ACOUSTIC SIGNALS AND STRIDULATORY APPARATUS IN *COPRIS INCERTUS* SAY (COLEOPTERA SCARABAEIDAE: COPRINAE).

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ABSTRACT

This paper concern the acoustic emissions and the stridulatory apparatus in the adults of *Copris incert us* Say species and is part of a comparative analysis on communication mechanisms in Scarab beetles (Coleoptera). The anatomical features were studied from the morphofunctional standpoint by observing the stridulatory movements in vivo and analyzing the structure of the sound apparatus through a Scanning Electron Microscope. The stridulatory apparatus is made up of a **pars stridens** and a **plectrum**; it works by rubbing the **plectrum** against the **pars stridens** due to the telescopic movement of the abdominal segments against the elytra.

Acoustic emissions of uneasiness and protest were recorded and analyzed to obtain time and frequency measurements. The sounds are typically emitted in long sequences; in accordance with the structure and morphology of the stridulatory apparatus, sounds consist in pulse-trains whose pulse-rate is modulated, but with relatively smooth variations.

Each emission consists of two subunits (disyllabic chirp), characterized by pulses with opposite phase, which are produced during backward extension of the abdomen and its subsequent return to the resting position.

The former subunit is highly constant while the latter, not always produced, is longer, with a lower and more variable pulse-rate, sometimes ending with pulses which are well spaced out. All the sounds analyzed are homogeneous as regards acoustic structure. As far as sex differences

are concerned, the time parameters are relatively homogeneous between males and females while the pulse-rate is significantly lower in males.

Key Words: Coleoptera, Scarabaeidae, Coprinae, acoustic signals, stridulatory apparatus.

R E S U M E N

El presente trabajo trata sobre la emisión sonora y el aparato estridulador de los adultos de *Copris incertus* Say y forma parte de los análisis comparativos sobre los mecanismos de comunicación en escarabajos (Coleoptera). Las características anatómicas fueron estudiadas desde el punto de vista morfofuncional a través de la observación de los movimientos estridulatorios en ejemplares vivos y el análisis de la estructura del aparato estridulador mediante el microscopio electrónico de barrido. El aparato estridulador está compuesto de una **pars stridens** y un **plectrum**, el sonido es producido cuando el **plectrum** raspa contra la **pars stridens**, debido al movimiento telescópico de los segmentos abdominales contra los élitros.

Los sonidos de protesta y molestia fueron registrados y analizados para obtener mediciones de tiempo y frecuencia. Los sonidos son típicamente emitidos en largas secuencias, de acuerdo con la estructura y morfología del aparato estridulador; los sonidos consisten en series de pulsos cuya proporción de pulsos es modulada, pero con variaciones relativamente uniformes. Cada emisión consiste de dos subunidades ("chirp" disilábico), caracterizado por pulsos con una fase opuesta, los cuales son producidos durante la extensión hacia arriba del abdomen y su subsecuente retorno a la posición de reposo.

La primera subunidad es altamente constante mientras que la última es larga y no siempre se produce, con una proporción de pulsos bajo y más variable, a veces terminando con pulsos bien espaciados.

Todos los sonidos analizados son homogéneos en relación con su estructura acústica. Con relación a las diferencias sexuales, los parámetros de tiempo son relativamente homogéneos entre los machos y las hembras, mientras que la proporción de pulsos es significativamente más baja en los machos.

Palabras Clave: Coleoptera, Scarabaeidae, Coprinae, señales acústicas, aparato estridulador.

INTRODUCTION

This research is part of an extensive project which is designed to analyze the communication mechanisms in organisms whose behavior corresponds to different levels of the ideal sequence of evolution of Scarab beetles' (Coleoptera) reproductive strategies. This sequence, which does not correspond strictly to the phylogenetic sequence of the taxa involved, begins with egg laying in or near the pabulum and develops to a pattern of complex nesting and parental care with presocial characteristics. In this context we study the sounds produced by a highly evoluted species, namely the *Copris incertus* Say. The

genus *Copris* is known to include about 200 species spread in the Afrotropical, Oriental, Palearctic, Nearctic regions and partly in the Extreme North of the Neotropical region. *Copris incertus* is one of the few American species which are truly related to the tropical environment and the only one which extends southward beyond the Panama isthmus, spreading from the tropical lowlands of Mexico to part of Colombia and Ecuador. Moreover, this species was successfully introduced into Hawaii, Western Samoa and New Zealand (Thomas, 1960). The biology of the genus *Copris*, like that of all coprophagous scarabs, is strongly conditioned by the characteristics of the food. This has a high energy content and is organized into discrete units randomly distributed in both space and time. In general such a condition causes a strong intra- and inter- specific competitive pressure. One of the evolutionary effects of this situation (Halffter & Matthews, 1966; Halffter & Edmonds, 1982) is the use of a **"food relocation"** strategy, which is fulfilled, in the genus *Copris,* through a foraging tactic called **hypophagic** (Zunino & Palestrini, 1986). The latter consists in digging first a subterranean chamber under the food source; subsequently the insect removes a consistent part of the pabulum and stores it in the chamber (feeding burrow), before its utilization as food.

The reproductive behavior, called "paracoprid" (Bornemissa, 1969), corresponds to the Pattern III described by Halffter & Edmonds (1982); accordingly to the latter Authors it derives directly from feeding behavior. Its main features are, first, the forming of the pair, followed by digging - usually under a dung pad - a single tunnel ending in a wide elliptic or cylindrical chamber. This receives a large quantity of food, which is manipulated to form a "cake", thus creating a free surrounding space. The food is worked by both males and females to condition the anaerobic fermentation processes (Halffter & Edmonds, 1982; Halffter, 1989). The female extracts some paedotrophic ovoids from the cake gradually isolating each egg previously laid in apical position. This food will suffice for the entire growth of each larva. The female stays inside the nest until she comes out with the offspring or until, during the last phases of the development of the progeny, she dies. In this phase she takes great care of the ovoids by moving them, removing fungi, repairing the cracks on the surface, and always keeping them with the apex pointing upwards. The male collaborates with the female to dig the nest and supply it with food, besides working the food into cake, but no role in taking care of the offspring has been observed. Indeed, he either leaves the nest or stays inactive in little blind tunnels. These general behavioral characteristics correspond to those we have observed in *Copris incertus* in captivity.

Mechanisms of interindividual communication, usually chemical or acoustic signals, are involved in this complex behavior. In *C.incertus* we have observed stridulation in overcrowded situations, when individuals were transferred to new

3

terraria, when they were subjected to sudden changes in lighting conditions or were managed, or even during their unsuccessful search for food.

The aim of this paper is to illustrate the characteristics of the stridulation of *C.incertus*, leaving the meaning of such signals out of consideration.

MATERIALS AND METHODS

The specimen examined come from the state of Hidalgo, Mexico (1). After a preliminary adaptation phase, characterized by several deaths, 10 pairs were housed in separate breeding boxes where they reproduced regularly and completed their nesting and breeding. The total length varies from 13.5 to 18.5 mm in both sexes, even though the general structure of the body is a bit sturdier in the female.

Manual immobilization of the insects caused sounds of uneasiness and protest, which were recorded through a Brüel & Kjaer Phonometer type 2230 equipped with a 1/2" 4176 type polarized condenser microphone and connected to a SONY TCD5 Pro cassette recorder (FeCr tape, Dolby off).

The sounds, produced by 2 males and 4 females, were recorded in constant environmental conditions (temperature of about 18° C), with a total of about 30' of sound emission. The recordings were analyzed with a Kay DSP 5500 real time digital Sonagraph interfaced to a Personal Computer equipped with software for signal handling and processing.

Measurements were taken directly on the monitor of the Kay Sonagraph through time and frequency cursors simultaneously available on sonagrams, oscillograms and instantaneous spectra.

The analyses were carried out in different ways according to the information to be obtained: for the preliminary analyses and the monitoring of the waveform, a 0-16 kHz band was used because the frequency range of the signals examined reached 12-14 kHz, the upper limit of the recording device; to carry out frequency-time measurements the signals were analyzed in the 0-4 kHz range.

Statistical analyses were performed with the package Statgraphics from STSC Inc.

The anatomy of the stridulatory apparatus was studied on 20 individuals of the same population, taking into account both those whose acoustic signal were already recorded and those which died during the breeding cycle.

The anatomical features and their morphofunctional significance were studied by observing the stridulatory movements in vivo and analyzing the sound-producing apparatus through a S.E.M. (Scanning Electron Microscope).

RESULTS

Stridulatory organ morphology

The stridulatory apparatus is made up of a **pars stridens** and a **plectrum** (Fig. 1). The pars stridens consists anatomically of a long longitudinal, juxtasutural rib which extends from the apex of the ventral face of the elytrum towards the head for about 6.5 mm. This rib has a width of about $40 \mu m$ (40.25 ± 0.63, $N = 20$) and consists of a series of transverse convex-shaped crests, each with 7 to 11 tooth-like structures (8.48 ± 0.15, $N = 33$), which are $5.4 \mu m$ long (5.38 ± 0.08, $N = 57$) and $1.7 \mu m$ wide (1.73 ± 0.04, $N = 55$) in the central part of the **pars stridens** (Fig. 2 A,B).
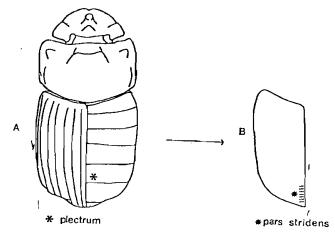

* plectrum   *pars stridens

Fig. 1 Dorsal view of an adult (A) with an elytra removed to highlight **plectrum** location and ventral view of the elytra (B) to show the location of the **pars stridens.**

There are at the most 4 (3.09±0.07, N=44) transversal crests at the same level every 10 μm, following the crest longitudinally.

In the cephalic position the **pars stridens** does not end sharply, but the structures of which it is made become gradually less well-defined till they merge with the squamous structure of the general microsculpture of the surface.

The **plectrum** consists, at the very least, of a median area of the 6th sub-trapezoidal abdominal tergum with a surface of about 0.1 mm^2. This area contains a series of about 20 transversal crests each about 13 μm apart (13.46±0.87, N=24) (Fig. 2 C,D). Laterally, the transverse crests extend considerably and have a thick series of sharp elements oriented towards the tail,
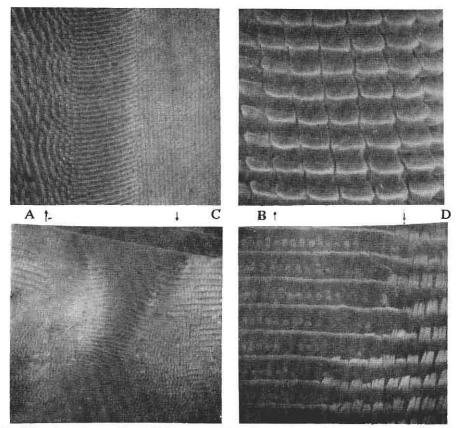

Fig. 2 Morphoanatomy of the stridulatory apparatus: A) central part of the **pars stridens;** B)detail of the transversal crests of the **pars stridens;** C) **plectrum** location in the median area of the 6th tergum; D) detail of the **plectrum.**

each about 16 μm long (15.70±0.22, N = 46) and about 0.8 μm wide (0.82±0.04, N = 35) gathered in groups of 4-9 (6.02±0.16, N = 65) (Fig. 3 A,B).

Each crest consists of discrete subunits with truncated and recessed surfaces; there are about 2 subunits every 10 μm (1.9±0.05, N = 25) with the following dimensions: length 5.5 μm (5.53±0.15, N = 33), breadth 1.7 μm (1.72±0.09, N = 30). The gaps are filled with longitudinally arranged bosses, with an average density of 2 per 10 μm and whose surface recalls that of worn molars (Fig. 3 C,D).
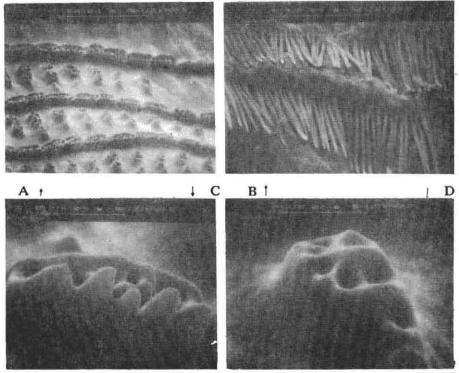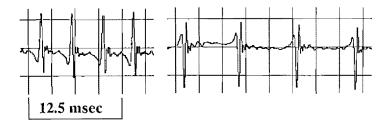

Fig. 3 Morphoanatomy of the plectrum: A) central part; B) lateral part with sharp elements; C) subunits of transversal crest; D) longitudinally arranged bosses.

The stridulatory apparatus works by means of the rubbing of the **plectrum** against the pars stridens which is caused by the telescopic movement of the abdominal segments against the elytra. The transversal extension of the plectrum crests and the possibility for the 6th abdominal tergum to extend or to partially introflect, suggests a possible variation in the sound emission involving different parts of the instrument.
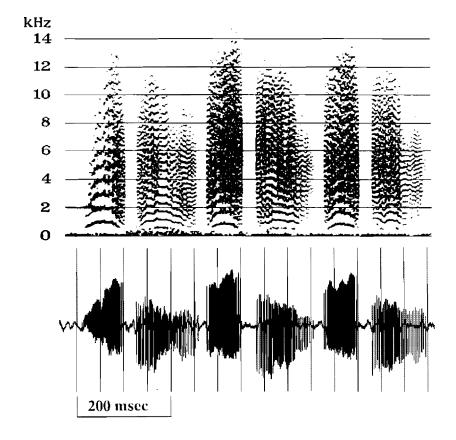
Fig.4 Envelope and sonagram in the 0-16 kHz band (bandwidth 120 Hz; y-axis division 2 kHz, χ-axis 50 ms) of three typical complete emissions. The oscillogram above (x-axis division 3.125 ms) shows the typical shape of the impulses of subunits A and B; each impulse is likely to be due to a single contact of one tooth of the **plectrum** on one crest of the **pars stridens.**

8

Sound analysis

Sounds are typically emitted in long sequences (the longest sequence recorded was about 30 seconds) even though they may also be emitted separately. During the recordings, some measurements of sound intensity were made; the acoustic intensity, measured at a distance of 1 cm, was on average $65 \, ^{dB}\text{SPL}$.

Accordingly with the structure and morphology of the stridulatory apparatus, sounds consist in series of impulses (pulse-trains) whose pulse-rate is modulated, but with relatively smooth variations.

A preliminary analysis in the 0-16 kHz band revealed sounds consisting of quite regular series of impulses (Fig. 4); hence sonagrams in the 0-4 kHz band (Hamming window, bandwidth 120 Hz, temporal resolution 6 ms) were made for spectral analysis and the acoustic parameters measurements, so as to obtain a harmonic band representation and to highlight pulse-rate modulation (Fig. 5 A-D).

The pulse-trains, with the pulses regularly spaced even though within modulated pulse-rate, are displayed with a clear harmonic structure being the interval between the pulses generally less than the time resolution given by the chosen bandwidth.

Moreover, as the pulses are simple and regularly spaced within the time-resolution window, the pulse-rate corresponds to the frequency of the fundamental (Tsao, 1984; Watkins, 1967).

Each complete emission consists of two functionally similar subunits (disyllabic chirp) which are generated during backward extension of the abdomen (subunit A) and its subsequent return to the resting position (subunit B). Subunit B can be missing, partially or entirely, if there is no contact between the **plectrum** and **pars stridens** when the former returns to the resting position. The intensity of B is generally lower then those of subunit A, perhaps because of reduced pressure between the parts involved.

The two subunits are characterized by pulses with opposite phase (Fig. 4); so we were able to establish the absence of subunit B in the incomplete emissions. Subunit A is characterized by a pulse-rate which first increases, reaching a maximum when it is about half-way and finally decreases in a relatively symmetrical way. Subunit B, not always present and with a lower intensity, is longer, with a lower and more variable pulse-rate, sometimes ending with pulses which are well spaced out (up to 8-10 ms). As regards the shape of the pulse-rate modulation, A appears to be highly constant, while B appears to be more
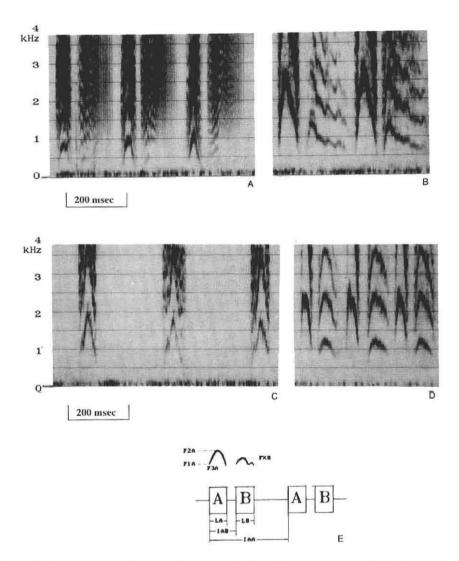
Fig.5 Sonagrams in the 0-4 kHz band (bandwidth 120 Hz, y-axis divisions 500 Hz, x-axis divisions 50 ms) of some emissions: a) complete emissions; subunit B with irregular pulse-rate and with isolated impulses b) complete emissions c) emissions consisting only in subunit A d) complete emissions e) diagram of the measured parameters.

variable. Both the subunits may reveal some isolated or irregularly spaced
pulses at the beginning and/or at the end.

Time and frequency measurements were carried out on a sample repre-
sentative of the recorded emissions to determine the typical acoustic features:
38 distinct sequences with a minimum of 3 emissions were selected; the total
emissions analyzed were 703, 519 of which were complete, namely consisting
of both subunits A and B (Tab. I). Time measurements, in ms, were carried out
on the oscillogram referring to the first and last impulse of each subunit with a
precision to within 3.125 ms; we considered length in time of A and B (**LA, LB**),
the interval between the beginning of A and beginning of B (**IAB**) and the interval
between the beginning of 2 consecutive A subunits (**IAA**) (Fig. 5 E).

From these measurements we obtained the following:

LAB emission length (**IAB + LB**)

PAB length of the gap between subunits A and B (**IAB-LA**)

Table 1

The number of complete and not complete emissions analyzed, per sex and
individual.

SEX	ID	COMPLETE	NOT COMPLETE	TOTAL
MALES	A	128	2	130
	I	105	3	108
FEMALES	B	8	119	127
	D	119	8	127
	G	10	41	51
	K	149	11	160
		519	184	703

PBA length of the gap between successive complete emissions (**IAA-IAB-
LB**)

ER emissions rate (**1000/IAA**) emissions per second

RSP sound/gap ratio **(LA + LB)/(IAA-LA-LB)**

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11

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Frequency measurements were made simultaneously on the sonagram and on the instantaneous spectrum relative to the position of the time cursor, with a precision of 20 Hz.

Regarding subunit A we have measured the initial, maximum and final frequencies, **F1A, F2A** and **F3A** respectively (Fig. 5 E). **F1A** and **F3A** were not always correctly measurable in the presence of not regularly spaced initial and final pulses; so the measurements made represent frequencies with an homogeneous trace relating to the fundamental frequency (or pulse-rate).

Concerning subunit B, which is more variable and modulated, we only could obtain the maximum frequency measured on the 2nd harmonic (**FX2B**), on the basis of which we calculated the value of the fundamental (**FXB**) with a precision of 10 Hz. In 99 out of 519 cases, subunit B was characterized by a low and irregular pulse-rate, so we were not able to measure it, since no trace to which to refer existed. Although subunit B is more variable, there is a strong correlation between **FXB** and **F2A** (linear regression $FXB = 0.3735 \times F2A + 136.942$, Corr.Coeff. $= 0.8576$).

As regards the time structure of the emission sequences we notice that **IAA** and related parameters are not affected by the absence or by the shortness of the subunit B: the interval between the end of a subunit A and the beginning of the next emission is in every case required for the return movement of the **plectrum** and so **IAA** is strongly correlated with **LA** (linear regression $IAA = 2.42188 \times LA + 104.41$, Corr.Coeff. $= 0.7225$) but not correlated with **LB.**

Time and frequency measurements of each individual are summarized in Tables 2-3 and in Fig. 6

All the sounds analyzed are homogeneous as regards acoustic structure. As far as sex differences are concerned, the time parameters (length of subunit A 53.57 ± 17.09 ms, length of subunit B 93.21 ± 34.29 ms, total length 174.96 ± 48.55 ms, emission rate 4.55 ± 1.24) are relatively homogeneous between males and females, while the maximum pulse-rate measured in both subunits was significantly different by means of ANOVA analysis (Fig. 7) (subunit A: females 1738.05 ± 484.15 Hz $N = 431$, males 966.55 ± 199.89 Hz $N = 238$, $F = 552$, $p < 001$; subunit B: females 867.9 ± 251.58 Hz $N = 195$, males 498.76 ± 108.76 Hz $N = 225$ $F = 398.6$, $p < 0.001$).

Table 2
Measured and calculated time parameters (ms)

	LA	IAB	LB	IAA
N	703	519	516	668
AVG	53.57	81.72	93.21	234.52
STD DEV	17.09	20.90	34.29	57.06
STD ERR	0.64	0.92	1.51	2.21
MIN	17.18	43.75	12.5	115.6
MAX	118.7	150	231.2	421.8
RANGE	101.52	106.25	218.7	306.2

	LAB	PAB	PBA	ER	RSP
N	516	519	499	668	499
AVG	174.96	28.48	238.89	4.55	0.549
STD DEV	48.55	7.78	64.67	1.24	0.083
STD ERR	2.14	0.34	2.89	0.05	0.0037
MIN	73.43	10.94	117.11	2.37	0.2604
MAX	318.7	64	490.5	8.65	0.7331
RANGE	245.27	53.06	373.39	6.28	0.4728

Table 3
Frequency parameters (Hz)

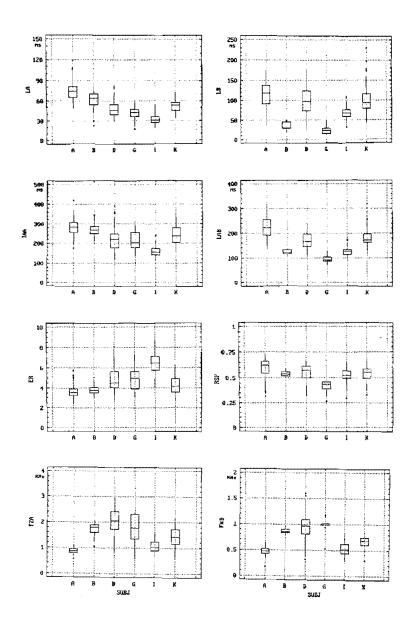|	F1A	F2A	F3A	FXB
N	545	669	533	420
AVG	680.51	1463.59	686.85	670.14
STD DEV	213.91	549.26	229.16	263.82
STD ERR	9.16	21.24	9.93	12.87
MIN	280	560	260	180
MAX	1600	2960	1600	1600
RANGE	1320	2400	1340	1420

Fig. 6 Box & Whisker's diagrams relating to the parameters measured for each individual.
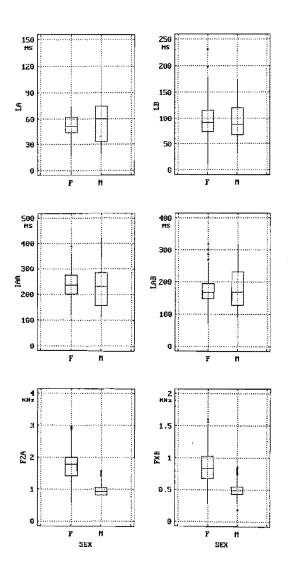
Fig. 7 Box & Whisker's diagrams comparing sound parameters between males (M) and females (F). The maximum frequencies of both the subunits are lower in males than in females, while the time parameters are relatively similar.

DISCUSSION

Among the Scarabaeidae, the genus *Copris* is a typical example of advanced paedotrophic nesting, with a co-operation between the sexes, accompanied by parental care until the emergence of the offspring. Our data on sound emission in *Copris incertus* Say show the morpho-functional features of the stridulatory apparatus. It consists of a **pars stridens** with a longitudinal, juxtasutural crest which extends from the apex of the elytrum towards the head, and a **plectrum** located on the 6th abdominal tergite. Our interpretation of the plectrum segment contrasts with that of Arrow (1904) and Matthews (1962) also accepted by Halffter & Matthews (1966). The study of a series of American, Afrotropical, Palearctic and Oriental species allows us in particular to report that only the 6th abdominal segment, according to the Jeannel & Paulian scheme (1944), is involved in the location and structure of the **plectrum.**

The study of sound emission caused by uneasiness and protest, integrated and correlated by the S.E.M. observations of the structures involved in sound production, namely **plectrum** and **pars stridens,** allow us to establish some bioacustic features of *Copris incertus* and represent the general and methodological basis for comparison with other phylogenetically related species. All the sounds recorded are homogeneous in structure. Our data do not permit us to describe the inter- and intra- individual variability, but as regards sex differences, we show that the time parameters are relatively similar between the sexes, while the maximum frequencies measured are significantly different. These observations would be better understood by deepening our knowledge of the morpho-functional aspects of the stridulatory apparatus and of the biological role of acoustic emissions as regards the interactions both among adults and between larvae and adults.

ACKNOWLEDGMENTS

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