The elytro-femoral stridulatory apparatus in Curculionidae (Coleoptera), with notes on the acoustic behaviour of *Arniticus hylobioides* (Boheman 1843) and *Erodiscus proximus* (Viana 1959), and thanatosis display in the latter species

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Abstract. The elytro-femoral stridulatory apparatus of two species of Curculionidae is described and figured: *Erodiscus proximus* (Curculioninae: Erodiscini) and *Arniticus hylobioides* (Molytinae: Hylobiini). Notes on sound generation, acoustical behaviour and phylogenetic implications are given. Thanatosis display is reported for the first time in *Erodiscus proximus*.

Résumé. L'appareil stridulatoire elytro-fémoral des Curculionidae, avec notes sur le comportement acoustique d'*Arniticus hylobioides* (Boheman 1843) et *Erodiscus proximus* (Viana 1959), et mise en évidence de la thanatose chez cette dernière espèce. L'appareil stridulatoire elytro-fémoral est décrit et illustré chez deux espèces de Curculionidae : *Erodiscus proximus* (Curculioninae : Erodiscini) et *Arniticus hylobioides* (Molytinae : Hylobiini). Des données sont apportées sur la génération du son, le comportement acoustique et les implications phylogénétiques. Le phénomène de thanatosis est rapporté pour *Erodiscus proximus* pour la première fois.

Keywords: Curculionidae, Erodiscini, Hylobiini, stridulation, morphology, acoustical behaviour.

The production of sound is widespread in Insecta, especially in members of the Orders Heteroptera, Orthoptera and Coleoptera. One of the most frequent methods is through stridulation, where two parts of the body, at least one of them ridged, are rubbed against one another.

As many as half of the total known diversity of the Curculionidae, the largest family of Coleoptera with approximately 50,000 species, stridulate (Lyal & King 1996). The biological meaning of sound production in weevils may be as diverse as alarm, conflict between members of the same sex and pre-copulatory or copulatory signalling between sexes.

The stridulatory apparatus is composed of two parts, the file and the plectrum. Distinction between these parts is not straightforward and more than one definition has been given. The file is usually more complex and static in relation to the plectrum, which has a simpler structure. This distinction is not absolute since in some cases both structures show parallel sophistication and/or move concurrently to one another. The most common method of stridulation in weevils is through use of elytro-tergal structures (Lyal & King 1996), other systems have been described: mesoscutum-pronotum; vertex-pronotal, gula-prosternal, ventrite I-femoral and elytro-femoral.

In Curculionoidea the elytro-femoral stridulatory apparatus, according to Lyal & King (1996), would be restricted to *Erodiscus* (Curculioninae, Erodiscini) as described by Vanin (1986). However, Kuschel (1955) redefined the genus *Arniticus* (Molytinae, Hylobiini) on the occurrence of such apparatus. The elytro-femoral stridulatory system turned out as a synapomorphy for both genera in the cladistic analyses conducted by Vanin (1986) for the Erodiscini and Gaiger (2003) for *Arniticus*.

The present paper intends to describe in detail the stridulatory system observed in one species of *Arniticus*, *A. hylobioides* (Boheman 1843) and one species of *Erodiscus*, *E. proximus* (Viana 1959). Both species were observed producing sound, therefore comments on the acoustic behaviour of these species will also be made.

Material and methods

The stridulatory apparatus were observed in 177 specimens of *Arniticus hylobioides*, and 21 specimens of *Erodiscus proximus*. Observations were made using a stereomicroscope with the magnification up to x50. Two specimens of each species, observed producing sound, were prepared as described by Gaiger (2001), for examination under a scanning electron microscope (SEM) to reveal key features of the system. Also, a brief account on collection data of the individuals that were observed stridulating is given below.

In September 4th, 1997, during a short stay of the second author at the Campus of the Universidade Federal Rural do Rio de Janeiro (Seropédica, RJ), a male specimen of *E. proximus* was collected. The weevil was found on the stem of a grass (*Panicum*

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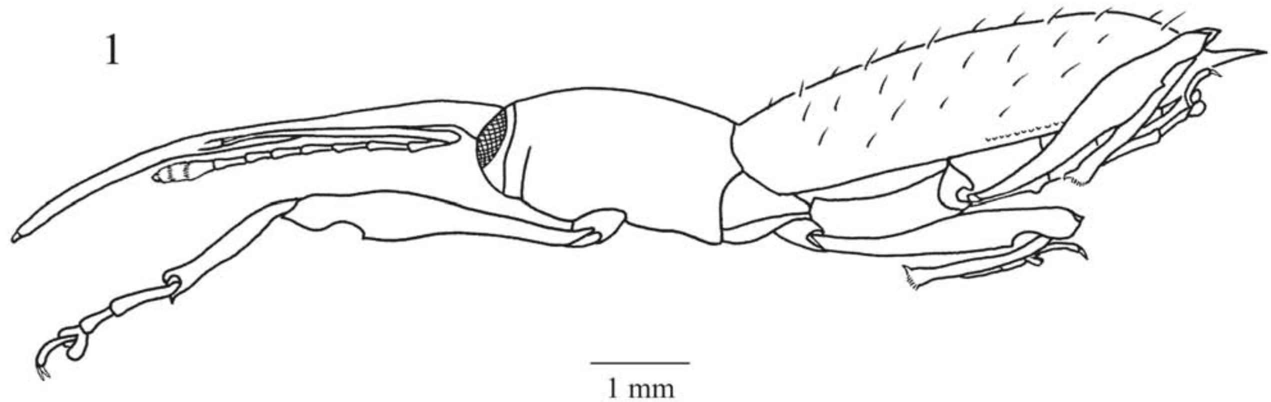


Figure 1
Erodiscus proximus (Viana 1959), sketch of the side view during thanatosis display.

sp., Gramineae) close to sunset. Although other individuals were searched for, only the single specimen mentioned was located (fig. 1).

One female specimen of *A. hylobioides* was collected at the Universidade de São Paulo (São Paulo, SP), inside the Zoology Department building (Ernst Marcus), in July 5th, 2000 by S.A. Vanin; a male specimen was found at the same locality in October 2000. Both individuals were observed stridulating.

Results and discussion

Morphology of the elytro-femoral stridulatory apparatus

Erodiscus proximus

The structures involved in sound production are located in the hind femora (plectrum) and in the elytral epipleura (file) (fig. 2-10). The plectrum (fig. 2-4) consists of a single keel on the internal surface of the hind femora that gradually disappear at the proximal and distal ends. The file covers about 50% of the elytral epipleura (fig. 5). It is composed by a series of grooved tubercles, spaced approximately 25 µm from each other with the tegument between the tubercles also displaying grooves (fig. 6, 7). The orientation of the grooves varies, both in the tubercles and in the tegument. From straight anteriorly and medially, their angle slightly increases towards the elytral apex (fig. 8-10). Dorsally to each tubercle there is a deep cavity that may act as a resonant chamber (fig. 7). The apparatus is equally developed in both sexes.

Arniticus hylobioides

The elytro-femoral stridulatory apparatus is located in the hind femora (plectrum) and in the elytral epipleura (file). The plectrum (fig. 11-12) consists of a series of keels on the internal surface of the hind femora, sometimes interconnected, composing a striated area. The number of keels gradually decreases toward the proximal and distal ends. Unlike *E. proximus*, the structure of the plectrum is as much complex as that of the file. The file covers about 70% of the elytral epipleura (fig. 13). It has approximately 34 transverse ridges per millimetre, which are spaced nearly 10 µm from each other (fig. 14-18). The tegument is smooth between each ridge (fig. 19). The orientation angle of the ridges varies, from acute anteriorly to right medially and finally oblique posteriorly, that is, its angle slightly increases towards the elytral apex (fig. 14-18). There is no deep cavity dorsally to the ridges. The sound structures are similarly built in both sexes.

Sound generation

Erodiscus proximus

Even though only a male specimen was actually observed producing sound, it is assumed the female is also able to generate sound, since both sexes have similar stridulatory structures.

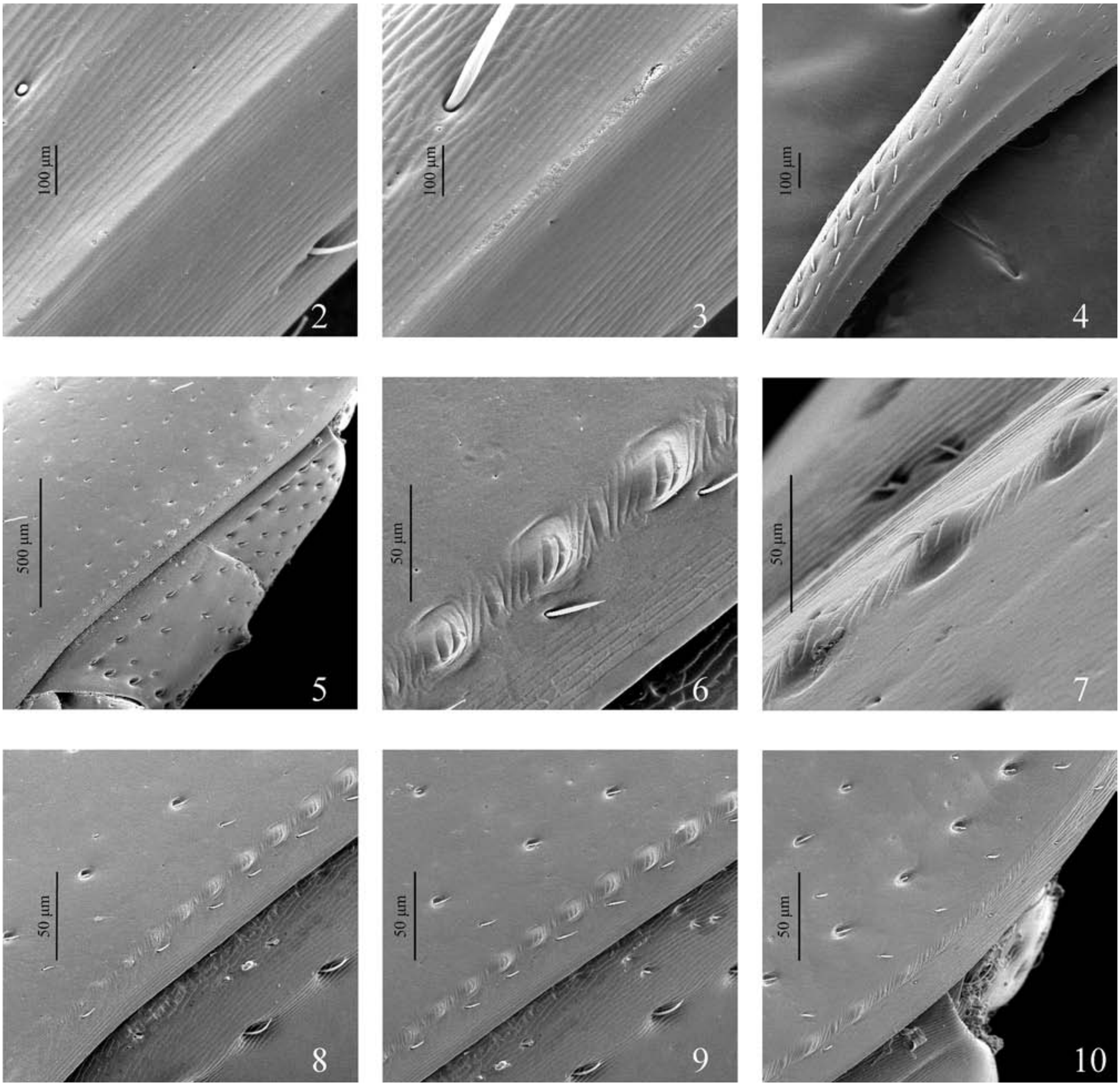
The sound is produced when the keel of the hind femur strikes the grooved tubercles and tegument of the elytral epipleura. There was no observation on which stroke of the hind femur, forward or backward, was mostly responsible for generation of sound.

The shifting orientation of the grooves, from the tubercles and tegument, can be inferred as a way to maximize the amplitude of sound. The intensity of sound depends on the quantity of energy transmitted to the sound producing structures throughout the hind femur movement, that is, the friction between the plectrum and the file. Thus, the shifting orientation of the grooves permits a steady and orthogonal orientation between the plectrum and file during the leg movement, therefore the friction is firmer enhancing sound amplitude, as described for the tiger beetle *Oxycheila tristis* (Fabricius) (Serrano *et al.* 2003).

Arniticus hylobioides

Both sexes of *A. hylobioides* were observed producing sound. The rubbing of the series of keels of the hind femur against the ridges of the elytral epipleura is responsible for the generation of stridulatory sound. An analysis of the video depicting the stridulation movements reveals that both strokes, forward and backward, are in charge of sound production. Concomitantly, abdominals movements were detected, which may influence the sound generated.

As explained above for *E. proximus*, the observed variation on the angle of the elytral epipleura ridges may be related to the increase of sound intensity.

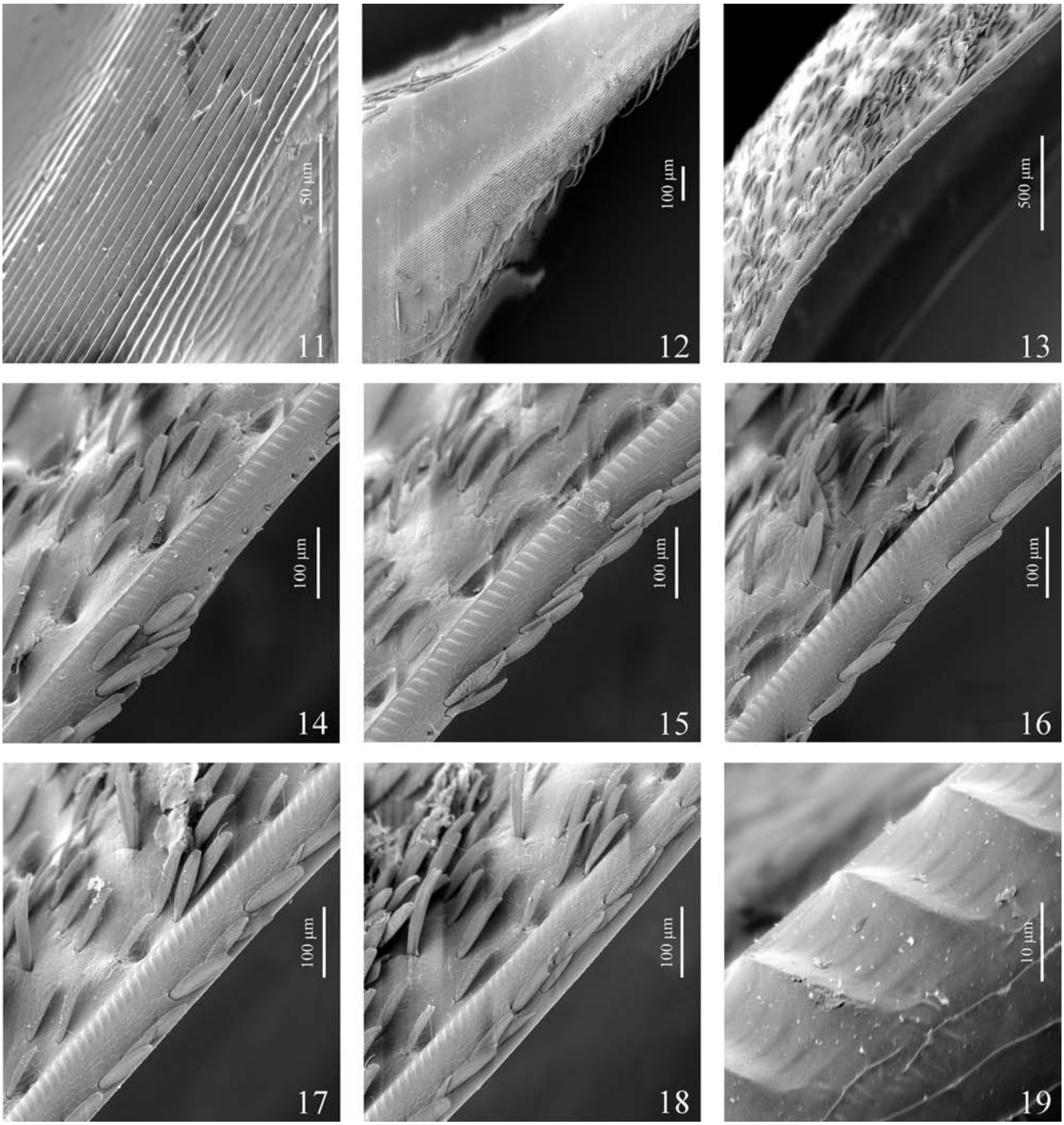


Figures 2-10
Erodiscus proximus (Viana 1959), elytro-femoral stridulatory apparatus. **2-4** Femoral plectrum. **2**, detail of apical portion; **3**, detail of mid portion; **4**, position in the hind femur. **5-10** Elytral file. **5**, position in the elytral epipleura; **6**, detail, lateral view; **7**, detail, dorsal view; **8**, detail of anterior portion; **9**, detail of mid portion; **10**, detail of posterior portion.

Sound generation and behaviour

Erodiscus proximus

The specimen collected was on the ground motionless with the head turned toward the ground. As soon as the second author grasped the individual, but leaving the hind legs free, the weevil began to stridulate, producing a low but audible sound. Both legs moved



Figures 11-19
Arniticus hylobioides (Boheman 1843), elytro-femoral stridulatory apparatus. **11-12** Femoral plectrum. **11**, detail; **12**, position in the hind femur; **13-19** Elytral file. **13**, position in the elytral epipleura; **14**, detail of the anterior portion; **15**, detail of the anterior-mid portion; **16**, detail of the mid portion; **17**, detail of the posterior-mid portion; **18**, detail of the posterior portion; **19**, detail of ridges, lateral view.

synchronously emitting sound for a few seconds and then repeating it two more times. This was a clear demonstration of sound generation associated with agonistic behaviour. No other behaviour associated with sound production was observed.

Interestingly, the experiment of grasping the specimen was repeated later in the laboratory but only once the weevil stridulated for about 15 seconds. However, in most experiments the individual displayed a completely different defensive behaviour, namely thanatosis, as soon as touched. Thanatosis is a reflex of tetanic immobility quick and easily evoked by mechanical stimuli (Crowson 1981). The thanatosis response was very variable, ranging from about one minute to nearly 140 minutes (30 observations, 4 days). The commonest position exhibited during the thanatosis display is pictured in figure 1. The antennae and legs were rigidly held close to the body, the anterior ones stretched forward, and the median and posterior pairs retracted. In some instances, all the legs were held stretched out from the body in irregular positions.

Arniticus hylobioides

The specimen collected produced sound as soon as it was grasped, providing the hind legs were free to move, sound produced was low but audible just as in *E. proximus*. Likewise, both legs moved synchronously emitting sound for a few seconds. The experiment was repeated many times, taking in account the occasion the weevil was videotaped stridulating. As in the case of *E. proximus* this was also a clear display of agonistic behaviour.

Another species of *Arniticus*, *A. brevicollis* Pascoe, was observed during its copulatory period. The male of this species moves both hind legs franticly throughout the copula (Bellizzi, personal communication), this movement probably causes stridulation. We were able to observe *A. hylobioides* stridulating, as an agonistic behaviour, and the movement is similar as described above. Hence, the sound production in *Arniticus* is probably also associated with copulatory signalling between sexes.

The elytro-femoral stridulatory apparatus and phylogeny

The elytro-femoral stridulatory systems found in the two discussed genera show many differences, such as position, structure and complexity. Concurrently, the systematic position of *Erodiscus* and *Arniticus* within the family Curculionidae is rather distinct. The most recent world catalogue places *Erodiscus* in the subfamily Curculioninae, while *Arniticus* is positioned as a Molytinae (Alonso-Zarazaga & Lyal 1999).

The very dissimilar morphology and position of the plectrum concurs with the presumed independent appearance of this structure on both genera. Therefore, in *Erodiscus* it is composed by a simple keel at the dorsal internal surface of the hind femora and appearing in *Arniticus* as a series of keels resulting in a somewhat complex structure at the ventral internal surface of the hind femora. Likewise, the file also shows differences that agree with the anticipated absence of homology among the structures. Thus, *Erodiscus* has a file comprised by a series of grooved tubercles above the elytral epipleura margin. Moreover, the tegument between each tubercle is also grooved. In *Arniticus* the file is located right at the epipleural margin and consists of a series of transverse ridges with a smooth tegument amid each ridge.

Nevertheless, the presence of an elytro-femoral stridulatory system resulted as synapomorphies for *Erodiscus* and *Arniticus* in the cladistic analyses carried out by Vanin (1986) and Gaiger (2003) respectively. Oddly, species from four other genera of Erodiscini examined by Lyal & King (1996) - *Hammatostylus* Champion, *Lancearius* Vanin, *Ludovix* Laporte and *Prosicoderus* Vanin - only the common mechanism of elytro-tergal stridulation was observed. Furthermore, in the cladistic analysis of *Arniticus*, the shape, position and size of the ridges of the stridulatory apparatus file turned out as important characters in establishing monophyletic groups (Gaiger 2003).

The restricted distribution of the elytro-femoral stridulatory system in Curculionidae provides little space for discussion on the use of this structure in a higher taxonomic level. The evidence gathered so far reveals that the system, as known in the Curculionidae, is quite restricted and apparently evolved independently in the two genera discussed. However, it surely provides valuable characters at the generic and specific level, as mentioned above.

Certainly, more comprehensive studies that disclose the actual distribution and variation of the system in Curculionidae may enlighten our knowledge on the evolution of the elytro-femoral stridulatory apparatus within the family.

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