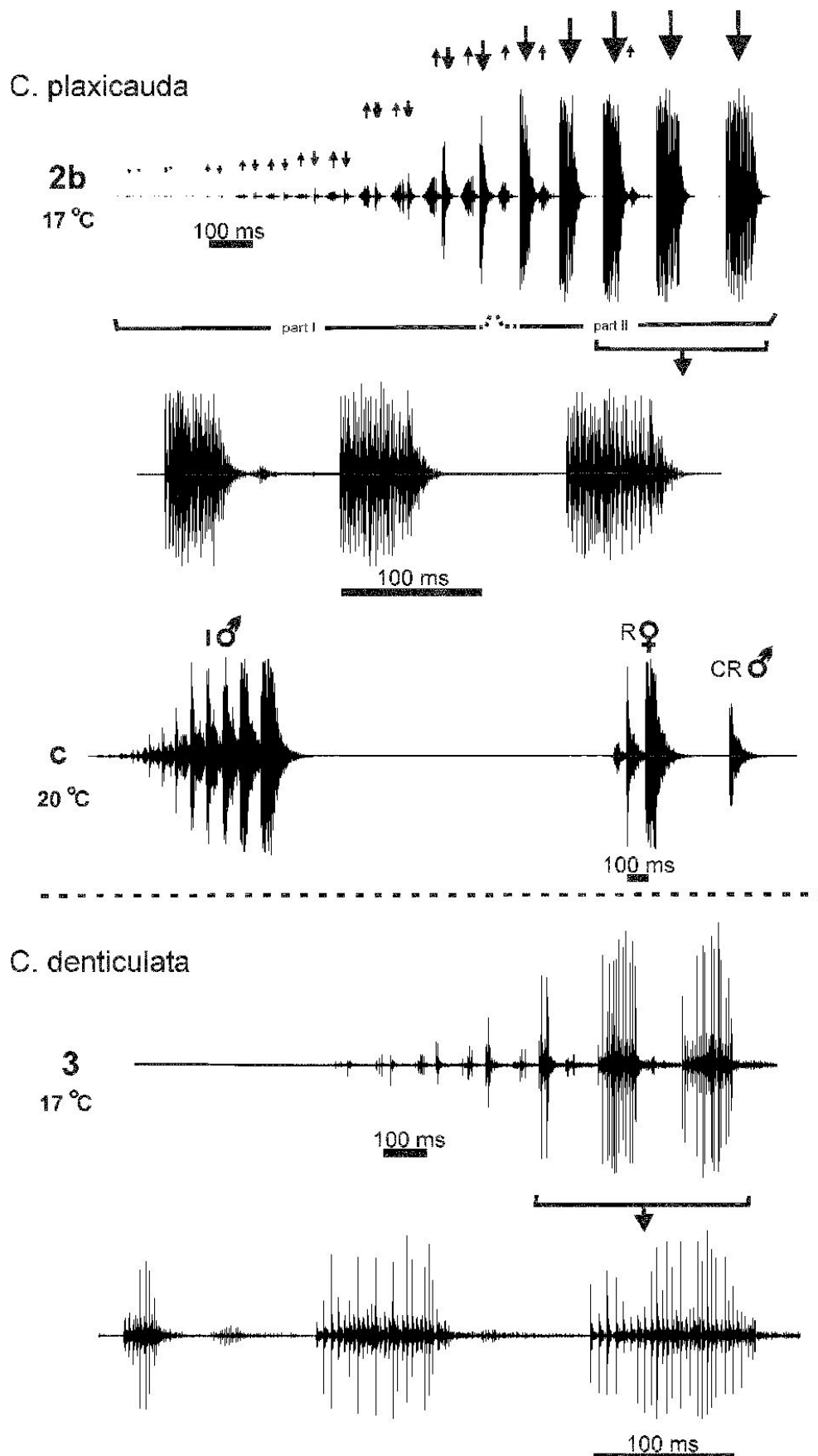


Fig. 2b, c; 3. *Callicerania plaxicauda* (Fig. 2b, c); *Callicerania denticulata* (Fig. 3).

became lower at the rather indeterminate boundary between part I and part II; normally they disappear inside the part II. The part II consisted of 1–5 especially loud CI-HS. Whereas the first 1–2 CI-HS were shorter, the following ones mostly exhibited an equal length, but were sometimes prolonged continuously. Although the loud CI-HS were much shorter than the part II-CI-HS of echemes of (the closely related) *C. ramburii* (*Platystolus ramburii* in Pfau 1996), the presence of a homologous part II is quite obvious. Compared to *C. ramburii* the total length of the initial song is approximately half as long at the same temperature.

During four weeks in captivity only one clear antiphony between a male and a female could be monitored (Fig. 2c). It is interpreted as an initial song (I♂), a female response (R♀; consisting of three hemisyllables) and a very short confirmatory response (CR♂), which was somewhat lower. Since male initial songs in some cases ended with similar very short and lowered hemisyllables, which are set farther apart (in one case such a delayed hemisyllable lasted only 15 msec at 21 °C), it seems that *C. plaxicauda*-males (just as *A. zapaterii*-males) sometimes append spontaneous confirmatory responses directly to the initial song.

C. plaxicauda performed a relatively high song activity at night: one male for example repeated his initial songs every 1–10 minutes (average 5.7 minutes; n=73) at about 20 °C. During daylight only few echemes could be heard. Disturbed animals produced series of sharp sounding longer syllables (not documented).

After one month of captivity one single surviving male produced much shortened echemes, which consisted only of part I.

3 *Callicrania denticulata* Barat, 2007

This species is closely related to *C. plaxicauda* (see Barat 2007), as demonstrated also in the structure of its initial song (Fig. 3). Potentially constant differences were the lower number of syllables in part I (3–7 syllables) as well as part II (2–4 syllables); furthermore the syllable-frequency was considerably lower at the same temperature (see Fig. 2b and 3, which are illustrated in the same time scale). The last two part II-syllables were markedly longer than comparable syllables of *C. plaxicauda*.

Furthermore there was an abrupt syllable-prolongation between the first and the second part II-syllable (factor of 2.5–4), which was not evident in *C. plaxicauda*; compared with the second part II-syllable the third (somewhat detached) syllable was equally long or slightly prolonged. The last part II-syllable exhibited 30–33 pulses, which were arranged less densely at the beginning. The comparable syllable of *C. plaxicauda* included only 20–28 more regularly arranged pulses, which appeared often very noisy (on account of accessory rubbing structures of the tegmina?).

The Op-HS were clearly visible in the oscillograms and became lower in part II, just as in *C. plaxicauda*; the Op-HS of the last syllable was particularly quiet or lacking.

In an outdoor-recording during darkness (21.00–22.00) the pauses between the echemes varied between 46 and 123 sec (at 17–14 °C).

4 *Ephippiger diurnus cunii* Bolívar, 1877

In contrast to different authors (cf. Ragge & Reynolds 1998) we follow Barat (2012) and consider *E. diurnus cunii* as a subspecies (and not a local form) of *E. diurnus diurnus* (see below).

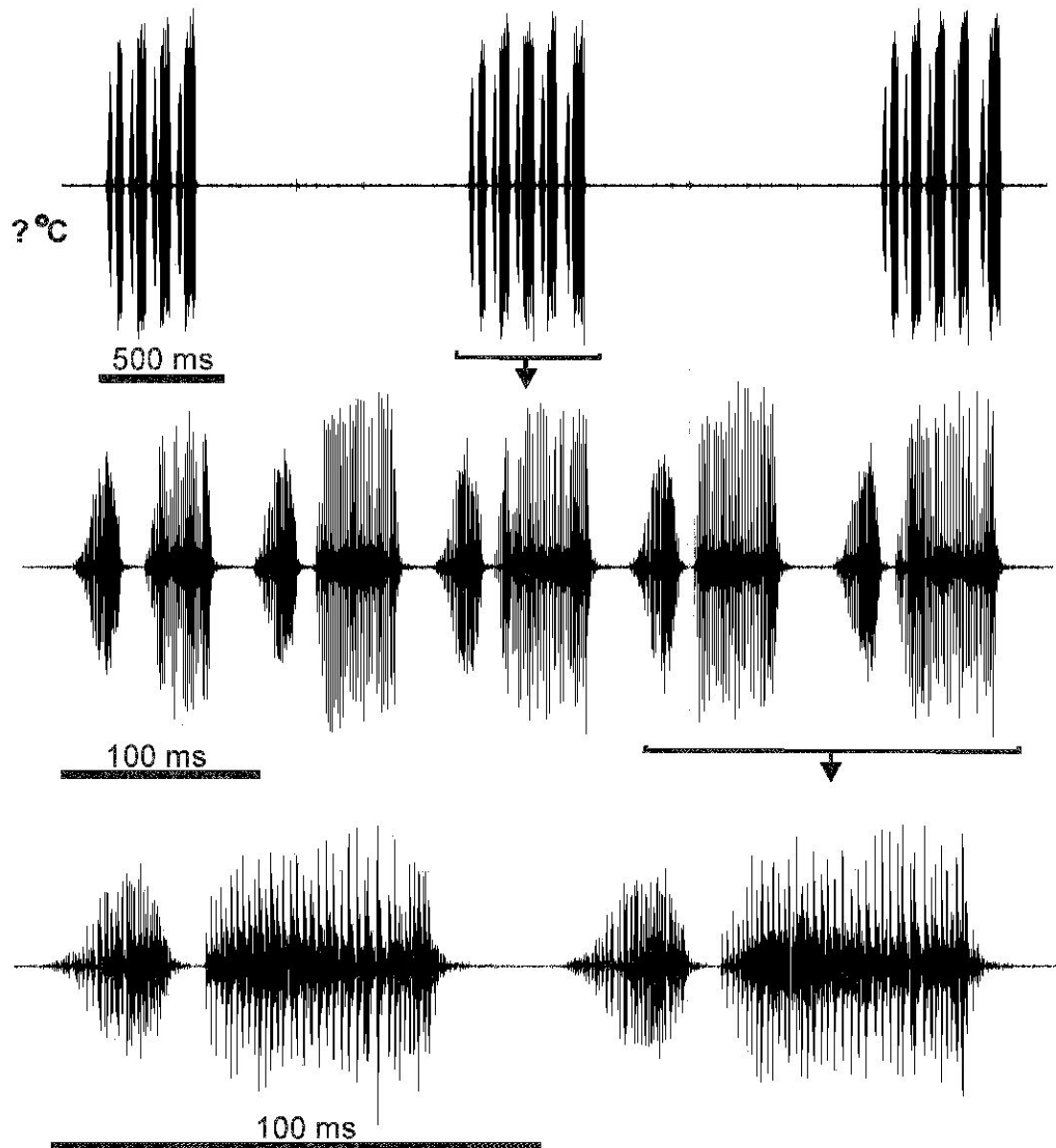


Fig. 4. *Ephippiger diurnus cunii*.

The echemes of males of *E. diurnus cunii* (Fig. 4) contained one to six syllables and were generally produced in long series, in which the pauses between the echemes often varied considerably. The first CI-HS of an echeme was usually somewhat lower, sometimes even below the loudness of its Op-HS. The length of the CI-HS increased slightly during the first 2–3 syllables and afterwards remained equal. In longer echemes with 5–6 syllables the period between the last and the penultimate syllable could be slightly extended (Fig. 4).

5 *Ephippiger diurnus diurnus* (Dufour, 1841)

The echemes of this well known species were composed of one to two syllables (Fig. 5a), which were produced primarily during the day (and sometimes also at night, cf. Ragge & Reynolds 1998) in long series. Among our recordings one curious beginning of a song sequence consisted of 4 syllables (Fig. 5b), which showed a

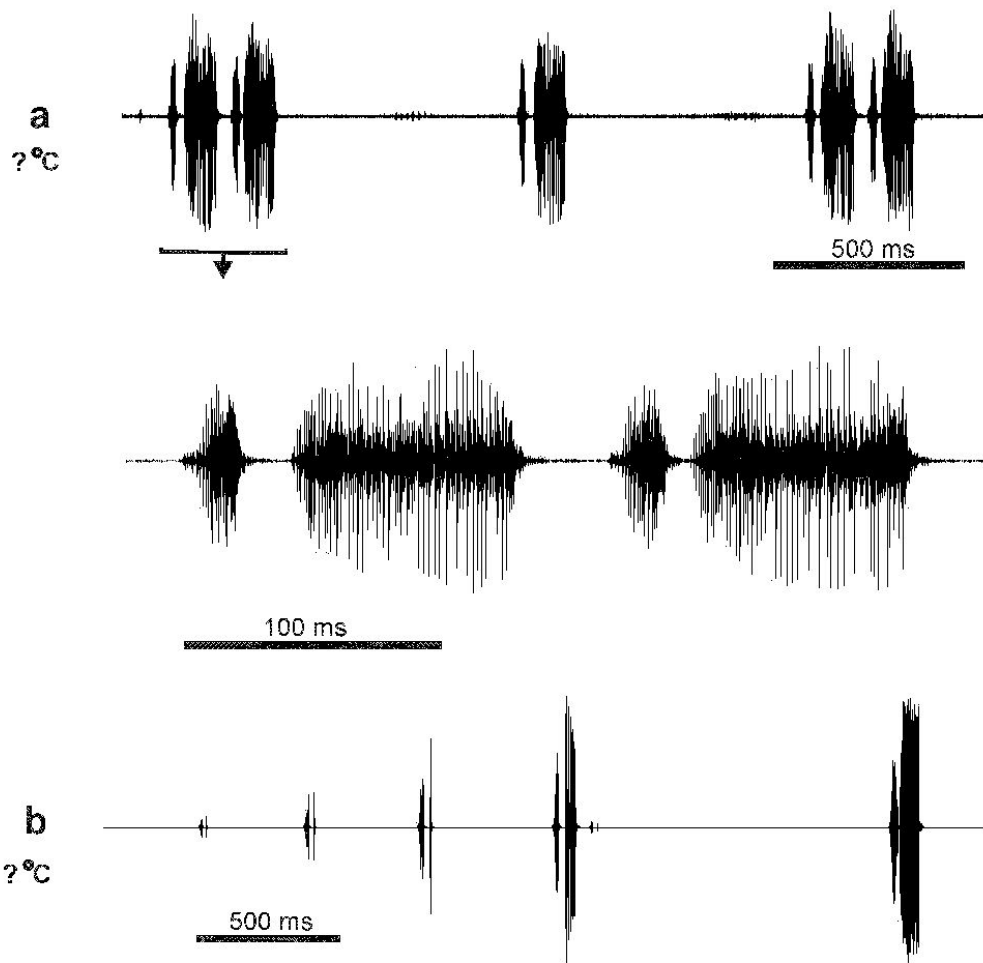


Fig. 5. *Ephippiger diurnus diurnus*.

clear crescendo as well as a CI-HS-prolongation; the fifth CI-HS exhibited apparently the normal syllable-length. This sequence is strongly reminiscent of the beginning of echemes of species with two-part songs (Figs 1–3, 10–13) and may point out that this type of echemes already existed in the phylogenetic ancestor of the genus (see also discussion).

6 *Ephippigerida areolaria* (Bolívar, 1877)

The echemes of *E. areolaria* consisted of 2–5 syllables (rarely only one syllable or up to seven syllables), which contained CI-HS of similar appearance; only the first CI-HS was often somewhat shorter and lower (Fig. 6a, b). The first Op-HS was the most suspicious one; the following Op-HS were shorter and became slowly longer in the course of the echeme (Fig. 6b). Compared to *E. diurnus diurnus* the echemes of *E. areolaria* (with only one or two syllables) appeared very similar, but the CI-HS were longer, approximately 1.6x at the same temperature; the syllable-frequency was slightly lower and the pulse-frequency of the CI-HS was less than 50 %.

Some series of echemes of males of *E. areolaria* showed a very constant repetition of echemes with an equal number of syllables. Several songs could, however, exhibit a rather regular switching between two and three (or four and five) syllables

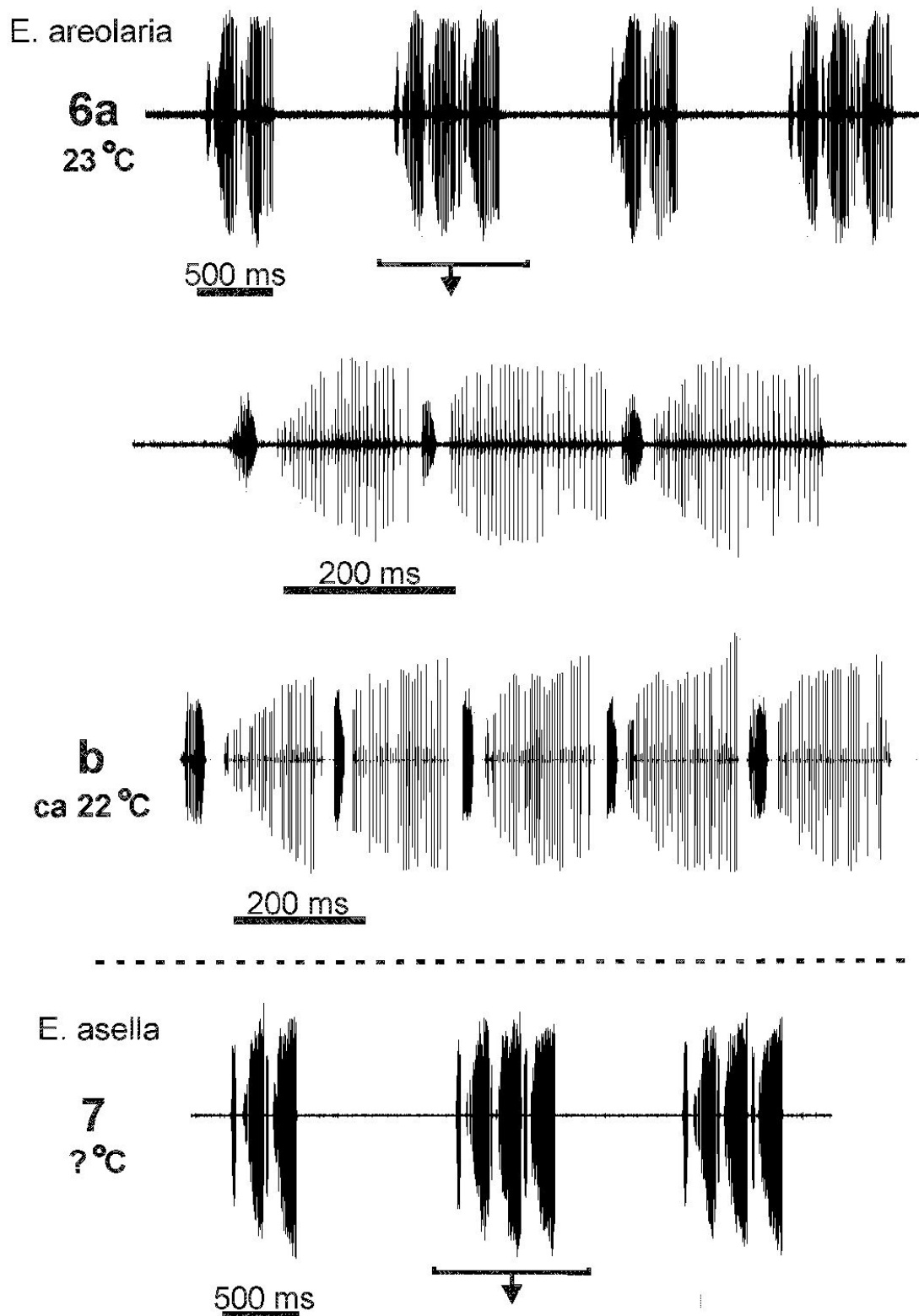


Fig. 6a, b; 7. *Ehippigerida areolaria* (Fig. 6a, b); *Ehippigerida asella* (Fig. 7).

or could repeat many syllables of an equal number and stochastically intersperse different echemes. After a long period in captivity (3.5 months) one male produced mostly echemes with 5, rarely even 7 syllables.

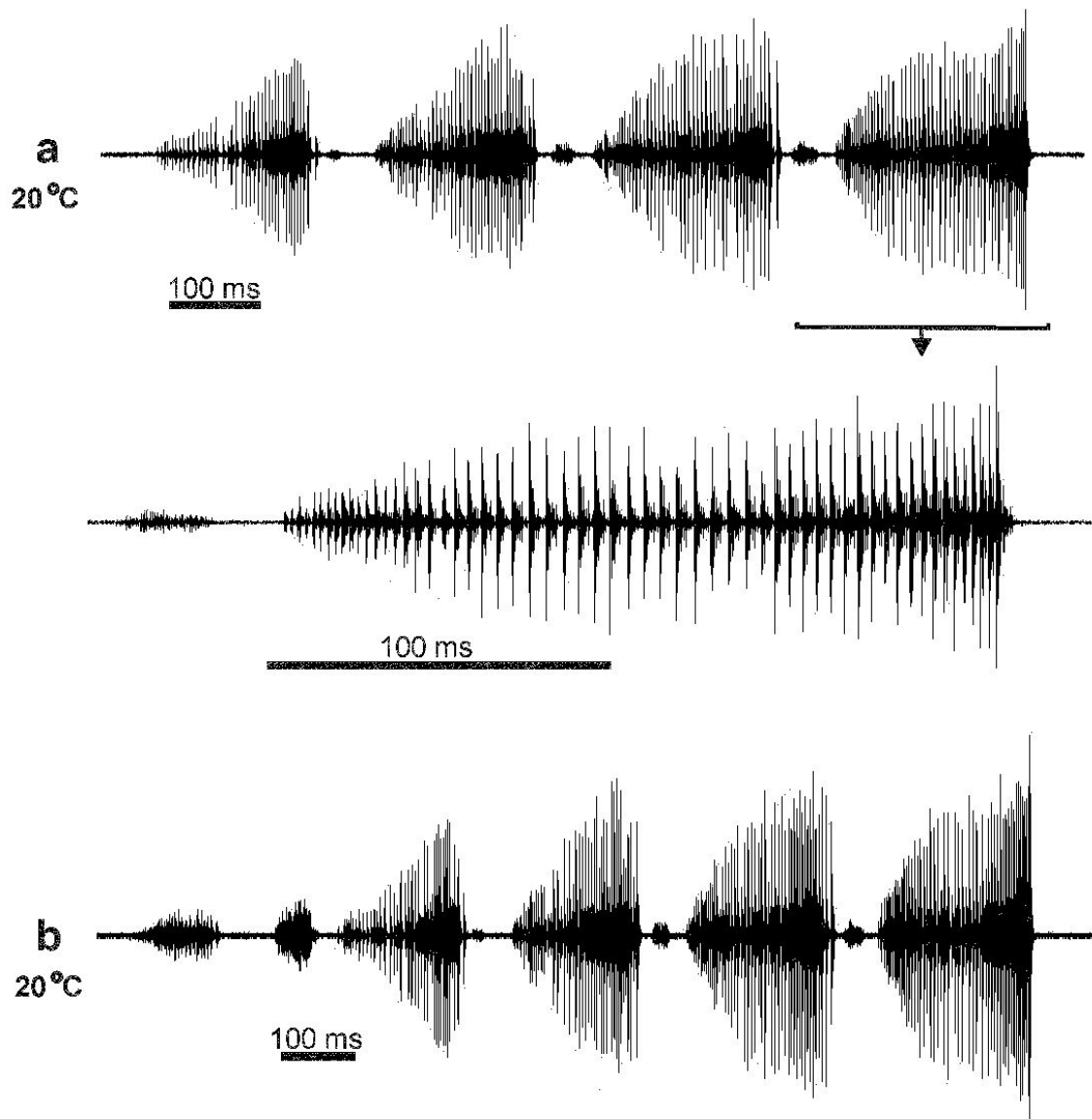


Fig. 8a, b. *Ephippigerida diluta*.

7 *Ephippigerida asella* Navàs, 1907

The recordings of echemes of a male «*E. areolaria*» specimen from the Sierra del Cadí (Fig. 7) are cited here under the name *E. asella*, since the location is situated within the range of this species. *E. asella*, recently rediscovered by J. Barat, is evaluated up to now as a valid species (Olmo Vidal 2006), in spite of the fact that the morphological differences between *E. areolaria* and *E. asella* are minimal (Barat, pers. comm.). The ensuing possibility that both names may be synonyms is supported by the very similar structure of the echemes.

8 *Ephippigerida diluta* (Bolívar, 1878)

E. diluta males sang echemes (Fig. 8a), which were at first view similar to those of *Ephippigerida pantingana* (see below). Sometimes *E. diluta* and *E. pantingana*, which were kept in cages close to each other, executed long alternating song-sequences, presumably due to the structural similarity of the songs (see Fig. 9c).



Fig. 8c; 9a. Tegminal files of *Ephippigerida diluta* (Fig. 8c) and *E. pantingana* (Fig. 9a).

Whereas in these antiphonies the echeme-frequency was equal at the same temperature, the syllable-frequency of the echemes was much higher in *E. diluta* (approximately 1.7x).

The echemes showed 4–5 (rarely 1–3 or 6) syllables and a slow crescendo, mainly concerning the first two to three syllables. The loudness of higher sound frequencies (about 16–22 kHz) increased from syllable to syllable. The length of the syllables increased slightly in the course of the echemes.

Op-HS were not detectable in many songs, but were sometimes distinct towards the end of an echeme; in some cases, however, the Op-HS of the first syllable was particularly loud (Fig. 8b; in this case a very low Cl-HS went ahead).

The CI-HS-length in the echemes of *E. diluta* was considerably smaller compared to *E. pantingana*-echemes at the same temperature. The pulse-frequency of the CI-HS, however, was higher (1.5–1.8x). In most CI-HS it was highest at the beginning and also at the end. The pulse-loudness was usually highest at the end of the CI-HS, but showed contrarily sometimes a decrease. The denticles of the stridulatory file are slightly more closely arranged than in *E. pantingana* (18 denticles/mm in the mid region); the file is less bent as a whole (Figs 8c, 9a).

9 *Ephippigerida pantingana* (Navàs, 1904)

E. pantingana had not been reported in the literature for almost a century; for its rediscovery and interesting biological data see Llucià-Pomares *et al.* (2009).

Echemes of this species were recorded in a steppe region near Ballobar in June 1992. The males began to sing at the beginning of darkness and were heard also in the early morning. The echemes showed 3–4 (rarely 1–2 or 5–7) CI-HS of equal loudness, except for the first one, which was somewhat lower (Fig. 9b). Compared with *E. diluta* the songs sounded finer, since frequencies below 7 kHz were practically missing. The syllable frequency was distinctly lower and the length of the CI-HS much greater. The pulse frequency of the syllables of *E. pantingana* was markedly slower at the same temperature.

Compared to *E. diluta*, the CI-HS of *E. pantingana* were different with respect to their rather steady pulse-frequency and their external shape (determined by the progress of pulse-volume). In Fig. 9c an oscillogram of an antiphony of *E. pantingana*- and *E. diluta*-males, which sat equidistant from the microphone, is illustrated; the louder echemes were produced by *E. pantingana*.

In Fig. 9d echemes of two males of *E. pantingana* are reported, which were almost synchronized; in the last echeme the louder male (which sat nearer to the microphone) produced only two, the male sitting farther away four syllables. The two males executed such simultaneous songs for minutes. No acoustic reaction was heard instead from a female which was nearby. In the immediate proximity to a female a male started to shake his body for one to two seconds, possibly producing vibration signals.

The denticles of the (relatively strongly bent) stridulatory file show a slightly more spaced arrangement than those of *E. diluta* (17 denticles/mm in the mid region; Fig. 9a).

10 *Lluciapomaresius nobrei* (Bolívar, 1898)

The recorded echemes of *L. nobrei* (Fig. 10a) consisted of a rapid series of crescendoing syllables (part I), which ended in a single accentuated prolonged part II-syllable. In most cases part I contained only Op-HS (in contrast to *Albarracinia zapaterii* or the closely related *Lluciapomaresius stalii*); the CI-HS are, however, visible in oscillograms of strongly overdriven recordings. The part II-CI-HS was 1.5–3.5 times longer than its Op-HS and often somewhat lower. In some cases one or two preceding CI-HS were more distinct and could even show characteristics of part II-syllables: the boundary between part I and II is evidently indistinct.

The pulse-frequency of the part II-CI-HS was lower than that of its Op-HS, in which the pulses were strongly condensed towards the end. Echemes of *Lluciapomaresius ortegai* (see below) were similar in several respects, but exhibited usually

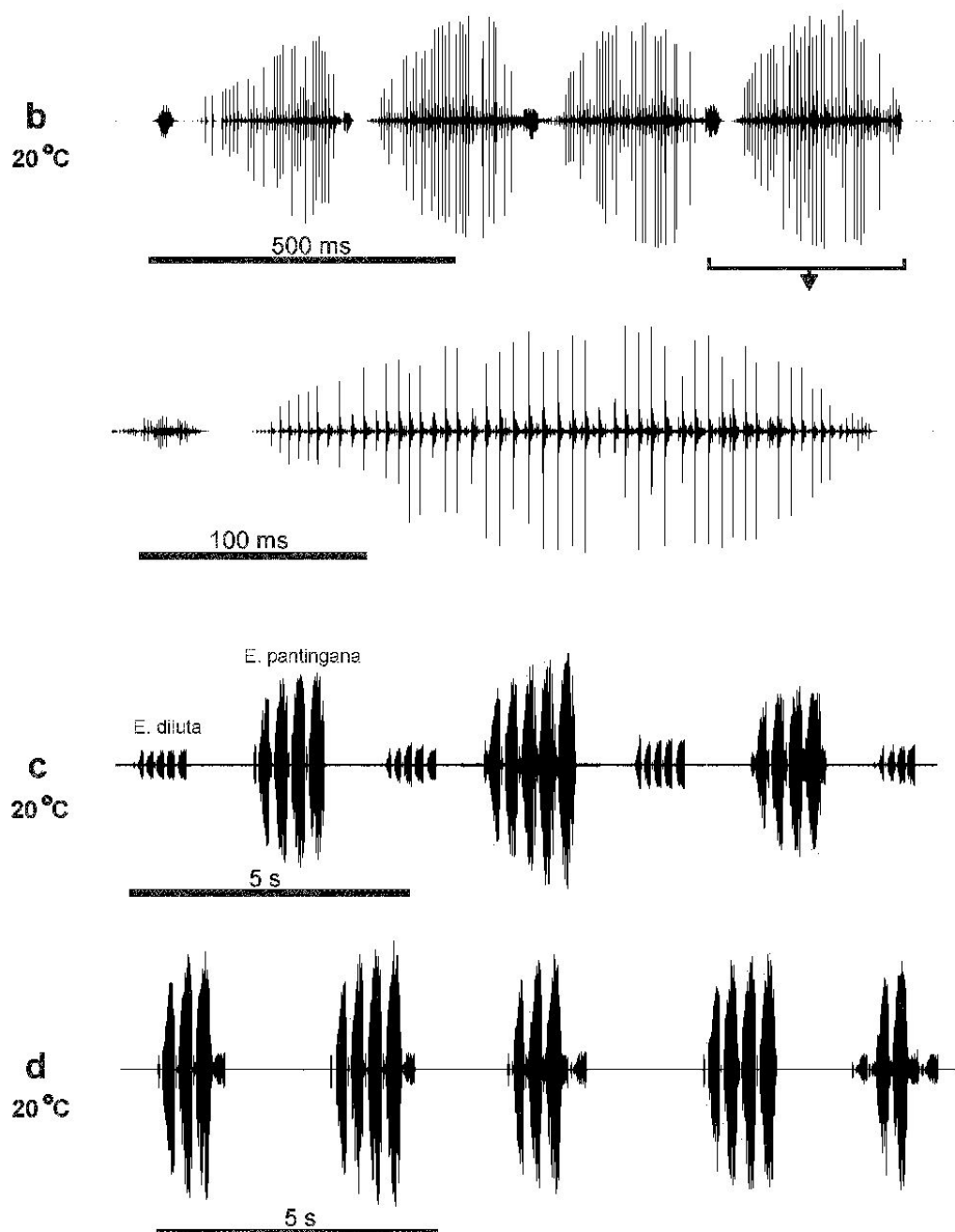


Fig. 9b–d. *Ephippigerida pantingana*.

a higher ratio of CI-HS/Op-HS-length of the last syllable, namely 3–4. In contrast to this, the quotient was only 0.5–2 in *L. stalii* (type A, see below). This parameter apparently represents an essential distinguishing song-feature and should be investigated more precisely in specimens from various locations.

The female of *L. nobrei* produced response calls immediately after (or slightly overlapping) the male initial song (Fig. 10b, c; R ♀). In some recordings, however, the female response, which was composed of two to five hemisyllables, showed a larger delay (up to 77 msec); 4 response-hemisyllables of an antiphony are reproduced expanded in Fig. 10d.

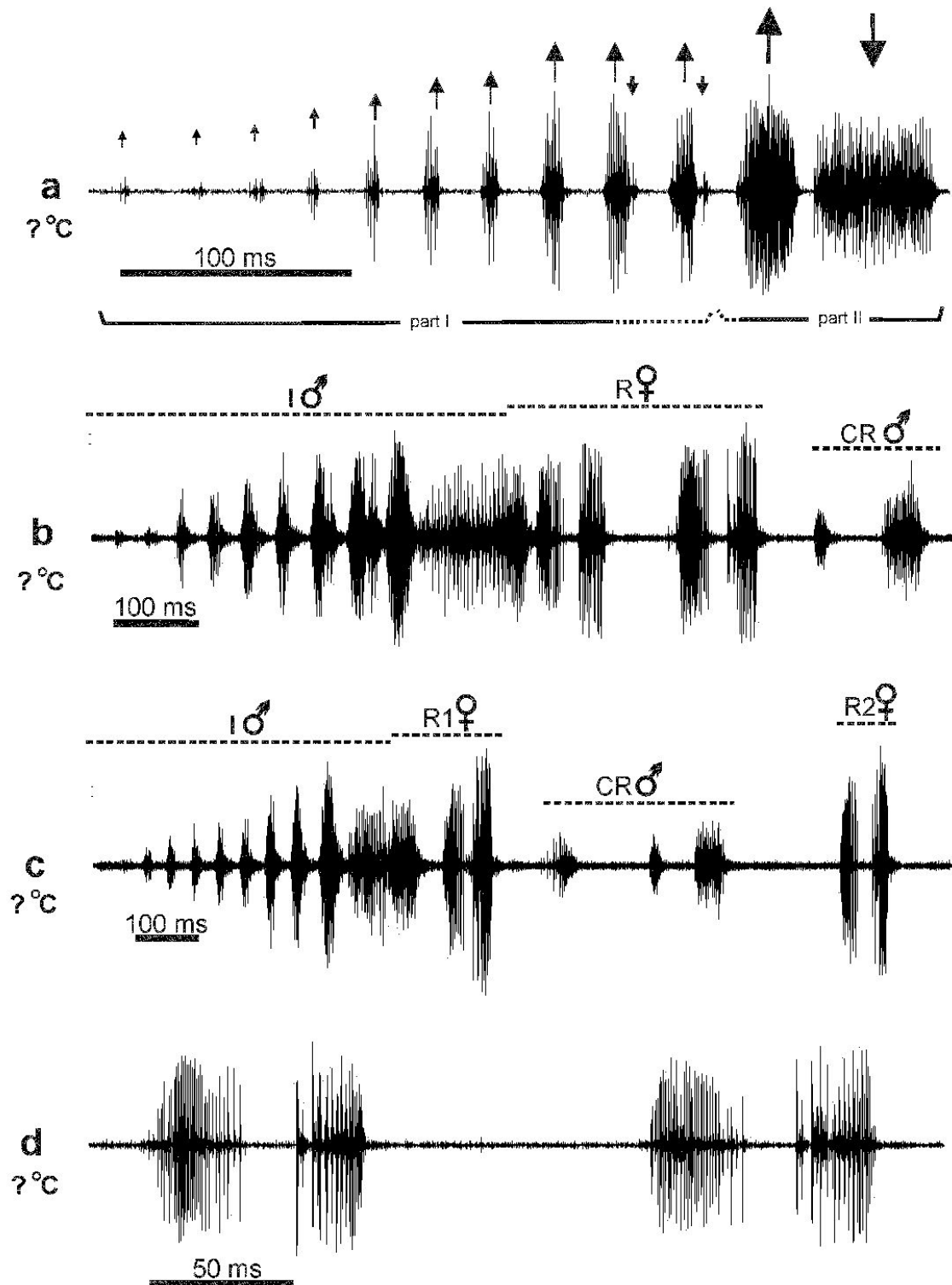


Fig. 10. *Lluciapomaresius nobrei*.

In Fig. 10b and c the female response obviously evoked a further reaction of the male, which is interpreted as the confirmatory response (CR♂). Sometimes this confirmatory response was followed by a further female response (Fig. 10c: R2♀); the male for his part could react with an additional confirmatory response, which could be responded in turn again by the female.

Initial songs of males of *L. asturiensis* from the north-western Iberian Peninsula are very similar to those of *L. nobrei*. Some examples of echemes, illustrated in Hartley (1993) and Ragge & Reynolds (1998), also show spontaneous confirmatory responses of some males, which were labeled as «secondary songs» and «further diplosyllables», respectively. *L. asturiensis* and *L. nobrei* possibly belong to the same species (Barat, pers. comm.).

Schmidt *et al.* (2009, Fig. 5) illustrated a very long echeme of *L. asturiensis* from the Serra do Alvão, northern Portugal: 16 syllables, lasting for 900 ms at 20 °C. This echeme showed a very low last CI-HS. In Fig. 7 these authors reproduced an oscillogram of *L. anapaulae* Schmidt, 2009 (recorded at 26 °C), which exhibited rather similar characters, but in this case the last CI-HS and the penultimate Op-HS represented the loudest hemisyllables. Considering the similar temperatures of Ragge & Reynolds' recordings of *L. asturiensis*, the syllable-frequency of the echemes of *L. anapaulae* is (according to the Fig. 7-legend: 11–13 syllables in 270–310 ms) significantly higher than that of *L. asturiensis* (resp. *L. nobrei*).

11 *Lluciapomaresius ortegai* (Pantel, 1896)

Initial songs of *L. ortegai* began with a short crescendo, consisting of 3–5 very short Op-HS and even shorter (and lower) CI-HS (Fig. 11a); these syllables constituted part I. Then, in a single last syllable (part II), the loudness was abruptly increased and especially the CI-HS was strongly prolonged. The last CI-HS was 3–4 times longer than its Op-HS.

In an outdoor-recording a female sitting nearby responded after 100–160 msec with 2–4 syllables; in the case of 4 response-syllables the last one was set further apart (Fig. 11b; R ♀). Since the male never responded to the female with a structurally different confirmatory response, but once produced a further echeme directly (60 ms) after the female response (Fig. 11c), it seems possible that a further complete echeme represents the confirmatory response of the male-female antiphony (similar to *Platystolus faberi*, cf. Pfau 1996).

12 *Lluciapomaresius panteli* (Navàs, 1899) (Fig. 12a)

The echemes of the males of *L. panteli* (Fig. 12b) were similar to those of *L. ortegai* (Fig. 11a); the very slowly crescendoing part I-syllables (up to 6 syllables) were even lower, in many cases not at all visible in the oscillograms. Therefore an echeme consisted in principle of only a single part II-syllable. The pulse-frequency of the part II-CI-HS was usually highest at the beginning; the pulses were then remarkably evenly arranged until the end (Fig. 12b is an exception in respect of the very last pulse).

In contrast to *L. ortegai* the pulses of the long last CI-HS exhibited a rather long crescendo at the beginning, which sometimes extended practically over the whole hemisyllable. In most cases the number of pulses was about 20, but varied in total between 7 and 24; the last 1–2 pulses were often extraordinarily loud (trigger pulses? See discussion).

The males sang mainly at daylight. One monitored specimen emitted 15 echemes in two hours (at 22 °C air temperature, under cloudy skies), but another male generated about 150 echemes in 1.5 hours (at about 21 °C). These differences

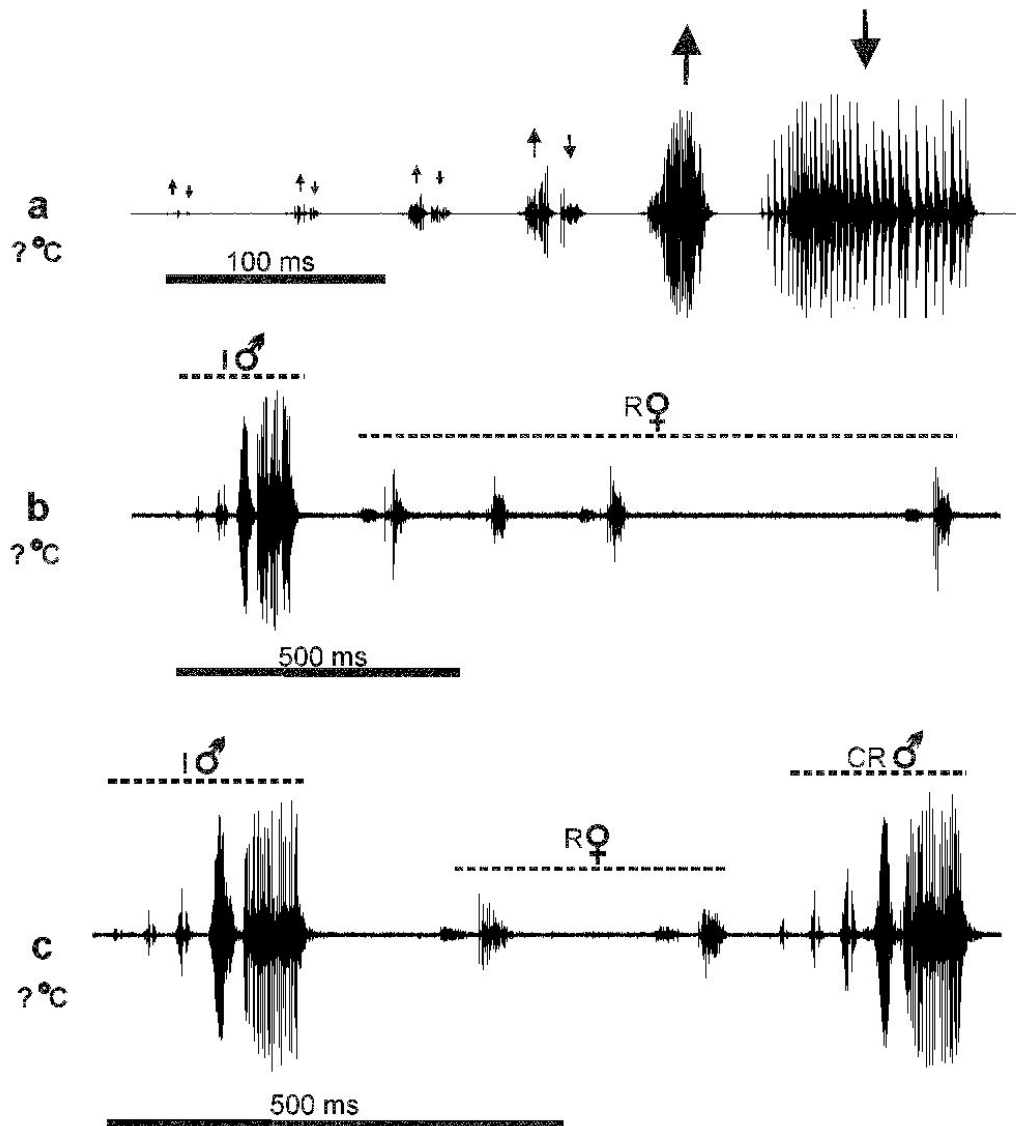


Fig. 11. *Lluciapomaresius ortegai*.

presumably reflect a different courtship motivation. Instead – during a whole night (21 °C to 19 °C; 7 h continuous recording) – only 11 echemes could be registered.

Female responses, following a male initial song, are illustrated in Fig. 12c (R1 ♀, R2 ♀). In this recording the microphone was targeted at the female; therefore only the loud part II-CI-HS of the male is documented anterior to the much louder female responses. Fig. 12d shows a case of a spontaneously produced female syllable (♀), which was followed by a prompt reaction of a male nearby sitting (CR ♂), apparently a confirmatory response.

Morphological characters (e.g. of the cerci; cf. Harz 1969, Barat 2004, Pfau *et al.* 2014) clearly show that *L. panteli* constitutes a true species. The highly differentiated subgenital plate of the female represents an essential further special character of *L. panteli*: This sclerite is a square plate with typical colors (Pfau *et al.* 2014, photo p. 48). The broad brown bands on both sides of the plate are more strongly sclerotized and elastic, whereas the light, yellowish region in between represents a more softly sclerotized compressible area. The subgenital plate will presumably be



Fig. 12a. *Lluciapomaresius panteli*, male (from Pfau *et al.* 2014).

impressed in its mid by the ovipositor, when the ovipositor is moved downwards during ovipositing. During the digging-movements of the ovipositor the lateral sclerite-bands will function as elastic elements, which are bowed during lifting as well as during lowering of the ovipositor at the exact location, where the bands make a turn to the upper side of the subgenital plate and make contact with the base of the ovipositor. The elastic counter forces should stiffen and limit the system ovipositor+subgenital plate in as well the up- as the downward directed movements, similar to technical steel band springs. This constitutes an autapomorphic peculiarity of *L. panteli* among the Ephippigerini.

It is suggested that the special capabilities of the subgenital plate enable the females of *L. panteli* to lay eggs with their robust short ovipositors in regions with a harder ground. In *L. ortegai*, which is presumably a very near relative, apparently a preliminary stage of this capability has been attained. In other species of the Ephippigerini (*L. stalii*, *L. nobrei*, *Parasteropleurus perezii*) the functions of the subgenital plate+ovipositor were found to be fundamentally different: there are joint-like areas in the side region of the subgenital plate, which are expected to ensure that the movement of the ovipositor run more smoothly, with a larger range. Reminiscences of formerly present joints are recognizable in *L. panteli*, but these regions obviously lost their former function.

13 *Lluciapomaresius stalii* (Bolívar, 1877)

The recordings of *L. stalii* from different locations exhibited conspicuous differences. Two extremes could be observed, but they could not be allocated clearly to certain geographic regions.

Type A: the echemes of type A-specimens were similar to those of *L. nobrei*, but the CI-HS were present from the beginning. Males from the Sierra de Urbión (Fig. 13a), as well as the Sierra de Gredos (Figs 13b, c) and the Sierra de Guadar-

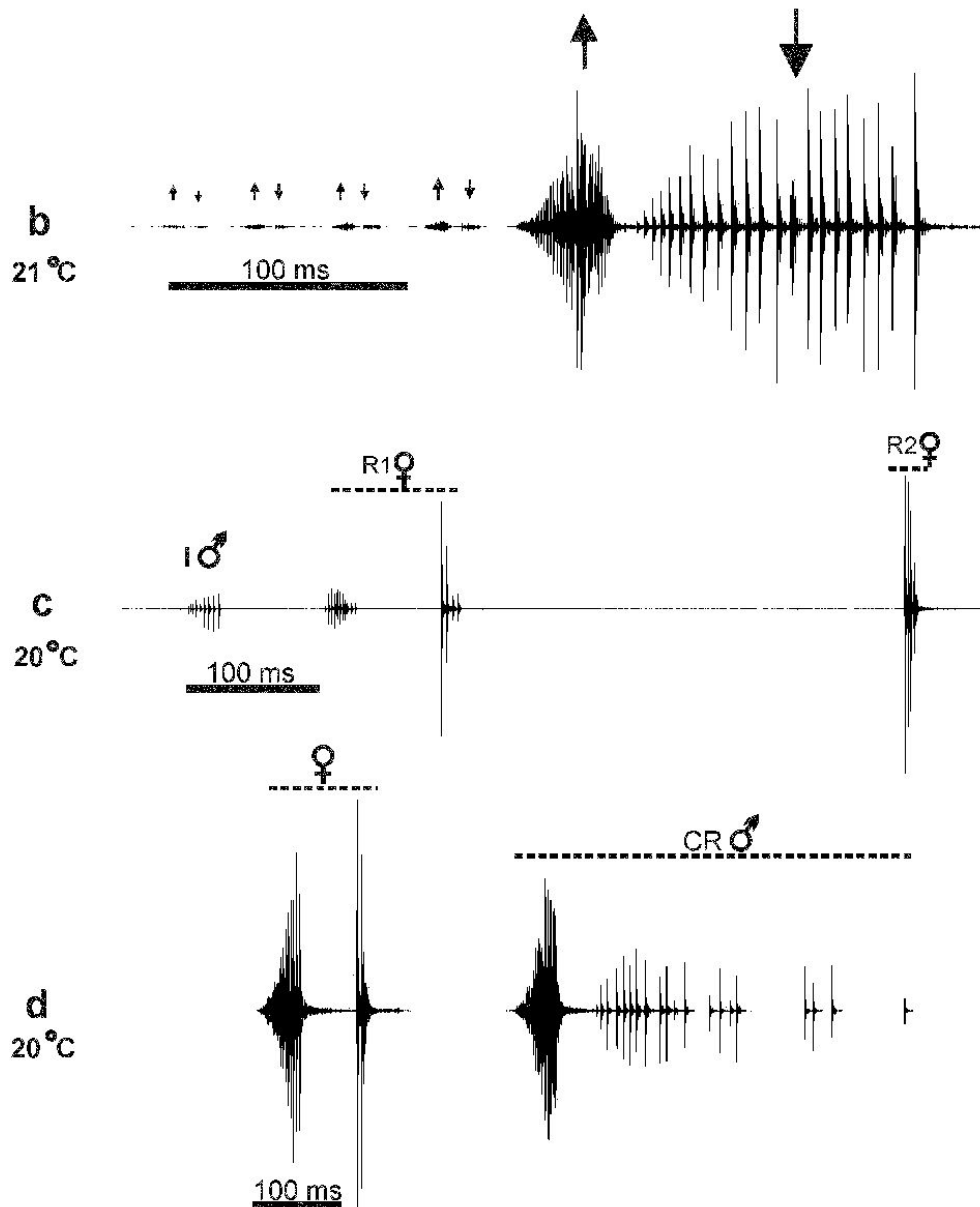


Fig. 12b–d. *Lluciapomaresius panteli* (from Pfau *et al.* 2014).

rama (Ragge & Reynolds 1998, Fig. 589), sang relative long echemes with a crescendo of syllables in the first half of part I, followed by several syllables of equal loudness (during the rest of part I) and a part II, consisting of 1–3 more or less longer CI-HS. The CI-HS of part II were gradually or abruptly prolonged, their pulses were typically (i.e. less densely) arranged. The very last CI-HS was shorter than in *L. nobrei*-echemes. It could exhibit the same length as its Op-HS, but could also be half or twice as long; it was often somewhat lower than its Op-CH, rarely much quieter or even missing. The Op-HS got normally successively longer during the echeme (Fig. 13a), but the first Op-HS of the part II was often abruptly increased in length. Sometimes the last part II-syllable was detached on account of a missing penultimate CI-HS.

In Fig. 13c an outdoor recording from the Sierra de Gredos (near to the Puerto del Pico) is illustrated. In this recording a response of a female nearby sitting was

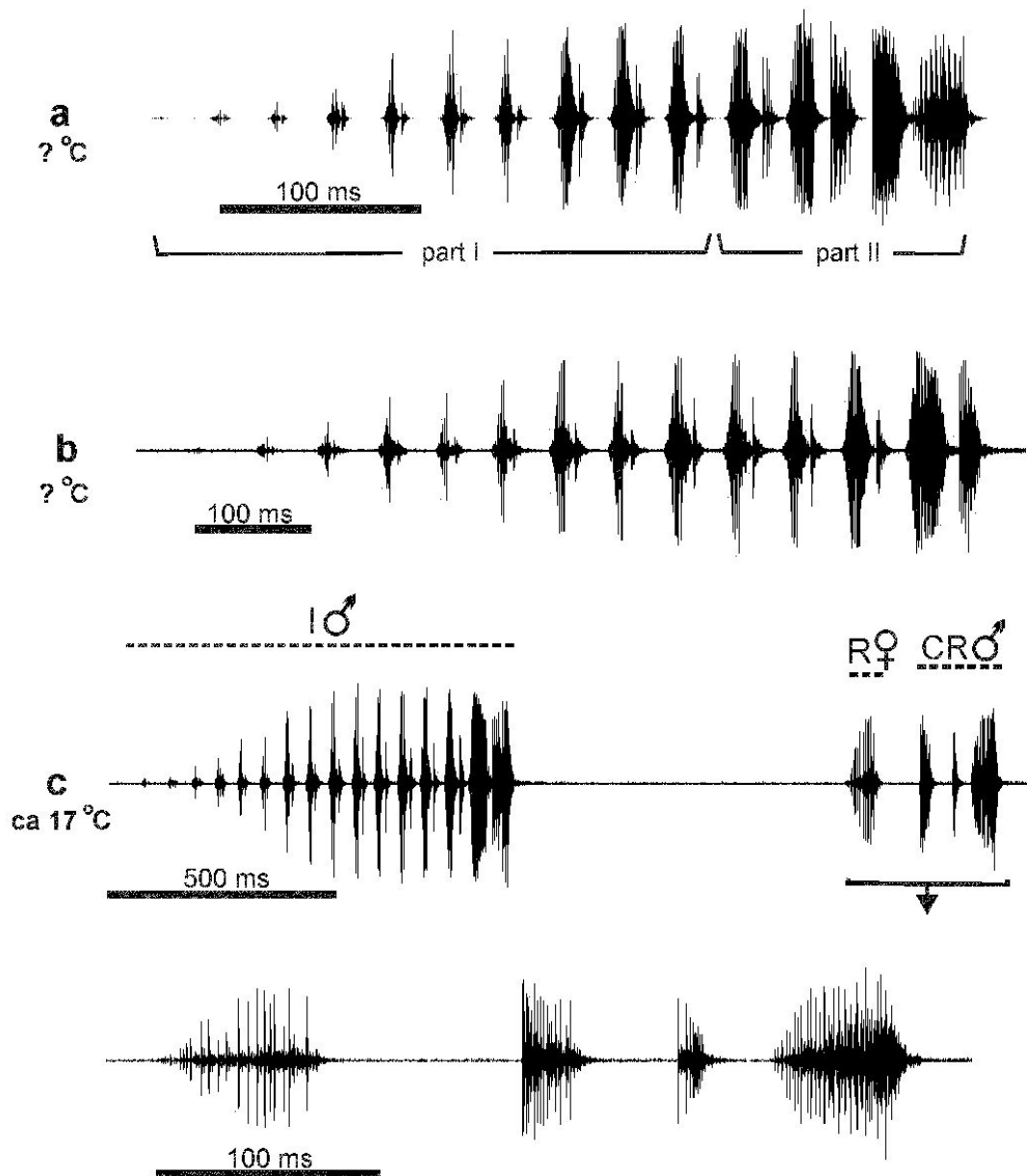


Fig. 13a–c. *Luciapomaresius stalii* (type A).

audible (R ♀), about 730 ms after the male echeme; the male then immediately produced a further signal, the confirmatory response (CR ♂), which consisted of three hemisyllables.

Type B: the echemes of this type contained fewer syllables (about 25–60 % of the syllable number of type A-echemes), which began very low and became only very slowly louder (Fig. 13d–f). The last 1–2 syllables were then abruptly intensified in loudness and length. The CI-HS of this part (mainly the last one) showed typical characters of part II-CI-HS. The last CI-HS was as long or up to 2.5 times longer than its Op-HS; its volume could surpass the Op-HS (Fig. 13e), but could also be lower (Figs 13f, g). Sometimes this hemisyllable was totally lacking. As in type A-echemes the last syllable could occur detached, if the penultimate CI-HS was suppressed (Fig. 13f).

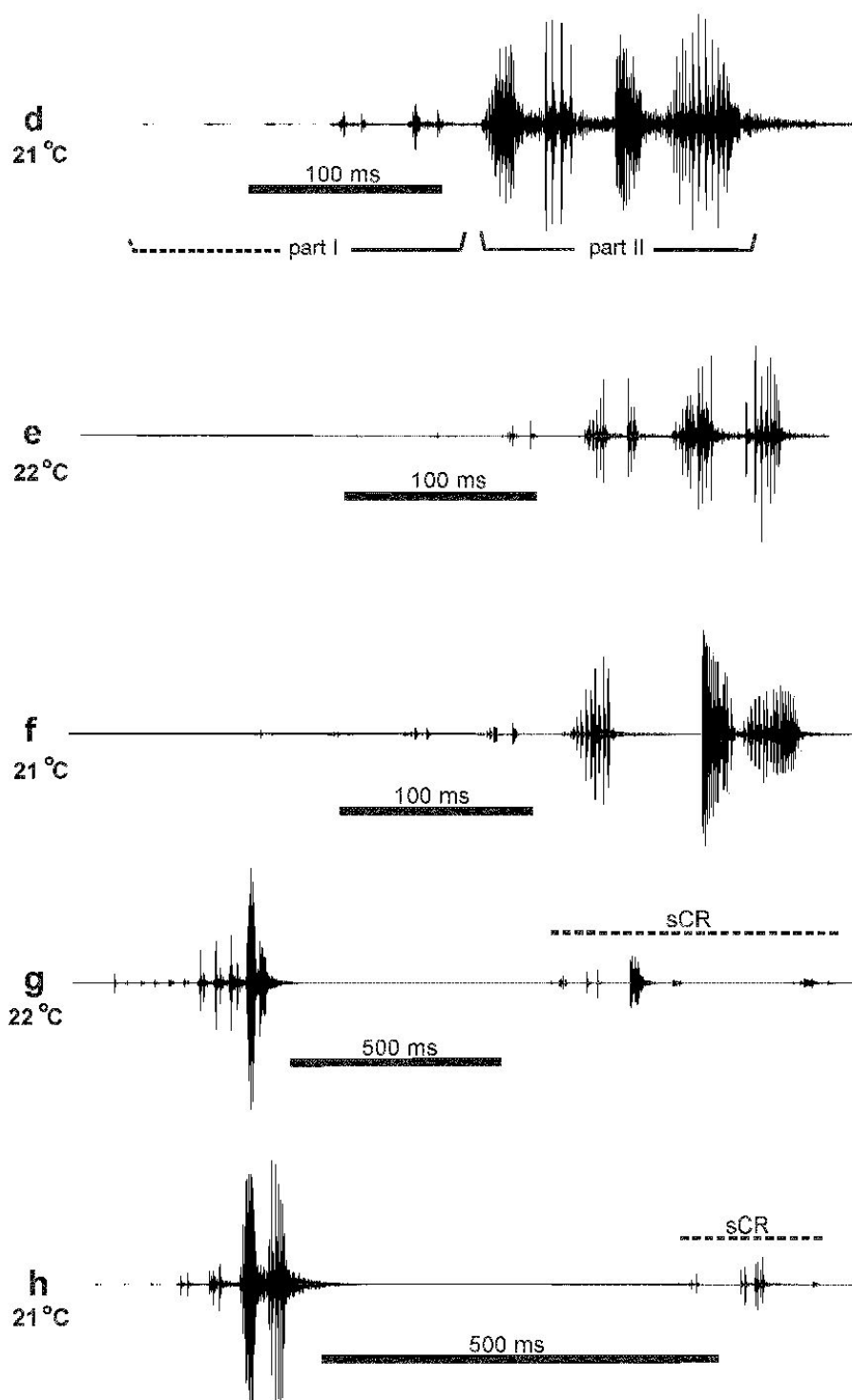


Fig. 13d–h. *Lluciapomaresius stalii* (type B).

On account of the fact that most introductory syllables (part I) were extremely low, only 1–4 part II-hemisyllables were prominent at all in type B-echemes. These echemes were in marked contrast to the much longer type A-echemes.

Spontaneous confirmatory responses were produced quite often by a male from Galve de Sorbe (Figs 13g, h). In an afternoon surveillance (5.10.2012) this male sang initial songs on average every 53 sec; every fifth echeme was on average

supplemented by a spontaneous confirmatory response. The spontaneous confirmatory responses were the result of tiny movements of the tegmina, which occurred between 0.37 and 1.8 sec after the initial song (at 21–22 °C); they were always much lower than the initial songs (in contrast to the CR of the type A-male, illustrated in Fig. 13c) and very variable.

The song activity of the male of Galve de Sorbe was remarkably high in some (relatively warm) nights: e.g. in the night of 5./6. 10. 2012, 620 echemes were produced (at 21–22 °C) in 6 hours and 10 minutes (1.7 echemes/min; average length of pauses: almost 0.6 min). In this night 24 spontaneous confirmatory responses were registered. Instead, in a relative cold other night (24. / 25. 9. 2012, 17–12 °C), only 124 echemes (= about 0.2 echemes/min) but not a single sCR was recorded in 10 hours.

Heller (1988, Abb. 81 A) documented a rather low appendage to a normal echeme, produced by a male from Atienza (a region which is quite near to Galve de Sorbe) by means of irregular movements of the tegmina, which were partly silent (l.c. p. 181). In terms of our analysis, this sequence constitutes a spontaneous confirmatory response. According to Heller's registration the loudest hemisyllable of the sCR in Fig. 13g could represent an Op-HS.

Both types, A and B, were documented by Ragge & Reynolds (1998, Figs 588, 589) from specimens of the same region in the Sierra de Guadarrama (Puerto de la Morcuera). On the other hand an echeme of *L. stalii* from the Puerto de Seranillos (recording «urst8401.wav» of K.-G. Heller; <http://www.biologie.uni-ulm.de/systax/>), a place near to the Puerto del Pico in the Sierra de Gredos (the locality of type A-songs; Fig. 13c), resembles typical type B-echemes, which were recorded from different places in the Sierra de Guadarrama (Heller 1988, Abb. 81 A, C). It is possible that additional recordings will show mediating characters between type A and B; these types would then constitute extremes of a larger scope of individual variation. Nevertheless, the differences in song-structure – and apparently also in special characters of the antiphonies between males and females – could indicate different subspecies or species in central Spain, which live close to one another (compare also the different titillators in the Figs 14h, i and *L. aff. stalii*).

14 *Lluciapomaresius aff. stalii*

Songs of *L. aff. stalii* were heard mainly during the day in the Sierra de Candalaria, a small mountain range near the northwestern Sierra de Gredos. The echemes (Fig. 14a) consisted of a relatively short crescendoing part I, composed of louder (and longer) Op-HS and lower (and shorter) CI-HS. A pronounced last CI-HS (as in *L. stalii*, *L. nobrei* and *L. ortegai*) was lacking; the last CI-HS, however, showed sometimes few pulses with a larger pulse distance than in the previous syllables, suggesting a «rudimentary» part II-CI-HS. In comparison with *L. stalii* the echemes sounded less harsh, since low frequencies (below 4 kHz) are very quiet.

The antiphonies between males and females were very variable (Figs 14b–d; cf. also Pfau 1996, Abb. 20). The females responded to the initial song with 1 to 4 syllables, which were of equal loudness or crescendoed (cf. Pfau 1996, Abb. 20 c, d); the last response-syllable was often detached (Fig. 14c; R ♀); the Op-HS of the response-syllables were lower or missing (Fig. 14d). The male produced 1–3 con-

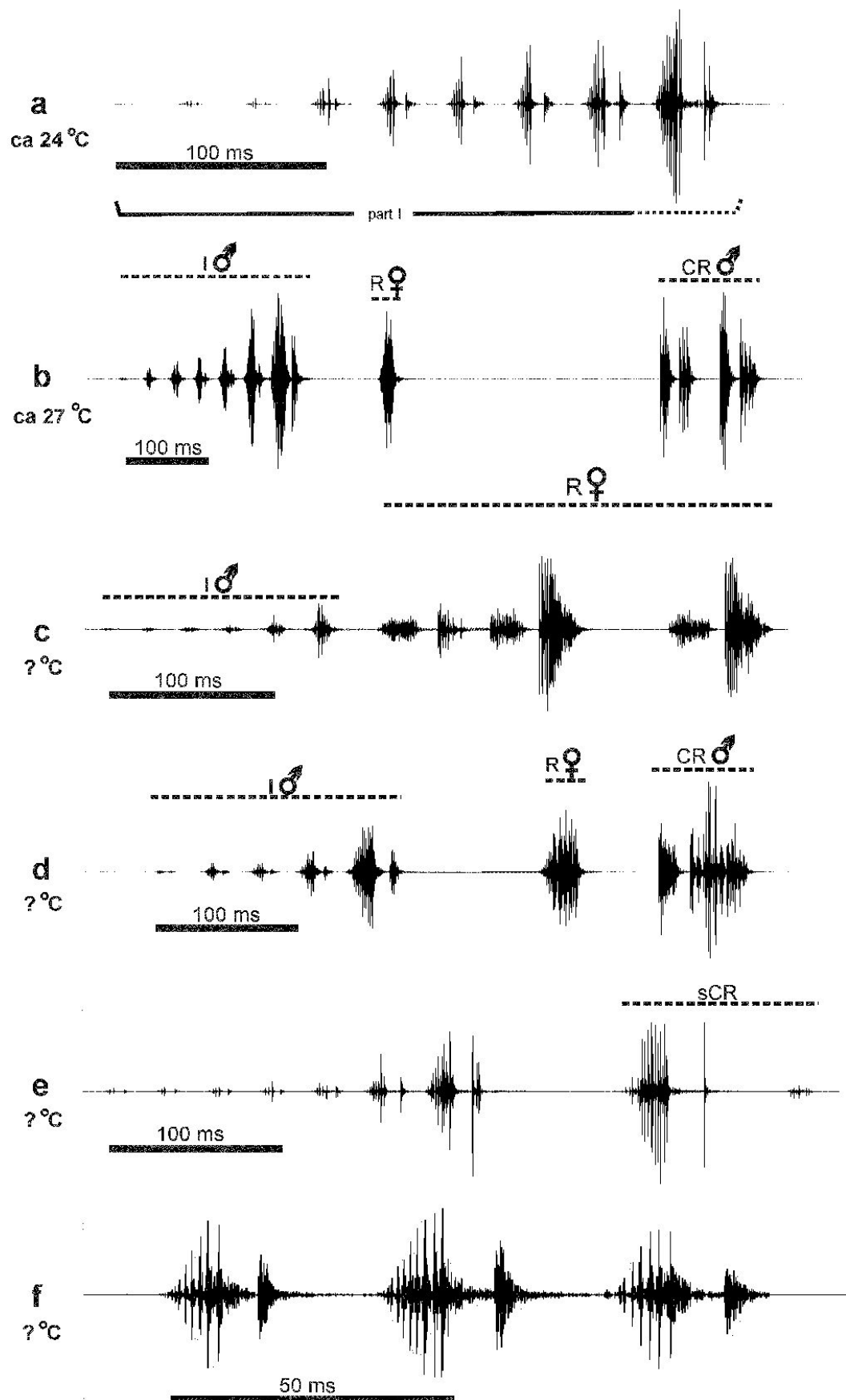


Fig. 14a-f. *Lluciapomaresius aff. stalii*.

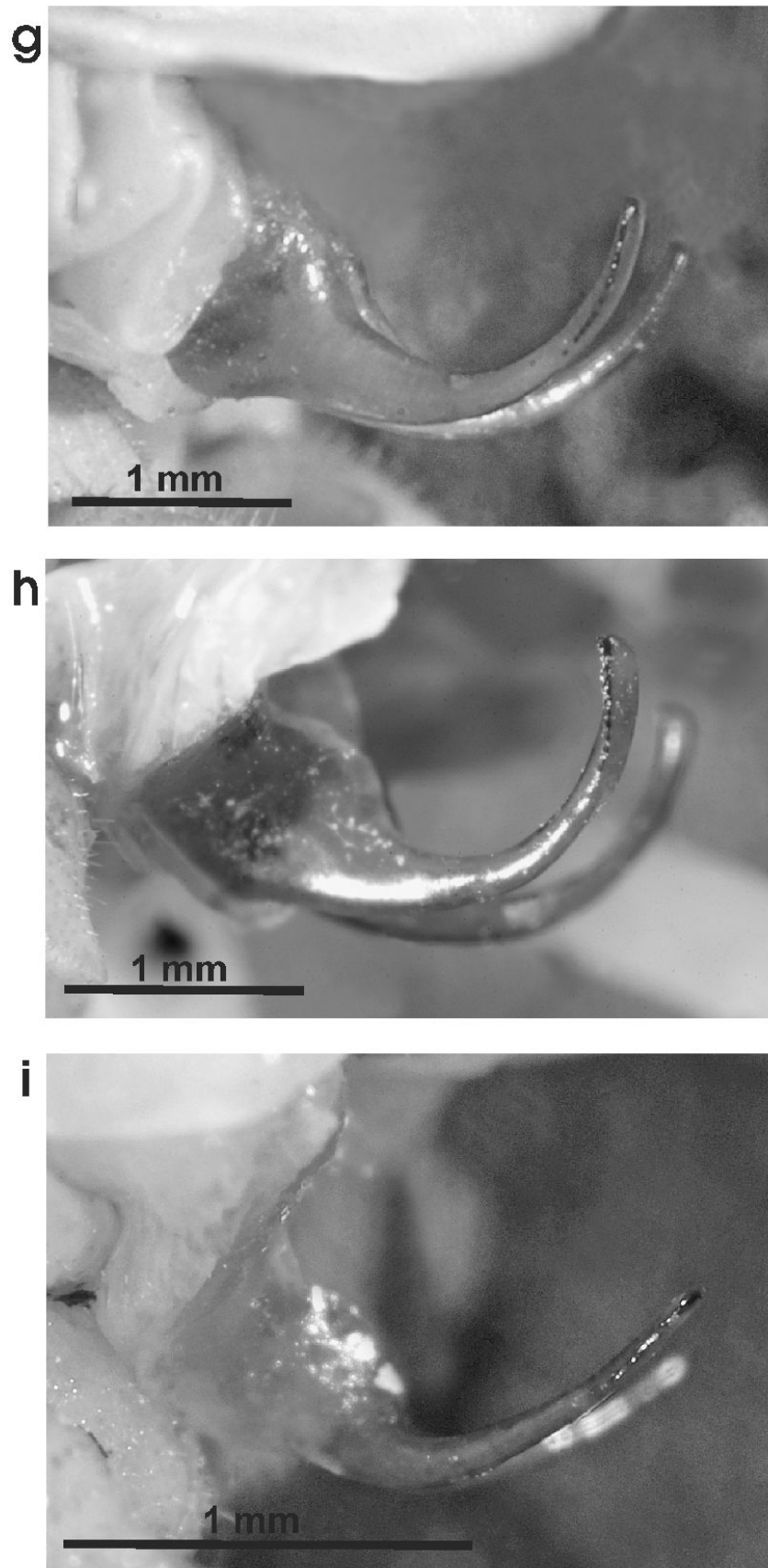


Fig. 14g–i. Lateral aspect of the distal parts of the titillators. (g) *Lluciapomaresius* aff. *stalii*, (h) *L. stalii* (Sierra de Gredos), (i) *L. stalii* (Sierra de Guadarrama).

firmatory response-syllables (Figs 14b, d; CR♂), of which the first were often lower or shortened (Pfau 1996, Abb. 20e–g); sometimes the confirmatory response consisted of only one hemisyllable, apparently an Op-HS (similar to the Op-HS of the sCR in Fig. 14e). Overall, *L. aff. stalii* showed a large variety of female responses and male confirmatory responses, especially with respect to the time intervals initial song/response (17–134 ms, up to 420 ms in one case) and response/confirmatory response (42–320 ms).

In spite of the variability of the confirmatory responses, an occasional similarity to part II-syllables of echemes of *L. stalii* is noteworthy: the CI-HS were as long as or up to 3 times longer than their preceding Op-HS and showed sometimes less densely arranged pulses (Fig. 14b), possibly again a reminiscence of formerly long part II-syllables in the initial song of antecedents.

A spontaneous confirmatory response (sCR), produced without preceding female response, is illustrated in Fig. 14e (cf. also Pfau 1996, Abb. 20f, g; in Abb. 20g two response-syllables of a female were induced by precursory male sCR-syllables – the female responses for their part were confirmed by a final male CR).

In the recording illustrated in Fig. 14c the microphone was targeted towards the female to show the syllable-structure of the response in details. Sometimes the female produced a quick series of syllables spontaneously (Fig. 14f), but in this case the syllables were different and resembled those of the male initial song.

The titillators of the males (Fig. 14g) are strongly bowed like in males of *L. stalii* from the Sierra de Gredos (Fig. 14h), which is presumably a synapomorphic character; nevertheless Pfau (1996) estimated the population of the Sierra de Candelario as a possible true subspecies or species on account of its structurally different initial song. In all other studied populations of *L. stalii* the titillators were bent less strongly (Fig. 14i) or were even nearly straight.

15 *Parasteropleurus martorellii* (Bolívar, 1878)

In the short inconspicuous echemes of this species the first syllable was very low; the second, already much louder syllable was followed by two or three approximately equally loud syllables, which increased slowly in length (Fig. 15). The syllables were structurally similar among each other and correspond to part I-syllables, except for the higher volume of the CI-HS. Interestingly, some other echemes of *P. martorellii*, recorded by Heller (as cf. *flavovittatus*; later determined as *P. martorellii* by Barat and Heller), show a prolonged last CI-HS with less densely arranged pulses, indicating that part II-syllables already existed in antecedents (see Fig. 25 and discussion).

Heller (1988) evaluated *P. martorellii* and *P. perezii* (see below) as bioacoustically and morphologically very similar and concluded that they may represent races of the same species. All our collected specimens of *P. perezii*, however, differ from *P. martorellii* considerably, with regard to the songs as well as to the morphology.

16 *Parasteropleurus perezii* (Bolívar, 1877) (Fig. 16a)

Fig. 16b shows a rather regular series of echemes of *P. perezii*, which was recorded in an open pine forest in the Serranía de Cuenca. At first glance the focused male (♂ 1, Figs 16c–f) appeared to vary the length of his echemes permanently. An

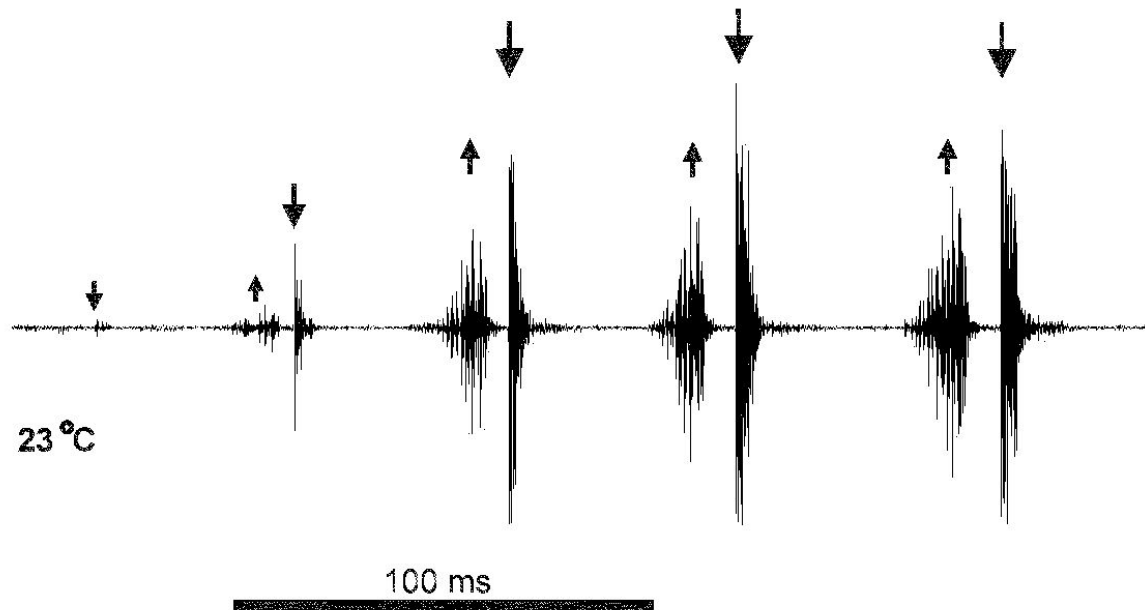


Fig. 15. *Parasteropleurus martorellii*.

analysis, however, showed that a female had responded very shortly after some of the initial songs and (already in the first echeme of the series – time-expanded in Fig. 16c) this female response (R ♀ 1) was followed (after 60 msec) by a male confirmatory response (CR ♂ 1). On the other hand, there was no female response in the third initial song of the series (Fig. 16d): the individual initial song represented a much reduced echeme, which consisted in principle of only a single loud CI-HS (for details, see below).

In the penultimate echeme of the series (Fig. 16e) the same female (♀ 1) apparently responded to another male (I ♂ 2, which was too far and low to appear at full size in the oscillogram) and our special ♂ 1 reacted again immediately with a confirmatory response. Fig. 16f illustrates an antiphony of another male and female (I ♂ 2, R ♀ 2, CR ♂ 2) to which ♀ 1 apparently also responded, provoking for her part again a confirmatory response of ♂ 1.

It was difficult to distinguish Op-HS and CI-HS in these recordings. With the help of Heller's registrations of the movements of the tegmina (Heller 1988, Abb. 82 A, B, I), the possible homology and structure of the sounds could be deduced. According to this, the first two loud sounds in Fig. 16c (I ♂ 1) represent both together a single CI-HS, which shows a relative large gap of ca 10 msec (first curved arrow), caused by a stagnating (or hooking-pause) of the tegminal movement. The CI-HS of the confirmatory response (CR ♂ 1) was even three-parted: the tegmina stopped for about 7 ms and then for 3 ms (two further curved arrows below the confirmatory response) before they snapped to the closed end-position. The two to three very low first hemisyllables of the (complete) initial song are accordingly also all indicated as CI-HS (Fig. 16d).

We found places with large populations of *P. perezii* in the pine forests of the Serranía de Cuenca. In spite of the very short and inconspicuous initial songs of the males, an impressive natural event was sometimes offered: numerous males and females produced antiphonies at the same time and the whole sunlit forest crackled mysteriously.



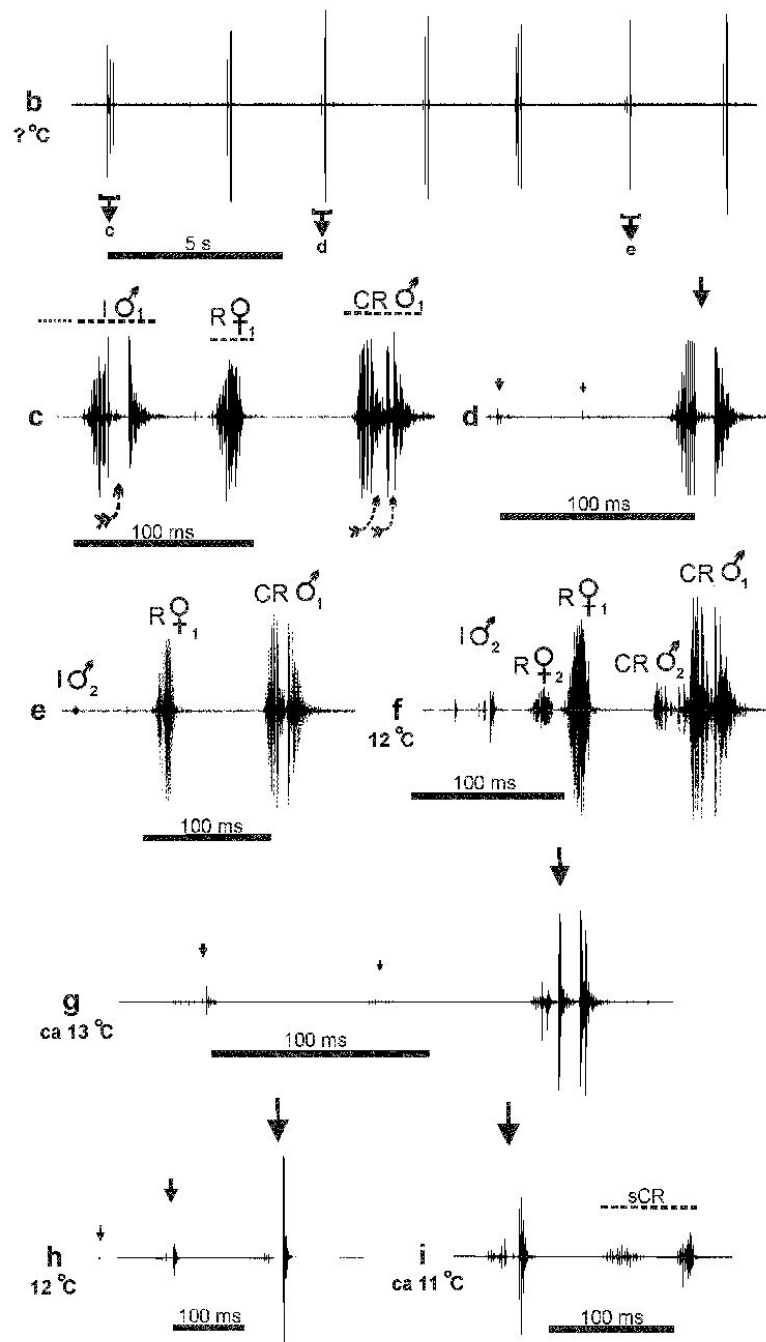
Fig. 16a. *Parasteropleurus perezii*, singing male.

Echemes of another male of *P. perezii* (from the Sierra de Montsant), which consisted of extremely short hemisyllables, are illustrated in Figs 16 g–i. In most cases (see Fig. 16g) the loudest last CI-HS of these echemes showed – in spite of its shortness – the typical specificity of the CI-HS of this species, which has been described above for the males of the Serranía de Cuenca.

This male of the Sierra de Montsant rarely sang two to three crescendoing «syllables» with very short «pulses» (Fig. 16h), reminiscent as a whole clearly of echemes of *P. martorellii* (Fig. 15). It should, however, be pointed out that the temperature during this recording was rather low, at least 10 degrees less than in the Figs 16b–f; therefore the sequence of Fig. 16h presumably consisted of three hemisyllables (more precisely: CI-HS with gaps!) – in contrast to *P. martorellii*, where complete syllables formed a superficially similar series.

In a surveillance at night (about 5.5 hours at 18–10 °C) the male from the Montsant sang 160 echemes with pauses between 1 and 11 minutes; the mean interval between the echemes was 2 minutes. Only in one case this male appended further sounds to an echeme (Fig. 16i); this whole sequence is interpreted as an initial song, which was followed by a spontaneous confirmatory response.

The high degree of secondary reduction and «disorganization» of the initial song of *P. perezii* is interpreted as an autapomorphic feature, allowing to separate this species (with rare exceptions, attributed to an accidental resemblance; see Fig. 16h) clearly from *P. martorellii*. Besides, there are morphological characters, which

Fig. 16b–i. *Parasteropleurus perezii*.

distinguish these two species: the much more spaced dentition of the tegminal file in *P. perezii* (and its different denticles; cf. Heller 1988, Abb. 157 B), the finer network of veins in the tegmina and the difference in the female abdominal sternites + subgenital plate (Harz 1969, p. 553; Barat 2012, Fig. 9).

17 *Sabaterpia taeniata* (de Saussure, 1898)

S. taeniata males sang very long steady series of short echemes, consisting of only one or two syllables, which were produced by tiny movements of the tegmina (Figs

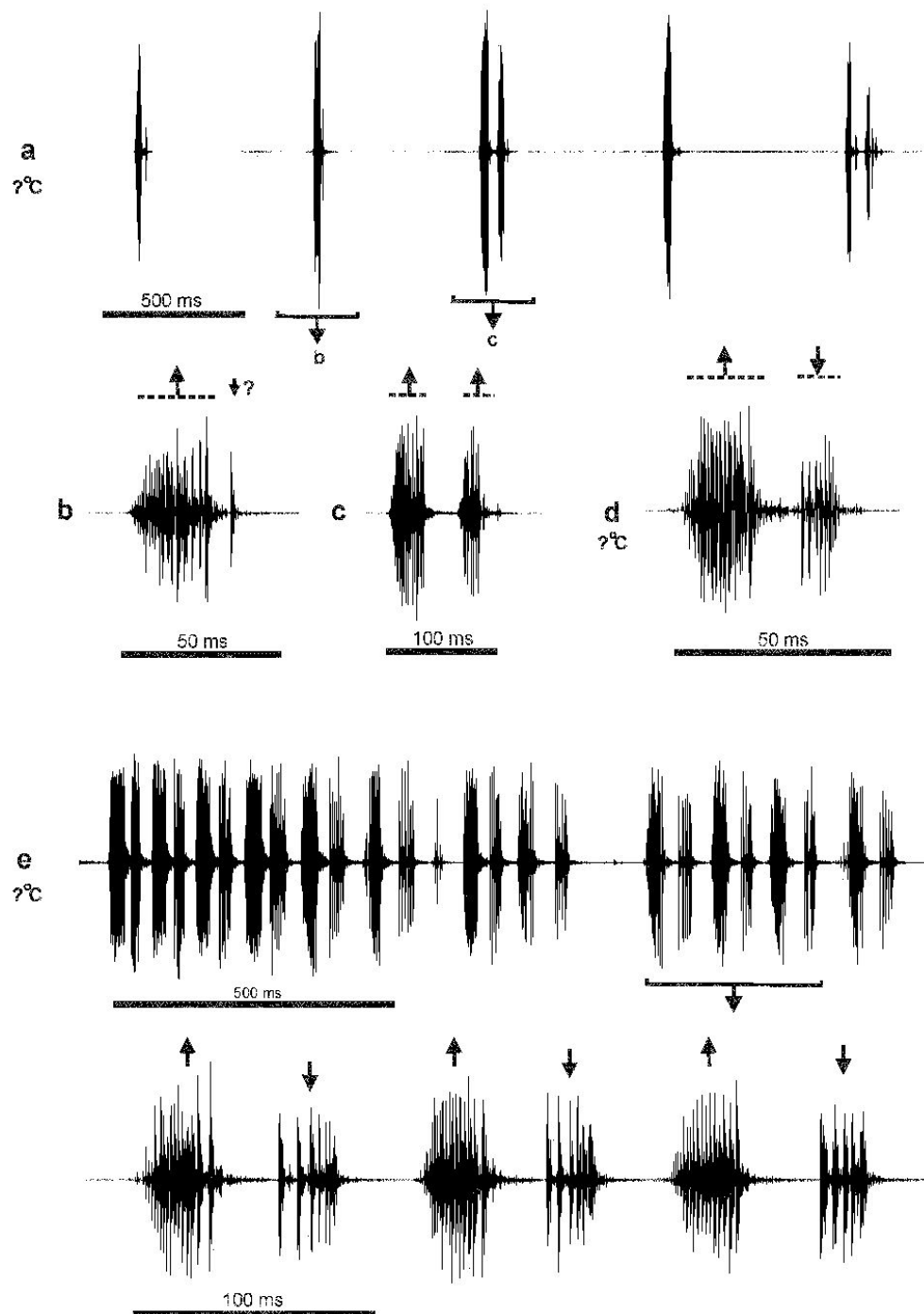


Fig. 17. *Sabaterpia taeniata*.

17a–d). A dense population occurring near Zahara de los Atunes in southern Spain produced an indescribably high level of noise.

Reminiscent of the ticking of a clock, these echemes are here called «ticks» (= «chirps» in Stiedl *et al.* 1994). In some of these ticks an Op-HS (according to Heller 1988, Abb. 79F) was followed by a lower and usually shorter CI-HS (Fig. 17d), but in others the CI-HS were very low or reduced. This concerned also the two-syllable ticks (Fig. 17c), either in the first or in the second syllable or in both.

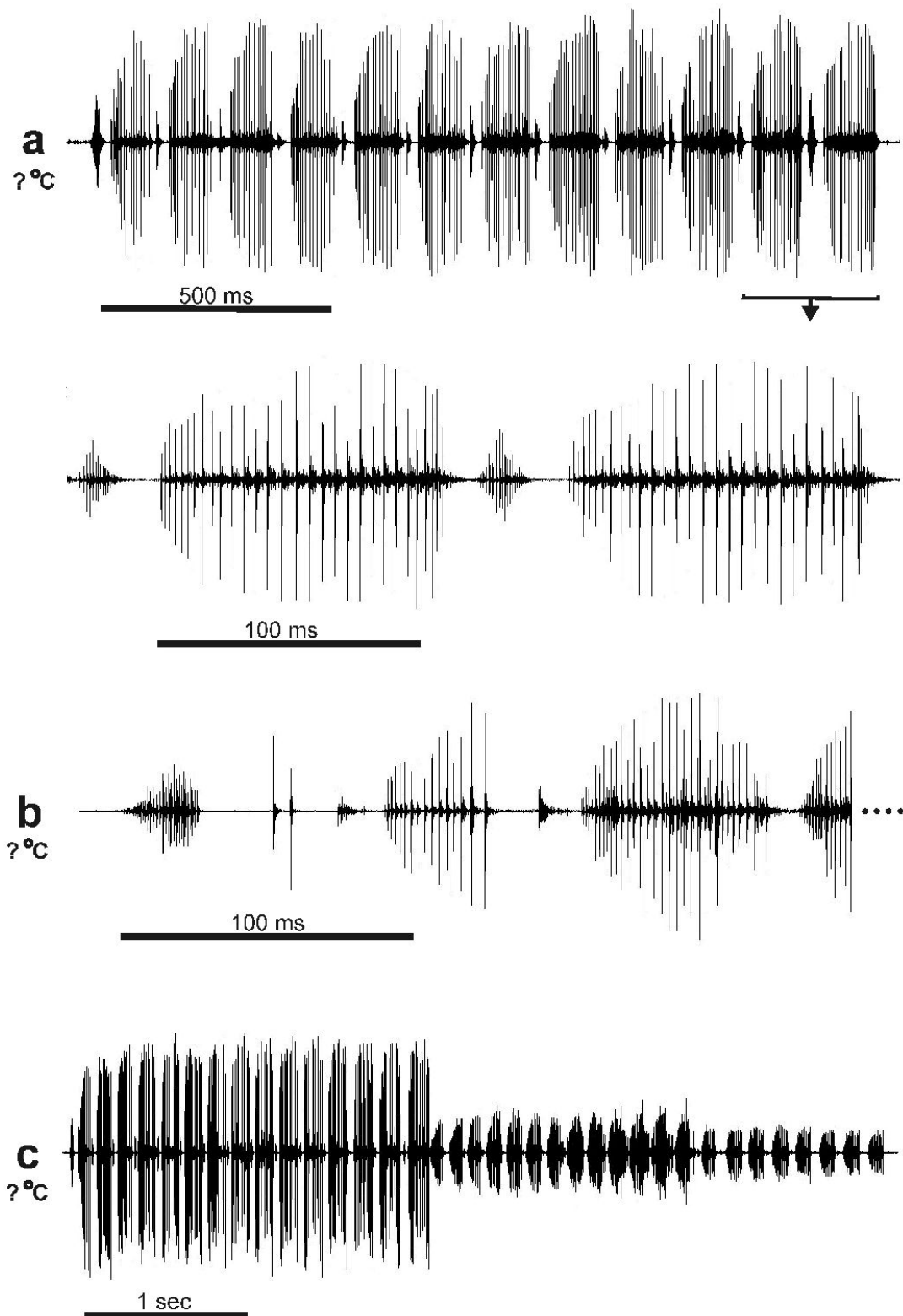


Fig. 18. *Sorapagus catalaunicus*.

Since the Op-HS was sometimes two-part – or presented a last pulse, which was detached – it was not possible to decide in every case whether a CI-HS was present or not (see e.g. Fig. 17b).

Antiphonies of two males (alternating tick-series) sometimes flowed into aggressive stridulations, i.e. very quickly emitted series of one syllable to more than a dozen loud syllables, which could be split into several parts (Fig. 17e). Concluded on account of the different pulse design (similar to the two hemisyllables shown in Fig. 17d), the sounds presumably represented Op-HS and Cl-HS; the Cl-HS showed all stages of reduction, just as in the ticks. However, the length of the Op-HS and Cl-HS was in aggressive songs usually nearly twice to three times as long as in the ticks. Sometimes aggressive stridulations and tick-series were produced alternately between different males for up to half a minute.

Aggressively singing males tried to approach one another and finally fought with each other (or possibly attempted to mate?).

In the field the animals showed a special hiding behavior: they stiffened and narrowed, and pressed the underside of the abdomen closely against stems or leaves of plants to appear like a part of that plant.

18 *Sorapagus catalaunicus* (Bolívar, 1898)

The echemes of *S. catalaunicus* consisted of rather long series of 8–16 similar syllables (Fig. 18a). The very first syllables exhibited sometimes a particularly loud Op-HS, followed by a shorter Cl-HS (Fig. 18b); then the Cl-HS increased in length. This indicates that the whole rest of the echeme constitutes the prolonged part II of an echeme.

In the middle section of the echemes several syllables showed the same length, whereas the last 3–4 syllables could be successively prolonged. The Op-HS were visible in several oscillograms, but much lower. The songs sounded rough on account of the presence of lower frequencies – in contrast to echemes of *Platystolus surcularius*, which in other respects showed a very similar overall structure.

During the beginning of the outdoor singing activity several males could line up their echemes as in Fig. 18c; sometimes, however, the echemes alternated for a longer time or were executed strictly simultaneously.

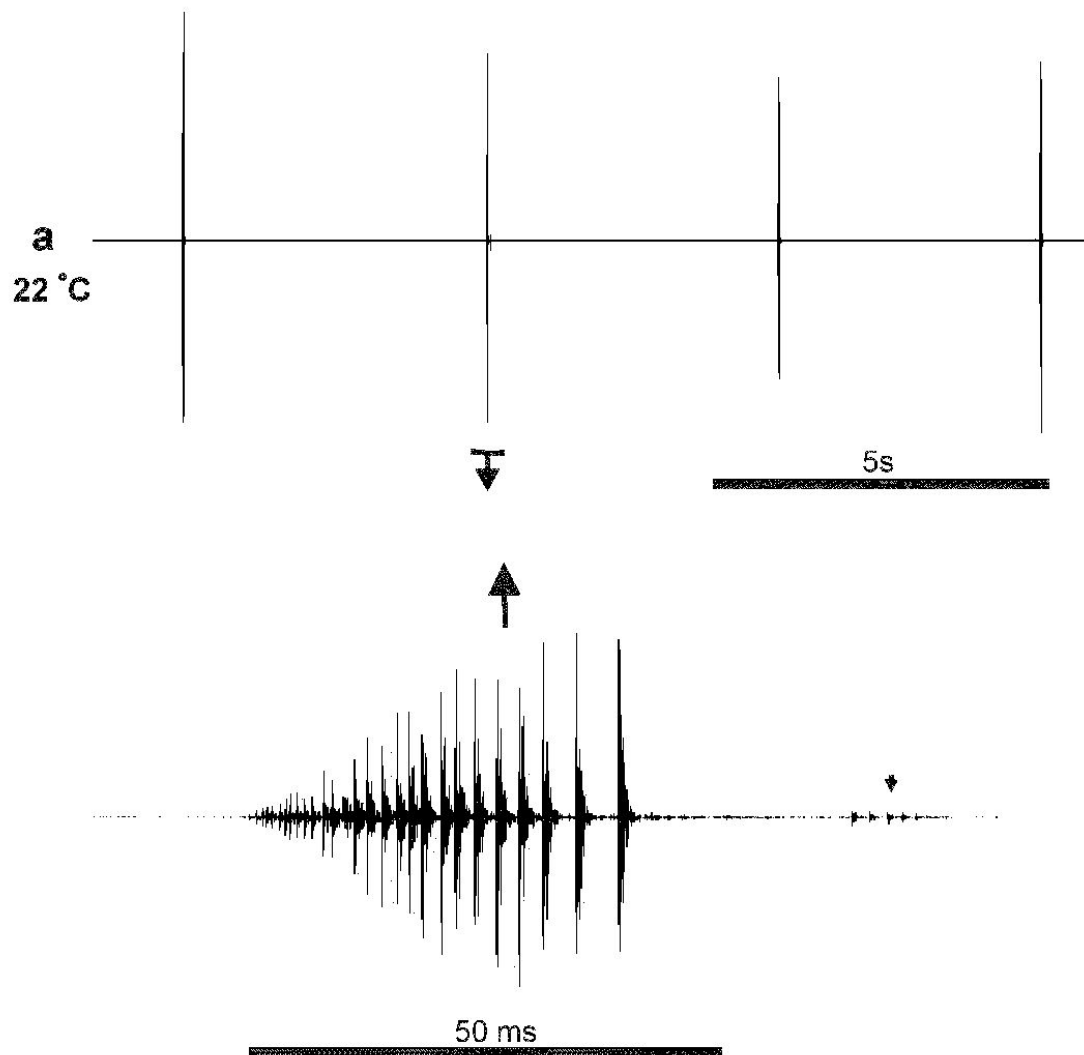
Sitting in nearby cages *S. catalaunicus* and *Ephippiger diurnus cunii* males stimulated one another to produce echemes. The syllable-frequency of *S. catalaunicus* was at the same temperature slightly higher than that of *E. diurnus cunii*.

19 *Steropleurus andalusius* (Rambur, 1839)

Fig. 19a shows a series of «echemes» of this species, a mere row of single hemisyllables, which – according to Heller (1988, Abb. 82F) – represent Op-HS. These Op-HS, which were apparently slightly shorter than those of *S. pseudolus* (Fig. 21), exhibited a typical crescendo of pulses and a decrease of pulse-frequency towards the end. The following Cl-HS were rarely visible as very inconspicuous hemisyllables in the oscillograms.

Recordings, published by Heller (1988) and Ragge & Reynolds (1998), originate apparently from *S. andalusius levantinus* Bolívar, 1908; the oscillograms of the echemes of this eastern subspecies show Op-HS, which are markedly longer (at 23 °C and more than 24 °C!).

Fig. 19b shows the ventral aspect of the end region of the female abdomen. If the ovipositor is completely outstretched, two hard sklerotized regions of the distal

Fig. 19a. *Steropleurus andalusius*.

subgenital plate are visible (arrow), which form sharp longitudinal medial borders. During ovipositing, the downward bent ovipositor will presumably impress the membranous caudal mid region of the subgenital plate, whereby the hard borders will function as lateral safeguards. Corresponding places were found to be only weakly sklerotized in the females of *S. pseudolus*.

20 *Steropleurus brunnerii* (Bolívar, 1877)

The echemes of *S. brunnerii* (Figs 20a–c) were very simple, consisting in many cases of only one Op-HS (Heller 1988, Abb. 82G), in which the pulse-frequency was high at the beginning and slowed down in the second hemisyllable-half. These Op-HS were considerably longer at (approximately) the same temperature than those of (western) *S. andalusius* (with rare exceptions; see Fig. 20c); the average pulse-frequency was somewhat lower. In some cases a lower and shorter second hemisyllable was distinct (Fig. 20b). This hemisyllable represented obviously a Cl-HS. An older animal (Fig. 20c) produced sometimes syllables with nearly equal loud Cl-HS, which were longer than the Op-HS and showed characteristics of a part II-Cl-HS.

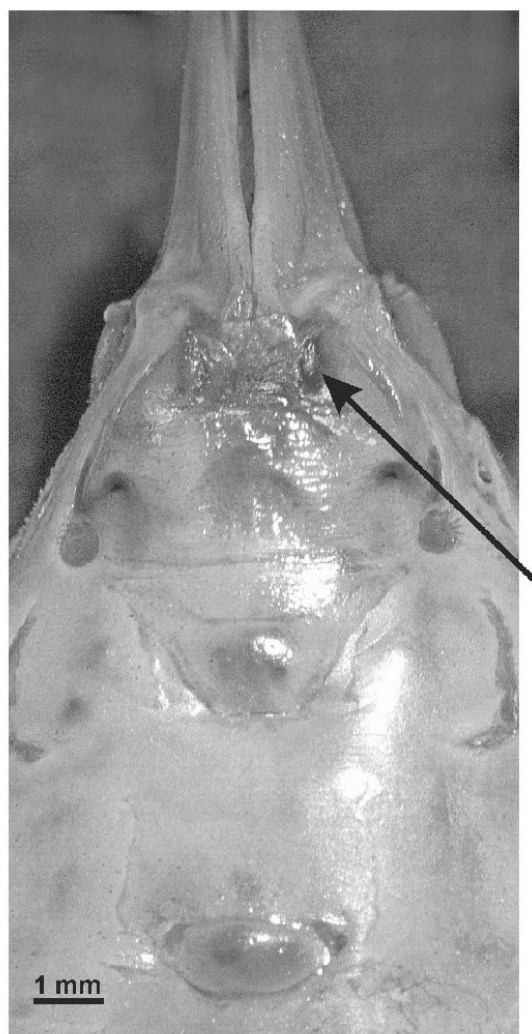


Fig. 19b. *Steropleurus andalusius*, ventral aspect of the female abdominal end (arrow see text).

21 *Steropleurus pseudolus* (Bolívar, 1878)

The loud first hemisyllable of the short echeme of this species (Fig. 21) is interpreted as an Op-HS (as in the closely related *S. andalusius*). Compared with *S. andalusius* (Fig. 19a: Op-HS = 28 pulses) the Op-HS were structurally very similar, but – containing more pulses (31 in Fig. 21) – somewhat longer; in addition the average pulse-frequency was a bit lower. The Cl-HS were recognizable in oscillograms of many echemes, slightly more conspicuous than in *S. andalusius*.

While sitting in the sun two males executed alternating echemes; the time distance between their echemes was 0.6–0.9 sec, rarely only 0.1 sec.

22 *Uromenus agareus* (Bolívar in Brunner v. W., 1882)

Males of *U. agareus* produced dense groups of syllables, which followed each other closely, forming often long series («songs»; Fig. 22a). Each syllable-group represented apparently an echeme (for explanation see below). Apart from few songs with single echemes, the number of echemes in the songs varied between 8

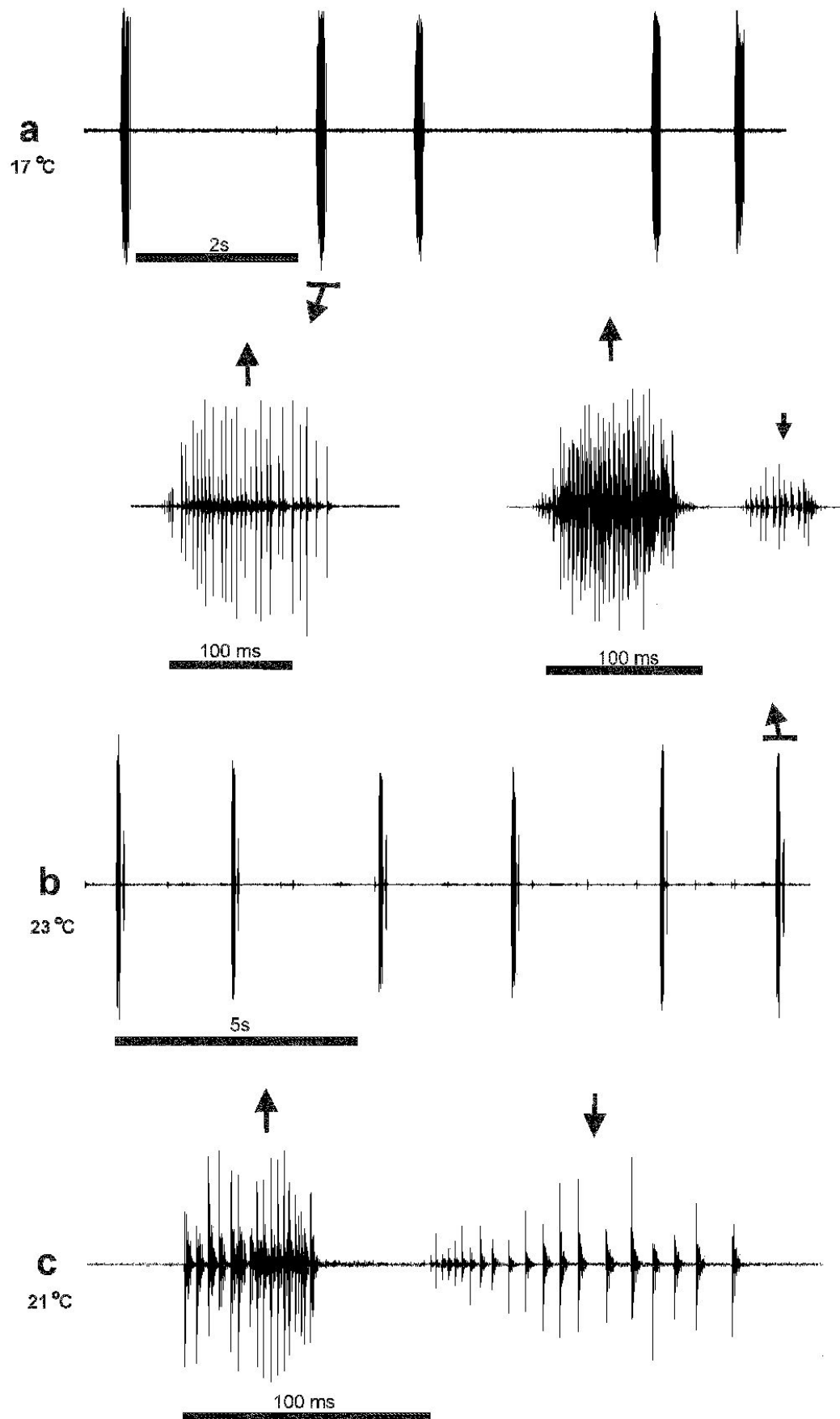


Fig. 20. *Steropleurus brunnerii*.

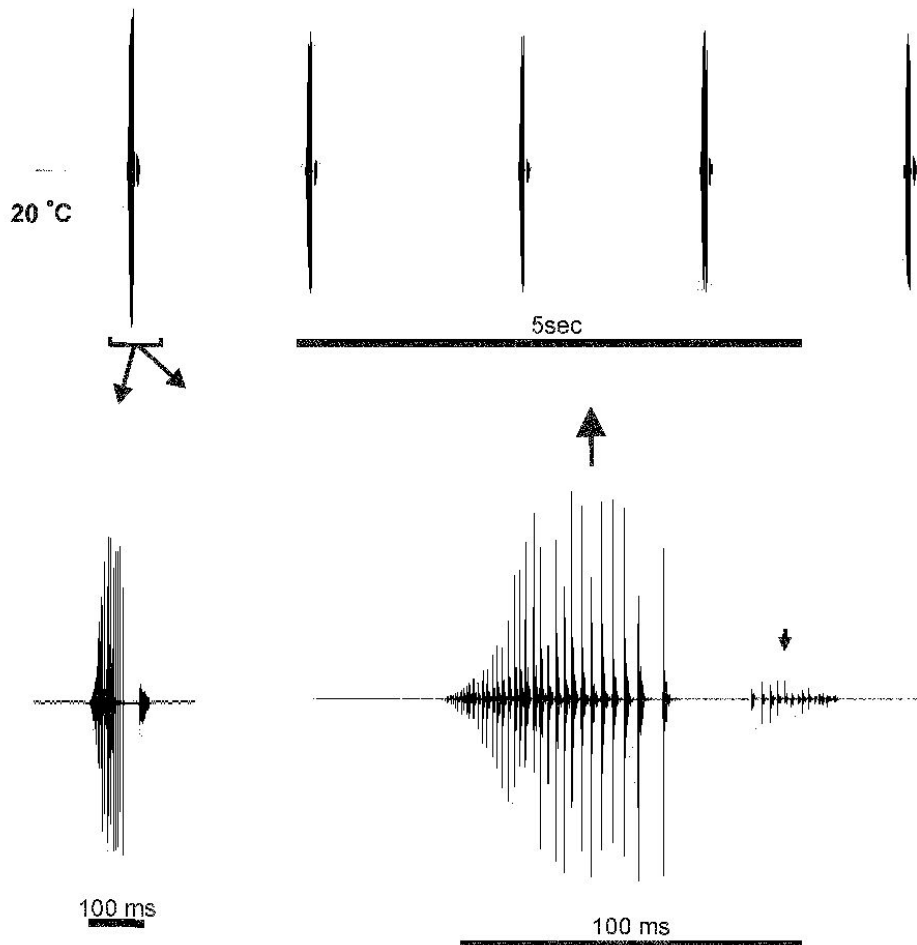


Fig. 21. *Steropleurus pseudolus*.

(Fig. 22a) and 68. A complete song with 42 echemes was 48 sec long (at 26 °C); the longest recording with 68 echemes lasted for 99 sec (at 22 °C).

In some songs the first echemes were shorter and lower and contained strongly crescendoing short syllables (Figs 22a–c). Only in these first echemes were the Op-HS and Cl-HS clearly different and reminiscent of the part I of initial songs of other species (e.g. *Albarracinia zapaterii* or *Lluciapomaresius stalii*). The next echeme already revealed a distinctive difference: the hemisyllables were longer, louder and more similar (Figs 22b, d, e). In spite of this similarity, the Op-HS and Cl-HS were usually distinguishable, since the Cl-HS remained slightly shorter and lower. The almost-equality of Op-HS and Cl-HS in most echemes apparently represents a rare feature among the species of the Ephippigerini.

While in some songs the first 2–4 syllables crescendoed slightly in each echeme (Fig. 22b), the echeme-aspect differed in others from the beginning in that practically no crescendo was apparent; these were possibly individual peculiarities of different specimens.

At the beginning of songs the time distance between the first and second echeme, and also between the echeme 2 and 3, could be up to two times larger than between subsequent echemes. More or less large «irregularities» could occur later inside the songs and also between syllables inside the echemes (Fig. 22e).

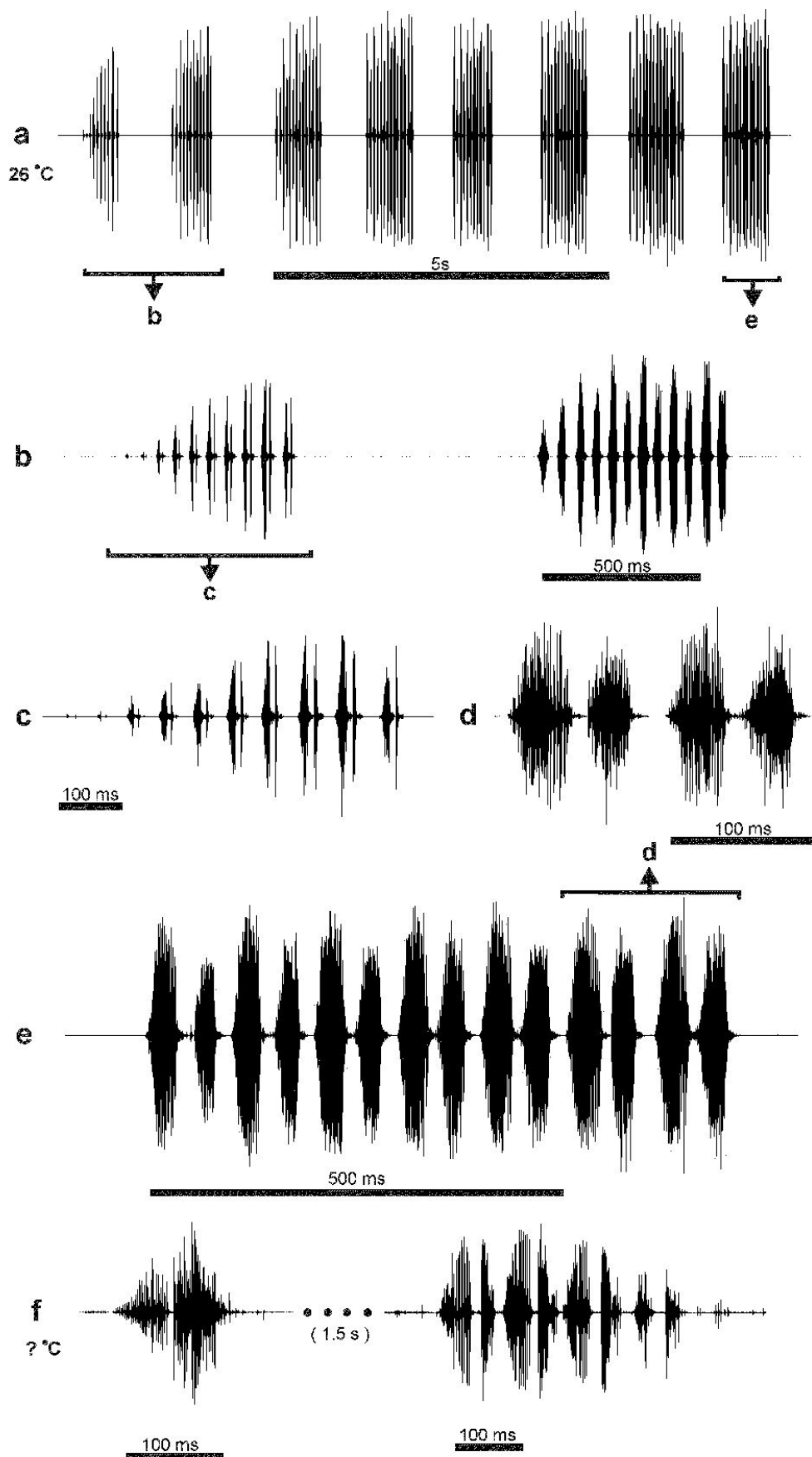


Fig. 22. *Uromenus agareus*.

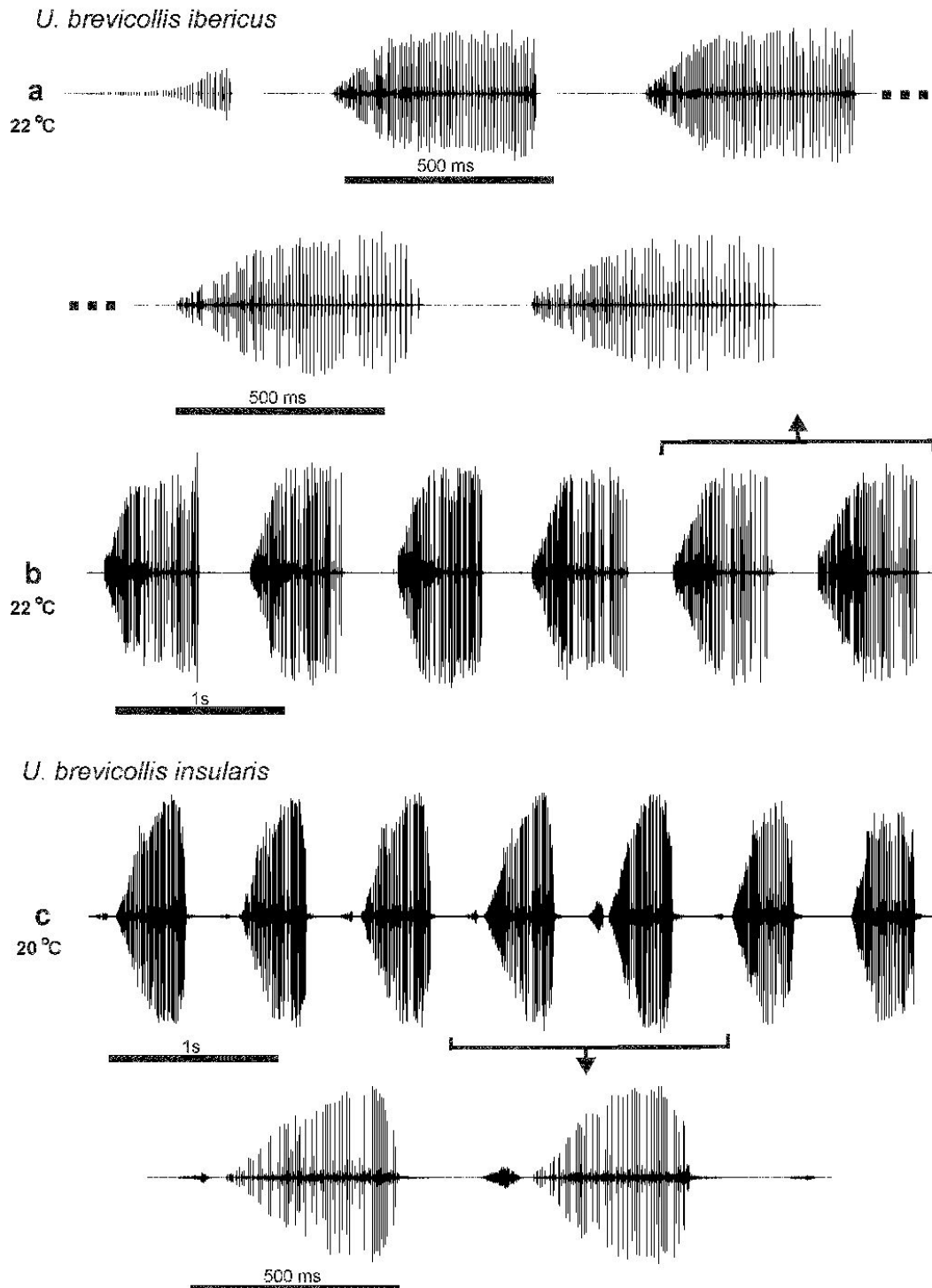


Fig. 23a–c. *Uromenus brevicollis ibericus* (Fig. 23 a, b); *Uromenus brevicollis insularis* (Fig. 23c).

Since the first echemes of some songs were strongly reminiscent of part I of two-part echemes – and on account of the presence of a gradual transition between the first and following echemes in some cases – each group of syllables is interpreted as a complete echeme, of which part II (of a formerly two-part song) presumably got lost.

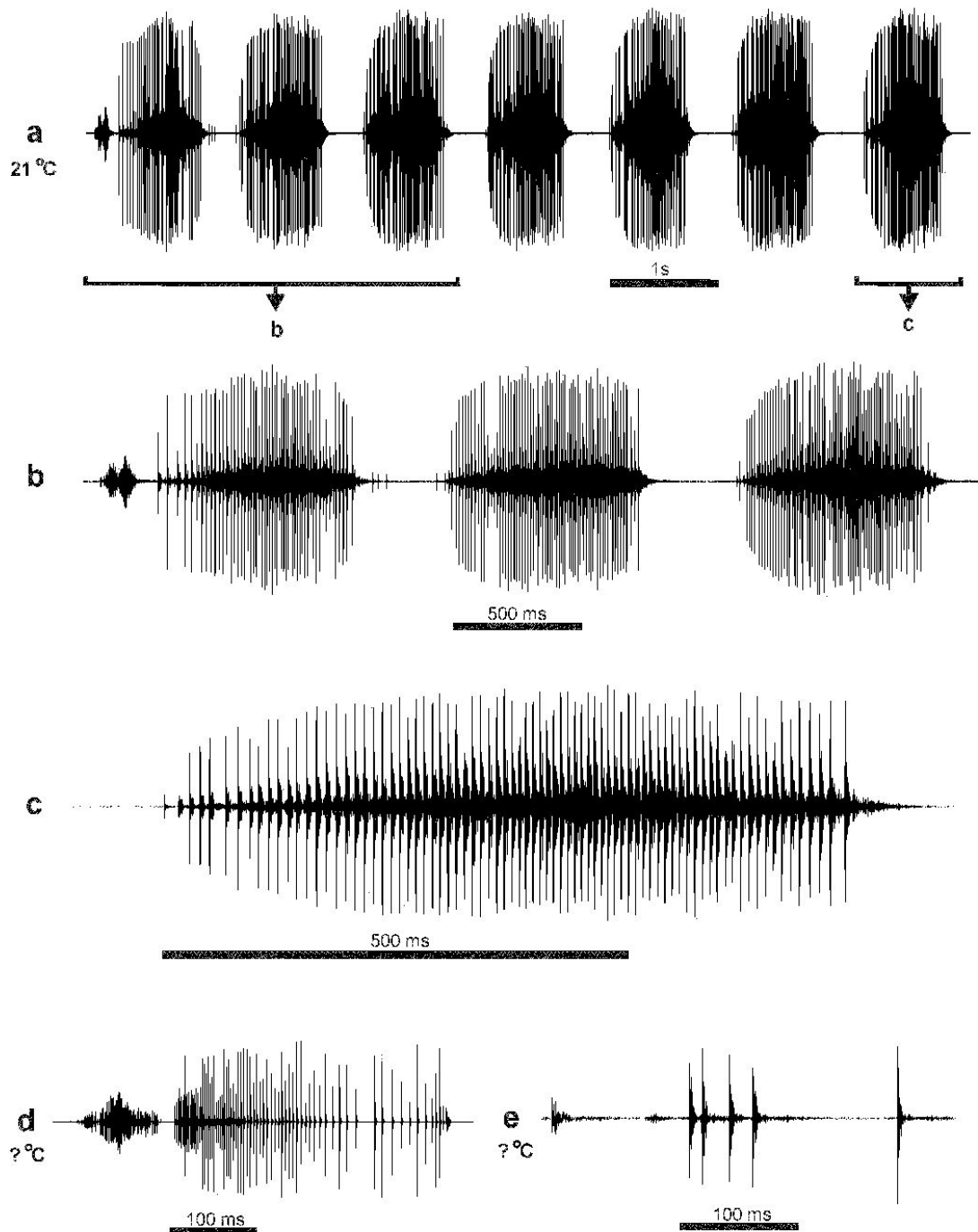


Fig. 24. *Uromenus rugosicollis*.

Structurally different aggressive songs were produced as a result of disturbance or interactions between males (Fig. 22f).

For some interesting behavioral habits of this agile and aggressive species see Schroeter & Pfau (1987).

23 *Uromenus brevicollis ibericus* Schroeter & Pfau, 1987

Fig. 23a shows three syllables of the beginning and two syllables of the end of a very short song (of in total eight syllables) of *U. brevicollis ibericus*. Compared

with *U. agareus* the CI-HS of this series were much longer and the Op-HS were missing. The whole series can be interpreted either a) in total as one very long part II-echeme or b) as a series of one-syllable echemes, each consisting of a single part II-CI-HS (for reasons to derive this song-type from two-part songs at all, see discussion).

Normally, all CI-HS were approximately equally long and loud, but in some series the first CI-HS was more or less lower and/or shorter (Fig. 23a). The pulse-frequency was usually highest at the beginning of the syllable and decreased slowly to the syllable-end (Fig. 23a; cf. the last two syllables). Sometimes, however, a considerable higher pulse frequency was presented also at the end of the syllables (Fig. 23a, syllable two and three). A pulse-crescendo often encompassed the first quarter (to first third or half) of the syllables; it was only rarely extended to the syllable-end (in contrast to *U. brevicollis insularis*, Fig. 23c).

In Fig. 23b the last six syllables of the song (illustrated partly in Fig. 23a) are represented in a different time scale to show some differences compared with songs of a male *U. brevicollis insularis* Chopard, 1923 from Sardinia (Fig. 23c; 6.10.2008, SW of Fonni, 1170 m). *U. brevicollis insularis* exhibited an approximately one third higher repetition rate of syllables and much shorter CI-HS (420 ms at 20 °C); the difference must be even more conspicuous at equal temperature. Complete songs of this male were often extremely long (up to 28 minutes!); we released it after three nights.

A recording of *U. brevicollis insularis* at 18 °C (Brizio & Buzzetti 2014, Figs 4, 5) indicates that the syllable-frequency corresponds approximately to the frequency of *U. brevicollis ibericus* at 22 °C.

Compared with *U. brevicollis trinacriae* La Greca, 1964 from Sicilia (Massa *et al.* 2001, Fig. 11) the syllable-repetition rate of *U. brevicollis ibericus* seems to be quite similar (if one calculates the different temperatures during recording).

The much different titillators of *U. brevicollis ibericus* and *U. brevicollis trinacriae* (cf. Schroeter & Pfau 1987, Abb. 1c; Massa *et al.* 2001, Figs 9D–F) indicate a possible species rank of both subspecies, but the nominate form *U. brevicollis brevicollis* (Fischer, 1853) from Algeria (for which no sound recordings have been published) should also be included in this comparison.

24 *Uromenus rugosicollis* (Audinet Serville, 1839)

This species produced series of CI-HS, which again can be interpreted either as a row of repeated part II-syllables (= numerous one-syllable-echemes forming a secondary assembly, a «song») or as single echemes, of which part II of a formerly two-part echeme is much elongated. These CI-HS-series were sometimes very short (containing one to few CI-HS; e.g. seven in Fig. 24a), but normally endured for many seconds or minutes, respectively. The repetition rate of syllables was considerably lower (about 30 %) than in songs of *U. brevicollis ibericus* (see above).

Short Op-HS were well audible in several songs, but were often totally lacking – particularly in the very first syllable and sometimes also some further syllables. The pulses inside the CI-HS appeared evenly arranged along the whole syllable in many cases (except for a slightly higher frequency at the beginning); in others the density was much lower at the beginning of the CI-HS, became then relatively high and was again lowered towards the end (Figs 24b, c); a reverse case is

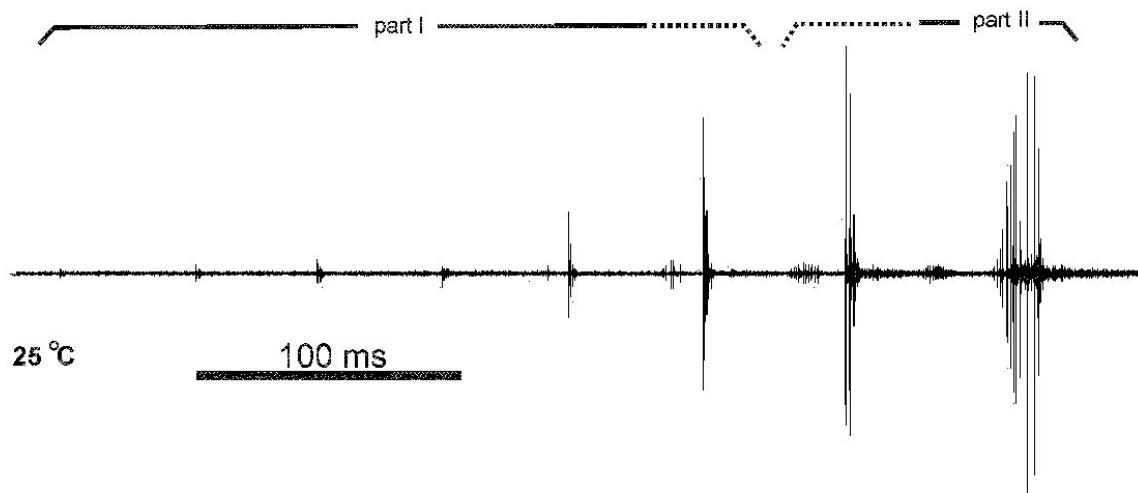


Fig. 25. *Parasteropleurus martorellii* (= *Steropleurus* cf. *flavovittatus* (Bolívar, 1878) in Heller 1988; Abb. 82E); record «urf18414_125.wa» (<http://www.biologie.uni-ulm.de/systax/>). The specimen was newly identified by K.-G. Heller and J. Barat (Barat, pers. comm.).

shown in Fig. 24d, a single syllable of an aged male, which often omitted one to several pulses inside his echemes.

The pulses crescendoed slowly at the beginning of the CI-HS (rarely up to the mid of the hemisyllable) and remained then evenly loud till the end; the syllable-end could sometimes also be enhanced or it could contrarily become lower.

An elder male, kept for 5 months, successively lengthened his songs by and by. These contained at the beginning of his captivity about 50 syllables, but were prolonged within three months up to 500 syllables, which lasted for about 10 minutes. In old age the Op-CH became more distinct. This animal changed his color drastically during its lifetime, from mainly green to brown-purple.

Cracking noises, produced by tiny movements of the tegmina (Fig. 24e), are possibly deterrence-sounds. In other cases, sharp sounding short syllables were spontaneously emitted (no recording).

On an afternoon in the Pyrenees many males could be heard singing in ferns and brooms at the same time, actually a mass singing. The singing then stopped abruptly. After a rather long time of silence one male again began to sing and was immediately followed by many others. The songs were assessed as relatively loud, but were in reality much lower as e.g. the initial songs of *Callicrania ramburii*; this was especially evident if the cages with these species were placed close to one another.

DISCUSSION

Evolution of song patterns within the Ephippigerini

There are indications that two-part songs are more widespread in the Ephippigerini than previously known: 1) typical elements of part I and/or part II could be detected in species with normally strongly different echemes, which could not be interpreted hitherto as derived or plesiomorphic (*Ephippiger diurnus*, *Uromenus agareus*, *Sorapagus catalaunicus*, *Steropleurus brunnerii*; see also *Parasteropleurus martorellii*, Fig. 25, and *Ephippiger apulus apulus*, Massa *et al.* 2012); 2) two-part songs

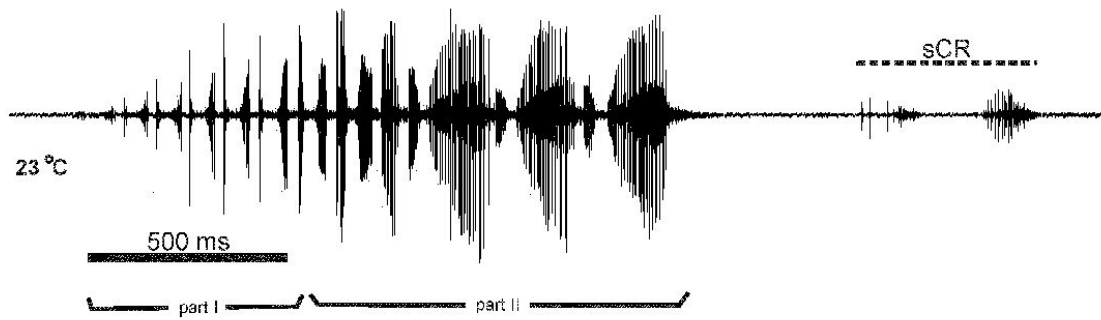


Fig. 26. *Uromenus maroccanus* (de Saussure, 1898) (= *U. cf. robustus* in Heller 1988; Abb. 80E); record «urmr8409s.wav» (<http://www.biologie.uni-ulm.de/syntax/>). The specimen was newly identified by K.-G. Heller (Heller 1995), according to Nadig (1994).

were found to be present also in *Uromenus maroccanus* (Fig. 26), a species of a genus, in which a different type of echemes is predominant.

Long two-part male songs are evaluated as relatively plesiomorphic. These songs are rather uniform in each part: there is a crescendo of short syllables in part I, whereas the CI-HS of part II are particularly loud and prolonged, with wider-spaced pulses. Shortened echemes (e.g. of several species of *Lluciapomaresius* and *Steropleurus*) – and also the much prolonged songs of species of *Uromenus* – are accordingly evaluated as derived, as the result of a transformation or reduction of part I and/or part II. Irregularities of pulses inside syllables and the reversal of the normal hemisyllable-succession are also estimated as secondary acquisitions. The question of the interpretation of series of long syllables with regular intervals (different species of *Uromenus*) is not solvable with certainty, since repetitive singers could simply have prolonged part II of a single echeme or could have used individual (to several?) part II-syllables to form sequences of strongly shortened echemes.

Nevertheless – on account of the hitherto unknown phylogeny of the genera of the Ephippigerini – we are unable at present to reconstruct the ancient song pattern of the stem species of the Ephippigerini.

Origin of the special duetting of the Ephippigerini

Pfau (1996) suspected a possible origin of the complex duetting of the genus *Platystolus* (*Callicrania*, *Platystolus*, *Neocallicrania* and *Synephippius* according to Barat 2012) prior to the last common ancestor of this genus – on account of complex duets, which had been found also in *Steropleurus* (= *Lluciapomaresius*) aff. *stalii*. A convergent origin was, however, not excluded at that time.

Looking closer at the existence and distribution of acoustic interactions of males and females in the Ephippigerini, new observations indicate that complex duets between the sexes are more widely distributed than previously expected. This opinion was at first based on the observation of spontaneous confirmatory responses in males of different species (*Albarracinia zapaterii*, *Lluciapomaresius nobrei*, *L. stalii*, *L. aff. stalii*). Since the spontaneous confirmatory response was also found to be present in most species of *Platystolus* (cf. Pfau 1996), the presence of spontaneous confirmatory responses was considered as a strong indication for the factual existence of three-parted male-female antiphonies. Accordingly we are now

able to make predictions for species, of which full antiphonies (with participation of females) have not yet been documented or even for species of which the female is unknown (for example *Uromenus maroccanus*, see Fig. 26).

The cases, in which the males attach confirmatory responses – which usually constitute the acoustic reaction to the female response – directly to a normal initial song without any factual female response, can be interpreted as a «song-enhancement», as the demonstration of a special courtship motivation, focused on all females in the vicinity. In antiphonies of *L. aff. stalii* the female was in fact sometimes stimulated to respond after a male had already produced one or two spontaneous confirmatory responses (cf. Pfau 1996, Abb. 20g). On the other hand, the observation that strongly motivated females are able to produce from time to time longer (but in most cases lower) spontaneous «songs» (cf. Pfau & Schroeter 1988a, Pfau 1996: *Platystolus martinezii*, *P. selliger meridionalis*, *P. miegii*, *P. surcularius*, *P. obvius*) indicates an equivalent method to check the surroundings for males, which could be stimulated to sing or reply.

For *Albarracinia zapaterii*, *Callicrania plaxicauda*, *Lluciapomaresius nobrei*, *L. ortegai*, *L. panteli*, *L. stalii* and *Parasteropleurus perezii* complete (= three-parted) antiphonies between males and females could be documented in this study for the first time. Due to the distribution of complex duets one could assume that a common ancestor of several genera of the Ehippigerini already performed this type of antiphony. Since the phylogenetic systematics of the Ehippigerini is unknown up to now, it is not possible to determine a probable evolutionary starting point of this capability – or to substantiate a still possible convergent evolution.

No matter whether mono- or polyphyletic, the three-parted male-female dialogue should have evolved *in succession* of the evolution of a female response, which could already have improved the coming-together of sexes (see v. Helversen *et al.* 2012 for a species of the Phaneropterinae). The new female capability to respond could then have led to a less repetitive, i.e. more sporadic singing of the male in coherence with the female response: with the knowledge of an interested approaching female in his vicinity, the male could add fewer and/or shorter echemes to keep in touch with the female.

Considering risks and advantages, one should keep in mind that strongly motivated repetitive singers have particular big disadvantages: their risk to be detected by predators is higher. This is a rather counterproductive situation. The change-over to a restricted repetitive singing – on a case-by-case basis, i.e. in the case of a responding and approaching female – presumably brought mutual benefits: the risks of the male during singing were automatically reduced and he could afford to move by himself; the female was disburdened accordingly.

Primitive confirmatory response songs, which are very similar to normal initial songs, are apparently still existing in certain species (*Platystolus faberi deman-dae*, *L. ortegai*?), but a secondary return to prolonged confirmatory responses cannot be excluded. In most species the confirmatory response has been transformed into a strongly shortened echeme or a single «left over» part of it, usually part II.

In this respect *Platystolus martinezii* represents a rather curious example (Pfau & Schroeter 1988a). In the very long initial songs of this species the confirmatory response could theoretically be interpreted as a delayed part II of the initial song, since the female response appears as brought forward, cutting a «normal» (= two-

part) initial song into two pieces. The confirmatory response of this species, however, more likely simply constitutes a much modified second echeme, which contains only part II-syllables, whereas in the long initial song it is just the part II, which has been reduced. Surprisingly the confirmatory response has been maintained also in the strongly shortened (but highly differentiated) rather low antiphonies of *Parasteropleurus perezii*.

Function of the special duetting of the Ephippigerini

Evolution and benefits of the duetting between males and females in the Tettigoniidae – more precisely: of the two-part duetting of many Phaneropterinae, which go off via male songs and female responses – were object in several comparative investigations (Heller 1990, 2006; Bailey 2003, 2006). In these studies certain Ephippigerini are included only as far as a «normal» (two-part) duetting is concerned, but respective findings, which de facto go beyond this knowledge, were not really noticed.

In the duets of the Phaneropterinae a very short female response is normally executed in a distinct time window, which often follows a special trigger syllable of the male echeme. These duets are in most cases relatively soft and appear to be less suited for a goal-oriented phonotactic movement over long distances. Characteristic trigger syllables at the end of the initial song, or extra loud trigger pulses are normally missing in the antiphonies of the Ephippigerini; they could possibly be present in *Platystolus martinezii* (Pfau & Schroeter 1988a) or *Lluciapomaresius panteli*. Furthermore, the relevant intervals inside the three-parted duets (between initial song and response, and response and confirmatory response) are apparently quite variable in the Ephippigerini.

The designation «confirmatory response» for the third part of the duet of the Ephippigerini implies that this part represents a confirmation for the female that her response has been heard, indicating a preliminary decision of the male. As in the case of the female response, the confirmatory response (its actual time interval, special structure, loudness) should contain different information: species, interest + motivation, fitness, distance + direction. A masking function («mate guarding»; Bailey 2006; Villarreal & Gilbert 2014) towards other males could theoretically also be implied in the case of loud duets or if the male-female antiphony is prolonged as a whole. However, there is currently no indication that the male confirmatory response is able to obfuscate the female response on account of its similarity.

The real sequence of the duetting of the Ephippigerini in the field should begin two-part as in other Tettigoniidae, when males and females are at first so far away from each other that only the female is able to hear the (usually louder) initial song of the male. In this case the female will presumably try to document her interest in this special male by producing her response and to reduce the distance by herself. As she approaches, the male, which is now able to hear the female's response, will also respond (= produce a confirmatory response) and move target-oriented by himself (observations on *Platystolus obvius* and *P. miegii*; Pfau 1996, p.64). His immediate signal-change informs the female that her response had been perceived. Near to one another no further normal male echemes are necessary – eventual further female sounds are only re-confirmed. Altogether a multi-parted antiphony between female and male is expected to lead to a continuous firmed binding of a

special male and a special female, which will have a better chance of moving not in vain; risks and energy costs should be minimized.

Simple experiments and field observations (Pfau & Schroeter 1988a, Pfau 1996) indicated that females sometimes indeed prefer certain male initial songs while disregarding others (observation on *Platystolus selliger meridionalis*; Pfau 1996, p.64f.). Furthermore, different females showed to be able to apply graduated reactions; their responses were prolonged and intensified, when the male had been located or had come nearer (observations on *Platystolus miegii*, *P. martinezii*, *P. obvius* and *P. ramburii*). Nevertheless, the contacting pairs could easily miss each other in dense populations, since there are distracting sounds from other males and females (observations on *P. martinezii* and *P. miegii*), which should cause corrections of the running and climbing direction in the branchwood. The firmed and accelerated mutual locating and finding of sexes via a complex antiphonic communication should demonstrate its evolutionary value especially in bad years (with low population density) and borderlands.

There are indications that species of some genera of the Ephippigerini secondarily returned to pure repetitive singing – co-ordinated with the loss of the female response. This raises evolutionary-biological questions. *Platystolus surcularius*, for instance, which is probably the sister species of *P. martinezii*, apparently secondarily colonized open landscapes of central Spain and in parallel simplified its communication system (Pfau 1996, pp. 37f., 65). The turning away from duetting was accordingly independent in other genera. The advantages of duetting are probably more limited in open areas: the echemes were now executed again in long sequences, which were repetitions of either part I- (*U. agarenius*) or part II-syllables (*Uromenus rugosicollis*, *U. brevicollis*). The different risks concerning predators or parasites were possibly lower (Greenfield & Roizen 1993) or counter-balanced, for instance, by shortening the echemes, lowering the loudness, accumulating in dense populations, applying a confusing chorus singing or acquiring an unpleasant taste.

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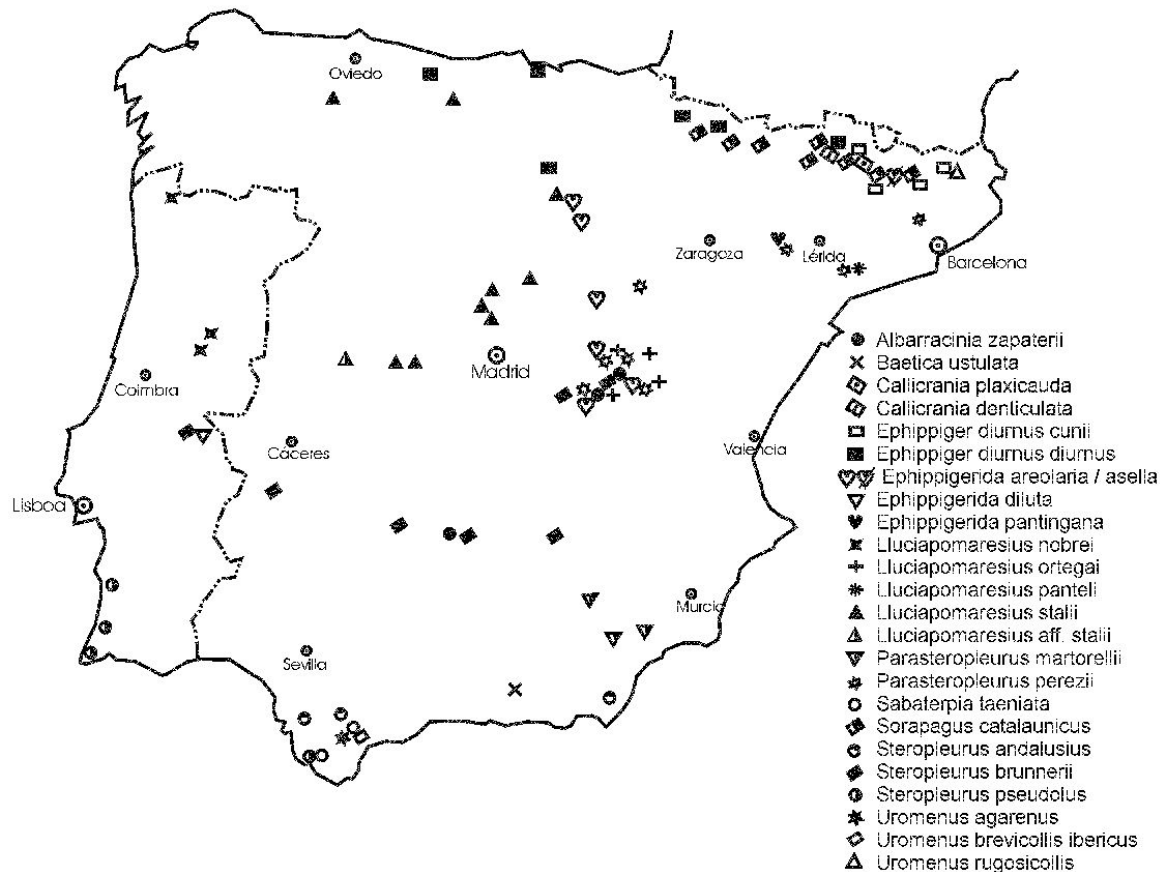
APPENDIX 1: SONG PARAMETERS, LOCATION DATA AND MAP

The parameters given are the result of random samples, in some cases based on few observations. These data should therefore be taken as a first orientation, because only a rather small section of the total variability (due to individual peculiarities and variations, which stem from age, provenance, motivation and local conditions, e.g. air temperature) is covered.

When selecting echemes for comparison, a similar range of temperature (19–23 °C) was preferred, but the total scope of temperatures is really much larger. 7°C in most cases means animals in the sunshine. Parameters of these songs are of relatively low comparative value. The wide scope of variation-possibilities becomes particularly obvious, when we consider the songs, which were recorded at rather low air temperatures: *S. catalaunicus* e.g. could be recorded at ca 15 °C; at this temperature an echeme of 17 syllables was 2.5 sec long (longest CI-HS: 135 ms)! The CI-HS of *U. rugosicollis* were up to 1200 ms long at 16 °C. *A. zapaterii* produced echemes of only 6 syllables at a temperature of 12 °C, which were 1.1 sec long; a single part II-CI-HS lasted for up to 190 msec. Early in the morning, when different males sang at places with different sun exposure, it appeared as if different species were present.

In the column «maximal hemisyllable duration» the longest syllable of a song was registered, without taking into account whether it represented an Op-HS or a CI-HS. Very long hemisyllables, which sometimes occur in confirmatory responses (see *L. panteli*) or in deterrent stridulations, are not taken into consideration, as well as extreme values from aged males.

species	echeme duration (syllable number in [])	syllable number / echeme	echeme - echeme pause	maximal hemisyllable duration
1 <i>Albarracinia zapaterii</i>	470 [6] - 575 [8] msec (21 °C)	(4-) 6-8 (-13)	1-5.2 sec	91 msec (21 °C)
2 <i>Callicrania plaxicauda</i>	0.6 [8] - 1 [11] - 1.25 [14] sec (20 °C)	(8-) 11-14 (-15)	4-25 min (av. 10 min)	70 msec (20 °C)
3 <i>Callicrania denticulata</i>	0.8 [6] - 1 [8] sec (17 °C)	6-8	46-123 sec	121 msec (17 °C)
4 <i>Ephippiger diurnus cunil</i>	180 [2] - 660 [6] msec (? °C)	(1-) 2-6	1-4.8 sec	100 msec (? °C)
5 <i>Ephippiger diurnus diurnus</i>	240 [1] - 520 [2] msec (20 °C)	1-2	0.5-2.7 sec	180 msec (20 °C)
6 <i>Ephippigerida areolaria</i>	460 [2] - 720 [3] msec (21 °C)	(1-) 2-5 (-7)	0.5-4 sec	210 msec (21 °C)
7 <i>Ephippigerida asella</i>	400 [2] - 700 [3] msec (? °C)	2-3	0.8-6.8 sec	175 msec (? °C)
8 <i>Ephippigerida diluta</i>	750 [4] - 900 [5] msec (20 °C)	(1-) 4-5 (-6)	0.8-1.2 (-2.5) sec	160 msec (20 °C)
9 <i>Ephippigerida pantingana</i>	0.95 [3] - 1.3 [4] sec (20 °C)	(1-) 3-4 (-7)	(0.4-) 1.5-3.5 (-6.3) sec	320 msec (20 °C)
10 <i>Liuciapomaresius nobrei</i>	205 [6] - 510 [10] msec (? °C)	6-13	0.6-8 sec	110 msec (? °C)
11 <i>Liuciapomaresius ortegai</i>	235 [3] - 375 [5] msec (? °C)	3-5	0.5-1.2 sec	100 msec (? °C)
12 <i>Liuciapomaresius pantelli</i>	170 [1] - 330 [5] msec (21 °C)	1-5 (-7)	1-10 min (av. 5.7 min)	130 msec (21 °C)
13 <i>Liuciapomaresius stalii</i> (type A) <i>Liuciapomaresius stalii</i> (type B)	450 [9] - 830 [15] msec (ca 17 °C) 100 [2] - 310 [7] - 355 [9] msec (22 °C)	9-15 (2-) 6-7 (-9)	11-25 sec 20 sec - 6 min (av. 54 sec)	55 msec (ca 17 °C) 40 msec (22 °C)
14 <i>Liuciapomaresius aff. stalii</i>	260 [6] msec (19 °C)	(4-) 5-6 (-10)	4.6-4.9 sec	27 msec (Op-HS) (19 °C)
15 <i>Parasteropleurus martorellii</i>	140 [3] - 230 [5] msec (23 °C)	3-5	14.5 sec	16 msec (Op-HS) (23 °C)
16 <i>Parasteropleurus perezii</i>	35 [1] - 170 [3] msec (20 °C)	1-3	0.7-2.6 (-4.5) sec	35 msec (20 °C)
17 <i>Sabaterpia taeniata</i>	17 [1] - 230 [2] msec (? °C)	1-2	0.35-1.8 sec	40 msec (? °C)
18 <i>Sorapagus catalaunicus</i>	0.59 [8] - 1.2 [14] sec (ca 25 °C)	8-17	0.4-3.1 sec	70 msec (ca 25 °C)
19 <i>Steropleurus andalusius</i>	70 msec (22 °C)	1	3.8-4.5 sec	44 msec (22 °C)
20 <i>Steropleurus brunnerii</i>	180 msec (Op-HS +CI-HS) (23 °C)	1	(0.5-) 3-13 (-22) sec	110 msec (23 °C)
21 <i>Steropleurus pseudolus</i>	91 msec (22 °C)	1	1.4-2.6 (-5.3) sec	52 msec (22 °C)
22 <i>Uromenus agareus</i>	0.8 [7] - 1.1 [9] sec (22 °C)	(3-) 7-9	0.25-1.1 sec	55 msec (22 °C)
23 <i>Uromenus brevicollis ibericus</i>	7 [9] - 27 [34] sec (22 °C)	(3-) 9-34	8.8-23 sec	600 msec (22 °C)
24 <i>Uromenus rugosicollis</i>	0.83 [1] - 60 [48] sec (21 °C)	1-48	2.7-7.4 sec	870 msec (21 °C)



- 1 *Albarracinia zapaterii* 23. 9. 1984 Altos de Cabrejas (W Cuenca) 1100 m [Fig. 1d]; 26. 9. 1984 Sierra de la Madera (NE Cuenca) 1300 m; 20. 9. 1986 Altos de Cabrejas (W Cuenca) [Fig. 1a,b,e]; 4. 7. 1987 Puertollano 870m [Fig. 1c].
- Baetica ustulata* 28. 6. 1987 Pico Veleta (Sierra Nevada) 2550 m (larva).
- 2 *Callicrania plaxicauda* 24.9.2012 Port del Cantó (E Sort) 1725m [Fig. 2a–c].
- 3 *Callicrania denticulata* 6.8.2014 Coll de Fades (W Laspaúles) 1480m [Fig. 3].
- 4 *Ehippiger diurnus cunii* 9. 9. 1981 Coll de Bracons (near Las Presas, Olot); 10. 9. 1984 Coll de Port (Sierra del Cadí, S Tuxent) 1600 m; 8. 9. 1984 NW Ripoll 900 m [Fig. 4]; 9. 9. 1984 S La Molina 1500 m; 24.9.2012 Port del Cantó (E Sort) 1725m.
- 5 *Ehippiger diurnus diurnus* 27. 9. 1983 Las Arenas (Picos de Europa) 400 m; 29. 9. 1983 Castro Urdiales (W Bilbao) 200 m; 14. 9. 1984 Puerto de la Bonaigua (NW Espot) 1500 m; 17. 9. 1984 Selva de Oza (N Hecho, Jaca) 1200 m; 19. 9. 1984 Las Arenas (Picos de Europa) 100–300 m [Fig. 5a]; 4. 9. 1986 Abaurrea Alta 1000m; 17. 8. 1991 Fresneda de la Sierra Tirón (Sierra de la Demanda, W Ezcaray) 1100 m [Fig. 5b]; 22. 8. 1991 Espinal (Camping Urrobi) 900m.
- 6 *Ehippigerida areolaria* 30. 9. 1981 Cañete (Serranía de Cuenca); 3. 9. 1983 Puerto de Sta. Inés (Sierra de Urbión) 1750 m; 4. 9. 1983 W Soria (Sierra de Cabrejas) 1150 m; 24. 9. 1984 S Sta. María del Val (Serranía de Cuenca, NW Tragacete, E Priego) 1300 m [Fig. 6b]; 20. 9. 1986 Altos de Cabrejas (W Cuenca); 11. 7. 1987 E Alcolea del Pinar (NE Guadalajara) 1200 m [Fig. 6a].
- 7 *Ehippigerida asella* 10. 9. 1984 Coll de Port (Sierra del Cadí, S Tuxent) 1600 m [Fig. 7].
- 8 *Ehippigerida diluta* 22. 6. 1992 N Alpahao (near Portalegre) 400 m [Fig. 8].
- 9 *Ehippigerida pantingana* 13. 6. 1992 steppe W Ballobar (NW Fraga) 200 m [Fig. 9].
- 10 *Lluciapomaresius nobrei* 11. 9. 1983 S Loriga (Serra da Estrela) 1000 m [Fig. 10a]; 13. 9. 1983 near Torre (Serra da Estrela) 1800m; 14. 9. 1983 S Penhas Doradas (Serra da Estrela); 15. 9. 1983 Rio Zézere (Serra da Estrela, near Manteigas); 20. 9. 1983 Lindoso 200 m [Fig. 10b–d].
- 11 *Lluciapomaresius ortegai* 30. 9. 1981 Cañete (Serranía de Cuenca); 25. 9. 1984 S Sta. María del Val (Serranía de Cuenca, NW Tragacete, E Priego) 1300 m [Fig. 11]; 20. 9. 1986 Altos de Cabrejas (W Cuenca); Las Majadas (Serranía de Cuenca) 1200 m.

- 12 *Lluciapomaresius panteli* 28.9.2012 W Albarca (Sierra de Montsant) 1000m [Fig. 12].
- 13 *Lluciapomaresius stalii* 12. 9. 1981 Rascafría (Sierra de Guadarrama) 1000 m [Fig. 14i]; 13. 9. 1981 Puerto del Pico (Sierra de Gredos) 1500 m; 16. 9. 1981 Puerto de Mijares (Sierra de Gredos) 1500 m; 3. 9. 1983 Sierra de Urbión 1600 m [Fig. 13a]; 5. 9. 1983 Puerto de Navafria (Sierra de Guadarrama) 1770 m; 7. 9. 1983 Puerto de la Morcuera (Sierra de Guadarrama) 1780 m; 25. 9. 1983 Puerto de Leitariegos, NW Villablino 1200 m; 21. 9. 1984 Alto Campo, Puerto de Piedrasluengas (W Reinosa) 1300 m; 8.9.1986 Puerto del Pico (Sierra de Gredos) 1500 m [Fig. 13b, c; Fig. 14h]; 20.9.2012 W Galve de Sorbe 1300 m [Fig. 13d–h].
- 14 *Lluciapomaresius* aff. *stalii* 27. 7. 1991 Candelario 1800 m [Fig. 14a–g].
- 15 *Parasteropleurus martorellii* 1. 7. 1987 Puebla de Don Fadrique 1400 m; 2. 7. 1987 Vélez Rubio 1100; 2. 7. 1987 Lorca 550 m [Fig. 15].
- 16 *Parasteropleurus perezii* 27. 9. 1981 Cuenca; 30. 9. 1981 Cañete (Serranía de Cuenca); 23. 9. 1984 Altos de Cabrejas (W Cuenca) 1100 m [Figs 16a–f]; 23. 9. 1984 SE Priego (Serranía de Cuenca, near La Frontera); 24. 9. 1984 Sta. María del Val (NW Tragacete, E Priego) 1300 m; 20. 9. 1986 Altos de Cabrejas (W Cuenca); 16.7.1991 Nuévalos; 22. 8. 1991 near Manresa 600 m; 2. 7. 1992 steppe W Ballobar (NW Fraga) 200 m; 28.9.2012 W Albarca (Sierra de Montsant) 1000m [Figs 16g–i].
- 17 *Sabaterpia taeniata* 26. 6. 1987 NE Zahara de los Atunes 40 m [Fig. 17]; 26. 6. 1987 SW Castellar de la Frontera (N Algeciras) 250 m.
- 18 *Sorapagus catalaunicus* 8. 9. 1984 NW Ripoll 900 m [Fig. 18]; 9. 9. 1984 S La Molina 1500 m; 11. 9. 1984 Tuxent (Sierra del Cadí) 1200 m; 14. 9. 1984 Laspaúles (S Benasque) 1500 m; 15. 9. 1984 SW Torla; 2.9.1986 Puerto de Monrepós; 3.9.1986 Jaca; 22.9.2012 Coll de Fadas (S Benasque) 1470 m; 23.9.2012 NW Laspaúles 1540 m; 24.9.2012 Port del Cantó (E Sort) 1725m.
- 19 *Steropleurus andalusius andalusius* 23. 6. 87 La Jara (W Arcos de la Frontera) 150 m; 30 5. 95 Grazalema 900 m [Fig. 19].
Steropleurus andalusius levantinus 30. 6. 1987 E Almería (desert «La Serrata»).
- 20 *Steropleurus brunnerii* 23. 9. 1984 Altos de Cabrejas (W Cuenca) 1100 m; 20. 9. 1986 Altos de Cabrejas (W Cuenca) 1100 m [Fig. 20]; 15. 6. 1987 NW Mérida (near La Nava de Santiago); 4. 7. 1987 Puertollano 870 m; 5. 7. 1987 W Villahermosa 950 m; 19. 6. 1992 Almadén (Llano de Alcudia, W Puertollano) 480 m; 22. 6. 1992 N Alpalhao (near Portalegre) 400 m.
- 21 *Steropleurus pseudolus* 19. 6. 87 Vila Nova de Milfontes; 20. 6. 1987 N Odemira 100 m; 26. 6. 1987 E Zahara de los Atunes (W Algeciras) 40m; 7. 6. 1995 Sagres 10 m [Fig. 21]; 8.6.1995 N Odemira 100m; 8.6.1995 SE Sines 30 m.
- 22 *Uromenus agareus* 26. 6. 1987 S Castellar de la Frontera (N Algeciras) 250 m [Fig. 22].
- 23 *Uromenus brevicollis ibericus* 26. 6. 1987 S Castellar de la Frontera (N Algeciras) 250 m [Figs 23a, b].
- 24 *Uromenus rugosicollis* 7. 9. 1984 Molló (SW Prats de Molló, France) 1100 m [Fig. 24]; 30.8.1986 Molló (SW Prats de Molló, France) 1100 m.