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The role of the Krauss's organ in sound production in Pamphagidae (Caelifera: Orthoptera)

B. Massa [a]

[a] Dipartimento Demetra, Università di Palermo, Palermo, Italy

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The role of the Krauss's organ in sound production in Pamphagidae (Caelifera: Orthoptera)

B. MASSA*

Dipartimento Demetra, Università di Palermo, Palermo, Italy

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Abstract
In Pamphagidae, the Krauss's organ is located on both sides of the 2nd tergite and its function is superficially known. It has been proposed to have a stridulatory function. This organ can be found in all Pamphagidae except the apterous genera. Rearing specimens of some species and observing mounted pamphagids allowed the author to observe that when the Krauss's organ is absent (most apterous species) the tympanum is also absent; further, he discovered specialized stridulatory structures on hind femurs of some taxa for sound emission. By rearing two Pamphagidae belonging to different genera, fragments of stridulations involving the Krauss's organ and specialized structures on the hind femur surface were obtained for the first time. Mapping the presence of these morphological characters onto the known Pamphagidae list revealed that specialization on the hind femur surface evolved multiple times in multiple geographical locations in winged species with a wrinkled Krauss's organ. The function of the sounds produced by the femur-Krauss's organ method remains to be studied.

Keywords: *Stridulation mechanism, femur-trochanter articulation, rubbing femur-Krauss's organ,* Acinipe calabra, Ocnerosthenus simulans

Introduction

In most Pamphagidae and some Acrididae (cf. Uvarov 1943), the lower anterior corners of the second abdominal tergite have specialized plates, called Krauss's organ (Uvarov 1943). This organ was originally described by Krauss (1878) in *Prionotropis hystrix* Germar, 1817. The organ is an oval plate with a rough, wrinkled, or ridged surface above the level of the tergite. Minute rounded tubercles on the inner hind femurs of *P. hystrix* were thought to rub against the Krauss's organ, suggesting that the latter had a stridulatory function (Krauss 1878). However, winged taxa of the tribe Thrinchini have the Krauss's organ but a different stridulating mechanism (Uvarov 1943). Therefore, Uvarov (1943) hypothesized that the Krauss's organ played a role in perceiving air pressure or protecting the second abdominal spiracle against the pressure of the hind femur on the body. In *Tmethis pulchripennis asiaticus* Uvarov, 1943 no specific sensory functions could be attributed to the Krauss's organ and no conspicuous nerves were connected to its integument (Shulov 1952). Furthermore, there was no evidence that this organ was involved in the response to light or air pressure or in the regulation of eating, courting, or mating (Shulov 1952). This lack of evidence for sensory function supports Uvarov's hypothesis that Krauss's organ is largely protective and structural. However, *Dhofaria splendens* Popov, 1980 of the subfamily Thrinchinae has been observed producing sound by rubbing the inner ridged base of hind femurs against the coarse surface of Krauss's organ (Popov 1997). Additionally, in both field and laboratory observations, *Glyphotmethis* individuals (mostly females) produced defensive sounds by rubbing the rough edges of the lamellate transverse antero-ventral edge of hind femurs on the wrinkled Krauss's organ and amplified them with their large tympana (Ünal 2007).

Here, it has been investigated the variation of Krauss's organ and associated sound-producing and sound-detecting organs in Palaearctic Pamphagidae,

*Correspondence: B. Massa, Dipartimento Demetra, Università di Palermo, Viale Scienze, 90128 Palermo, Italy. Tel: +39 09123896018. Email: bruno.massa@unipa.it

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using specimens of most genera, either sampled in the field or deposited in museum collections. To investigate the function of the Krauss's organ, some male and female of pamphagids were reared.

Material and methods

Males and females of squamipterous genera *Acinipe*, *Pamphagus*, *Pseudoglauia*, *Ocneridia*, *Prionosthenus*, and *Ocnerosthenus* were reared in containers (20 × 20 × 20 cm). They were fed with cereals and maintained at spring-summer weather conditions (20–25 °C), waiting for sound production. Sound emissions were recorded using an Edirol R09HR digital recorder, and song fragments were analysed with Cool Edit Pro version 2 (Syntrillium Software, USA). Morphological variation in femurs and Krauss's organ using fresh and museum specimens has been investigated. Some specimens were dissected and mounted on microscope slides. A series of images in different focal planes were taken using a Nikon Coolpix 4500 digital camera mounted on a Stereomicroscope Wild M5, and a composite image was generated using CombineZP (Hadley 2008). A series of specimens were studied at Muséum National d'Histoire Naturelle (Paris), Naturhistorisches Museum (Wien), Museo Nacional de Ciencias Naturales (Madrid), Museum für Naturkunde (Berlin), Museo Regionale di Scienze Naturali (Turin), Museo Civico di Storia Naturale (Milan) and Museo Civico di Storia Naturale (Genoa).

Results

The presence or absence of potential stridulatory structures (tegmina, Krauss's organ, tympanum, hind femur surface specialization) in Pamphagidae subfamilies are listed in Table I. Generally, tympanum and the Krauss's organ are present in taxa in which at least one sex has wings. By contrast, the Krauss's organ is absent from most apterous taxa, or with vestigial tegmina, or without tympanum. Among the subfamilies, Pamphaginae includes species with traces of wings in the metanotum and species with no wings. In the former case, they have a wide tympanum and Krauss's organ, and in the latter case they may have neither the Krauss's organ nor the tympanum. The exception in the subfamily Pamphaginae was *Ocneridia*, which has three species with varying degrees of tegmina and wing development; all three species have tympana and none have the Krauss's organ. Within the family Pamphagidae, some squamipterous species have a slightly bumpy ridge on the inner base of the hind femurs, similar to stridulatory pegs (Figures 1–6). These pegs were absent from all other squamipterous and apterous species. When present, these structures faced the Krauss's organ (Figures 7–10). The inner surface of the hind femur have three distinct morphologies: 1) a ridged surface was observed in *Dhofaria*, *Glyphotmethis*, *Prionotropis*, *Tmethis*, and other Thrinchinae; 2) ridged pegs (minute tubercles) on the surface were observed in some Akicerinae, Porthetinae, and Pamphaginae (*Euryparyphes*, *Paraeumigus* and *Paraeuryparyphes* from N Africa, and *Ocneropsis*, *Ocnerosthenus* and *Prionosthenus* from Middle East); and 3) rows of bristles on the surface were observed in Porthetinae (African genera *Lobosceliana* and *Stolliana*). Taxa of the subfamily Echinotropinae, which have fully developed, lobiform or absent tegmina, present or absent tympanum, and no Krauss's organ, have no known stridulatory mechanism.

No physiological relation between Krauss's organ and tympanum or other organs was observed (cf. also Shulov 1952). In squamipterous species, such as *Pamphagus marmoratus* Burmeister, 1838 the tympanum is located very close to the Krauss's organ on the 1st and 2nd tergites. Most squamipterous species have a small atrophic wing concealed under the tegmen (Figures 11–14). In lab-reared females *Ocnerosthenus simulans* (Bolivar, 1911) from Lebanon and *Acinipe calabra* (Costa, 1836) from Sicily, sound was produced rubbing their hind femurs on Krauss's organ. When producing sound, the females' hind legs were raised and moved up and down against the Krauss's organ. Similarly, a small sequence of clicks was recorded from one *O. simulans* female. These clicks were produced by rubbing the tegmina against the atrophic wing joined to the metanotum, and were similar to those recorded in *Acrostira* (Enderlein, 1929) and *Purpuraria* (Enderlein, 1929) (López et al. 2008).

Femur and Krauss's organ morphology affect the sound. For example, sounds produced by *A. calabra* (without ridges of pegs, but with a very rough inner base of hind femurs) and *O. simulans* (with ridges of pegs on inner side of hind femurs) were observably different (Figures 15–18). *A. calabra* sound was lower in frequency (max: 5825 Hz, power: 64.4 dB; min: 3475 Hz; power: 66.5 dB) than the *O. simulans* sound (max: 16,416 Hz; power: 44.0 dB; min: 13,543 Hz; power: 46.4 dB). Additionally, these sounds differed in frequency modulation as *A. calabra* had a deeper but more intense sound than *O. simulans*. Pause times were shorter in *A. calabra* (0.542 s) than in *O. simulans* (0.214 s).

Table I. Presence or absence and characteristics of tegmina, Krauss's organ, tympanum and hind femurs specialization in the five subfamilies of the family Pamphagidae.? = unavailable information.

	Tegmina	Krauss's organ	Tympanum	Hind femurs specialization
Echinotropinae Dirsh, 1961				
Echinotropis Uvarov, 1944	vestigial	absent	absent	unknown
Geloiomimus Saussure, 1899	apterous	absent	absent	unknown
Parageloiomimus Dirsh, 1961	♂ winged, ♀ squamipterous	absent	♂ present, ♀ vestigial	unknown
Thrincotropis Saussure, 1899	vestigial or apterous	absent	absent	unknown
Akicerinae Bolívar, 1916				
Akicera Serville, 1831	♂ winged, ♀ lobiform	present	wide	?
Adephagus Saussure, 1887	♂ ♀ winged	present	wide	?
Batrachornis Saussure, 1884	♂ ♀ winged	present	wide	?
Batrachotetrix Burmeister, 1838	winged, lobiform or apterous	present, smooth	Present, vestigial in apterous species	ridges of pegs
Eremotettix Saussure, 1888	♂ winged, ♀ winged or apterous	present, smooth	wide	ridges of pegs
Glyphanus Fieber, 1853	1st pair, brachypterous	wrinkled	wide	no
Porthetinae Bolívar, 1916				
Aphantotropis Uvarov, 1924	♂ winged, ♀ apterous	present	wide	?
Bolivarella Saussure, 1887	♂ squamipterous, ♀ apterous	present, smooth	wide	?
Cultrinotus Bolivar, 1915	♂ winged, ♀ apterous	present	wide	?
Hoplolopha Stål, 1876	♂ winged, ♀ apterous	present	wide	?
Lamarckiana Kirby, 1910	♂ winged, ♀ apterous	present, smooth	wide	minute tubercles
Lobosceliana Dirsh, 1958	♂ winged, ♀ apterous	present, wrinkled	wide	rows of bristles
Pagopedilum Karsch, 1896	♂ brachypterous, ♀ apterous	present	wide	?
Porthetis Serville, 1831	♂ winged, ♀ apterous	present	wide	?
Puncticornia Dirsh, 1958	♂ winged, ♀ apterous	present	wide	?
Stolliana Bolivar, 1916	♂ winged or brachypterous, ♀ apterous	present, wrinkled	wide	rows of bristles
Trachypetrella Kirby, 1910	lobiform	present (stridulatory organ below Krauss's organ)	wide	?
Transvaaliana Dirsh, 1958	♂ micropterous, ♀ apterous	present	wide	?
Vansoniacris Dirsh, 1958	♂ brachypterous, ♀ apterous	present	wide	?
Xiphoceriana Dirsh, 1958	♂ winged, ♀ apterous	present	wide	ridges of pegs
Thrinchinae Stål, 1876				
Asiotmethis Uvarov, 1943	winged	wrinkled	wide	transversal lamellate ridges
Atrichotmethis Uvarov, 1943	winged	wrinkled	wide	?
Beybienkia Tsyplenkov, 1956	♂ winged, ♀ brachypterous	wrinkled	wide	?
Dhofaria Popov, 1985	winged	wrinkled	wide	transversal lamellate ridges
Eoeotmethis Zheng, 1985	♂ winged, ♀ squamipterous	wrinkled	wide	?
Eotmethis Bei-Bienko, 1948	♂ brachypterous, ♀ squamipterous	wrinkled	wide	?
Eremocharis Saussure, 1884	winged or brachypterous	wrinkled	wide	no
Eremopeza Saussure, 1888	winged	just wrinkled	wide	no
Eremotmethis Uvarov, 1943	winged	wrinkled	wide	no
Filchnerella Karny, 1908	winged or squamipterous	wrinkled	wide	?

(*Continued*)

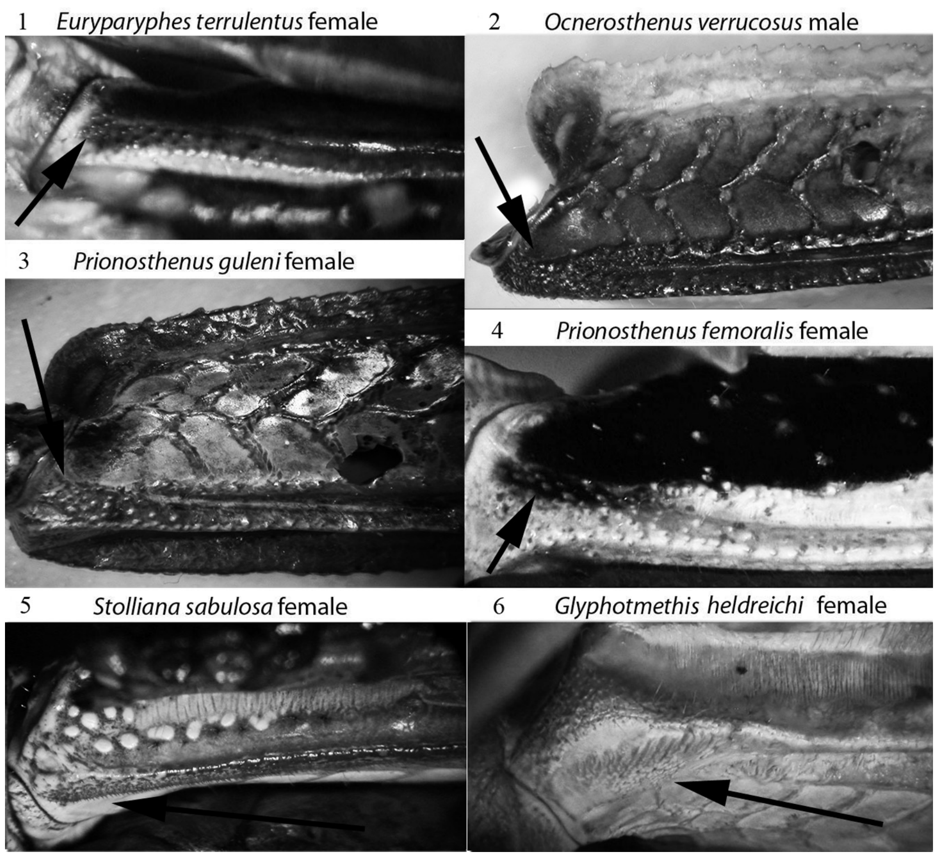
Table I. (*Continued*).

	Tegmina	Krauss's organ	Tympanum	Hind femurs specialization
Glyphotmethis Bei-Bienko, 1951	brachypterous or winged	wrinkled	wide	transversal lamellate ridges
Iranotmethis Uvarov, 1943	winged	just wrinkled	wide	?
Kanotmethis Yin, 1994	winged	wrinkled	wide	?
Melanotmethis Uvarov, 1943	winged	wrinkled	wide	?
Mongolotmethis Bei-Bienko, 1948	♂ brachypterous, ♀ squamipterous	present	wide	?
Paratmethis Zheng et He, 1996	winged	present	wide	?
Pezotmethis Uvarov, 1943	winged or brachypterous	wrinkled	wide	?
Prionotropis Fieber, 1853	brachypterous	wrinkled	wide	minute rounded tubercles
Pseudotmethis Bei-Bienko, 1948	winged or brachypterous	wrinkled	wide	?
Rhinotmethis Sjöstedt, 1933	♂ brachypterous, ♀ squamipterous	wrinkled	wide	no
Sinotmethis Bei-Bienko, 1959	♂ winged, ♀ brachypterous	wrinkled	wide	?
Strumiger Zubovski, 1896	winged	wrinkled	wide	no
Thrinchus Fischer von Waldheim, 1833	winged	wrinkled	wide	?
Tmethis Fieber, 1853	winged	wrinkled	wide	one line of small tubercles
Tuarega Uvarov, 1943	winged	wrinkled	wide	some transversal lamellate ridges
Utubius Uvarov, 1936	winged	just wrinkled	wide	no
Pamphaginae Burmeister, 1840				
Acaeropa Uvarov, 1927	squamipterous	present	present	?
Acinipe Rambur, 1838	1st pair, squamipterous	smooth	wide	no
Acrostira Enderlein, 1929	absent	smooth	reduced	no
Araxiana Mishchenko, 1951	absent	absent	absent	?
Bufonocarodes Mishchenko, 1951	absent	absent	absent	no
Cryptonothrotes La Greca, 2004	traces on metanotum	absent	wide	no
Ebnerodes Ramme, 1951	absent	absent	present	?
Eumigus Bolivar, 1878	1st pair, squamipterous	smooth	wide	no
Eunapiodes Bolivar, 1907	1st pair, squamipterous	smooth	wide	no
Eunothrotes Adelung, 1907	traces on metanotum	absent	wide	no
Euryparyphes Fischer, 1853	1st pair, squamipterous	just wrinkled	wide	ridges of pegs
Finotia Bonnet, 1884	absent	absent	absent	no
Glauia Bolivar, 1912	1st pair, squamipterous	smooth	wide	no
Glauvarovia Morales Agacino, 1945	1st pair, squamipterous	smooth	wide	no
Haplotropis Saussure, 1888	micropterous	present	wide	?
Iranacris Mishchenko, 1951	absent	absent	absent	?
Kurtharzia Koçak, 1981	1st pair, squamipterous	smooth	wide	no
Mistshenkoella Cejchan, 1969	♂ brachypterous, ♀ micropterous	wrinkled	wide	no
Nadigeumigus La Greca, 1993	1st pair, squamipterous	smooth	wide	?
Neoparanothrotes Mirzayans, 1990	absent	absent	present	?
Nocaracris Uvarov, 1928	traces on metanotum	absent	absent	no
Nocarodes Fischer von Waldheim, 1846	absent	absent	absent	no
Ocneridia Bolivar, 1912	1st and 2nd pair, squamipterous or apterous	absent	wide	no
Ocnerodes Brunner von Wattenwyl, 1882	1st pair, squamipterous	smooth	wide	no
Ocneropsis Uvarov, 1942	1st pair, squamipterous	smooth	wide	ridges of pegs
Ocnerosthenus Massa, 1995	1st pair, squamipterous	smooth	wide	ridges of pegs
Orchamus Stål, 1876	1st pair, squamipterous	smooth	wide	no
Oronothrotes Mishchenko, 1951	traces on metanotum	present	wide	?
Paktia Pfadt, 1970	♂ micropterous, ♀ traces on metanotum	present	wide	?

(*Continued*)

Table I. (*Continued*).

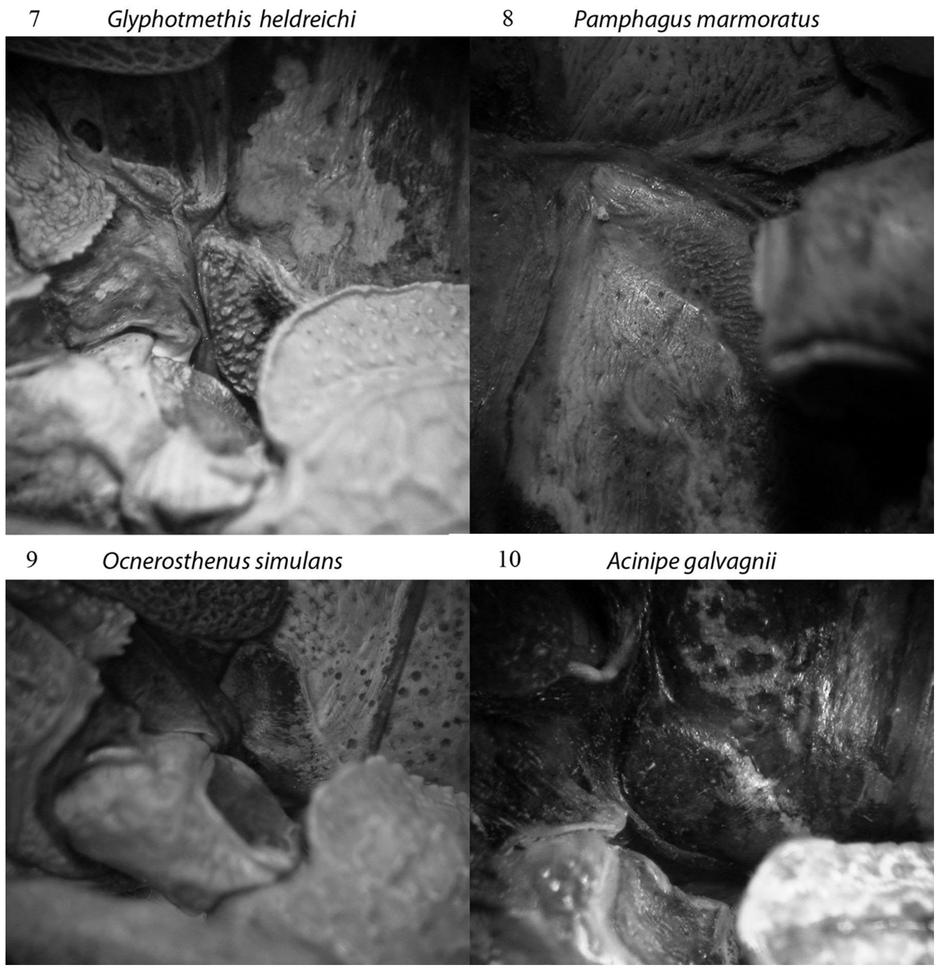
	Tegmina	Krauss's organ	Tympanum	Hind femurs specialization
Pamphagus Thunberg, 1815	1st pair, squamipterous	wrinkled	wide	no
Paracinipe Descamps et Mounassif, 1972	1st pair, squamipterous	smooth	wide	no
Paraeumigus Bolivar, 1914	1st pair, squamipterous	just wrinkled	wide	ridges of pegs
Paraeuryparyphes La Greca, 1993	1st pair, squamipterous	just wrinkled	wide	ridges of pegs
Paranocaracris Mishchenko, 1951	absent	absent	absent	no
Paranocarodes Bolivar, 1916	traces on metanotum	just visible	wide	no
Paranothrotes Mishchenko, 1951	traces on metanotum	absent	wide	no
Prionosthenus Bolivar, 1878	1st pair, squamipterous	smooth	wide	ridges of pegs
Pseudamigus Chopard, 1943	1st pair, squamipterous	smooth	wide	?
Pseudoglauia Morales Agacino et Descamps, 1968	1st pair, squamipterous	smooth	wide	no
Purpuraria Enderlein, 1929	traces on metanotum	smooth	reduced	no
Savalania Mishchenko, 1951	absent	absent	absent	?
Saxetania Mishchenko, 1951	traces on metanotum	absent	wide	no
Tropidauchen Saussure, 1887	traces on metanotum, *T. marginatum* is winged	absent	wide	no



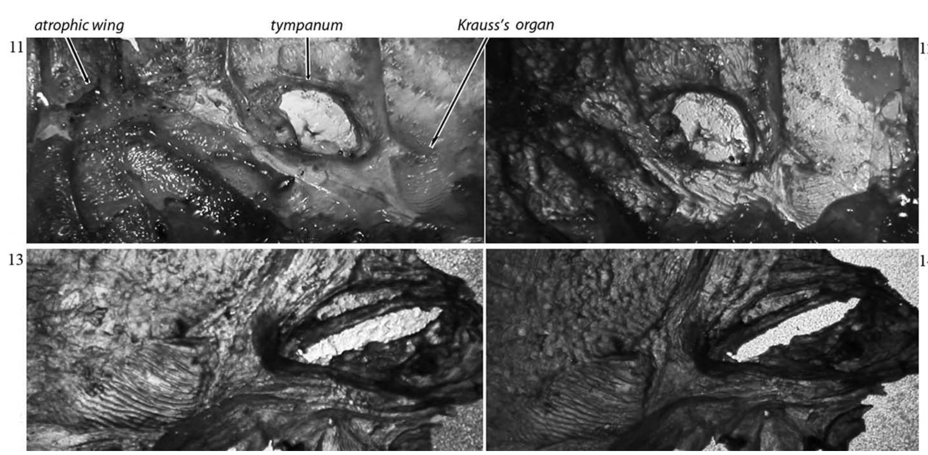
Figures 1–6. Specialized structures on the inside of hind femurs of Pamphagidae.

Discussion

The secondary loss of the Krauss's organ is a phylogenetically informative character used to divide Pamphagidae into subfamilies and tribes (Storozhenko & Paik 2011). The presence of Krauss's organ in winged taxa (Akicerinae, Porthetinae and Thrinchinae) is ancestral or plesiomorphic, and its secondary loss in squamipterous tribes (Pamphagini Burmeister, 1840, Euryparyphini La Greca, 1993, and Haplotropiidini Sergeev, 1995) and apterous



Figures 7–10. Krauss's organ morphology in four Pamphagidae species.



Figures 11–14. The tympanum and Krauss's organ in a freshly dissected (11, 13) and in a slide preparation (12, 14) *Pamphagus marmoratus*, 11, 12: outer view, 13, 14: inner view. A small atrophic wing is concealed under tegmina, which was removed to show it.

taxa (tribes Finotiini Bolívar, 1916 and Nocarodeini Bolívar, 1916 and subfamily Echinotropinae) is apomorphic. Morphological diversification of the hind femur surface evolved in winged species with a wrinkled Krauss's organ but was not observed in taxa with reduced or absent wings. The parallel loss of sound

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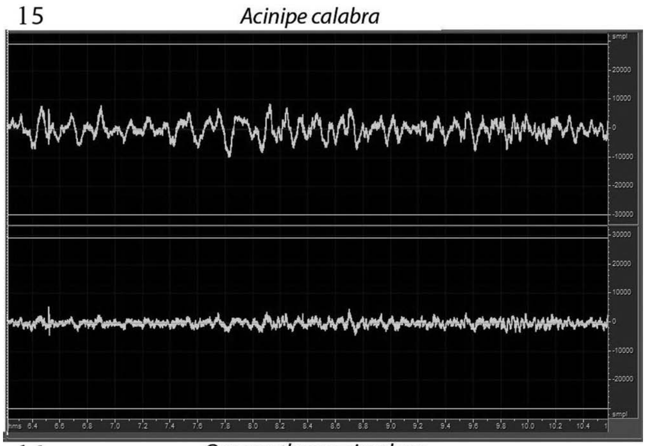

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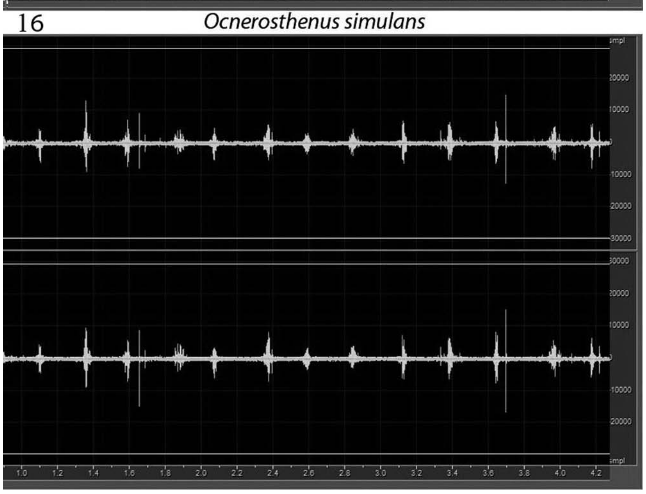

Figures 15–16. Oscillograms of sounds produced by *Acinipe calabra* and *Ocnerosthenus simulans* rubbing hind femurs on the Krauss's organ.

producing and detecting organs suggests that they are functionally related.

In Pamphagidae, alternative mechanisms of stridulation that do not involve the Krauss's organ have been described (Johnsen 1972; Ingrisch 1983; Llorente et al. 1995; García et al. 1996; Presa et al. 2000; López et al. 2008), but few studies suggested that Krauss's organ itself produces sounds. In some Thrinchinae, the upper side of middle tibiae have a row of teeth or tubercles that are rubbed by the wing, producing sound that is amplified by the tympanum. *Dhofaria* and *Glyphotmethis* species produce sound by rubbing the femur and the Krauss's organ (Popov 1997; Ünal 2007). In Porthetinae, the costal region of tegmina (fully developed or shortened) is enlarged and covered by dense, parallel, ridge-like veinlets for stridulatory specialization. In *Trachypetrella*, a femur-abdominal stridulatory mechanism includes the Krauss's organ and stridulatory ridges below it (Dirsh 1965).

Pamphagidae are thought to have originated in the early Tertiary or Cretaceous (Flook & Rowell 1997). If Krauss's organ is ancestral, the first Pamphagidae could have communicated using stridulations from the femur and Krauss's organ. Based on the known Pamphagidae phylogeny, the most ancestral form of this communication involved a wrinkled Krauss's organ rubbing against the inner side of the femur. Later in Pamphagidae evolution, specialized structures, such as bristles or lamellate ridges, on the inner femur surface led to a range of sounds. For example, oscillograms from *Acinipe* and

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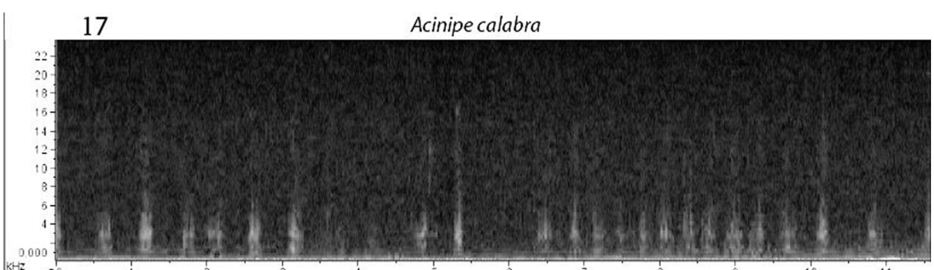

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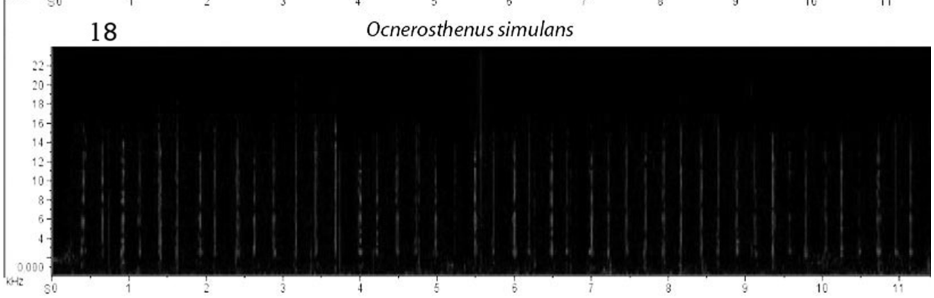

Figures 17–18. Frequency of sounds produced by *Acinipe calabra* and *Ocnerosthenus simulans*.

Ocnerosthenus (Figures 15 and 16) revealed how surface rugosity affects the sound produced. The ridged pegs on the femur surface in *Ocnerosthenus* yielded oscillograms with well-defined syllables. By contrast, in *Acinipe* with no such pegs, oscillogram syllables were not clearly defined.

Over the course of the evolution of Palaearctic Pamphaginae, three distinct femur-Krauss's organ mechanisms evolved. In early-diverging Pamphaginae, such as *Euryparyphes* and *Prionosthenus*, ridged pegs on the hind femurs produce sound by rubbing against a smooth Krauss's organ. In most squamipterous Pamphaginae, the Krauss's organ is slightly wrinkled but still produces sound rubbing against the inner side of the femur. In the most recently diverging Pamphaginae lineage, the tegmina were completely lost, and there is no evidence of the Krauss's organ. Many of these species exhibited a parallel loss of tympana. This pattern of Krauss's organ presence/absence is concordant with the theory that the Baetico-Riffan plate in the western Mediterranean was the centre of Palaearctic Pamphagidae evolution (La Greca 1999). In this scenario, Asian apterous taxa would be the most recently diverging.

Concerning the kind of sound emitted by rubbing femurs against Krauss's organ, in Pamphagidae, hind femurs have an attenuated lobe for the femur-trochanter articulation, which permits both femurs and trochanters to rotate on their axis more than in Acrididae (where the lobe is more prominent). This arrangement brings the lower edge of the femoral base in contact with Krauss's organ (cf. Uvarov 1943). The femur-abdominal mechanism does not require that the Krauss's organ is a true organ, but simply requires that this chitinous portion of the 2nd abdominal tergite plays a role in sound emission, possibly in addition to other sound mechanisms involving generally tegmina or their remains. Thus, it is more precise to name the structure Krauss's plate. The function of the sounds produced by these stridulations should be the focus of future studies. Here it has been demonstrated this mechanism in species from genera with (*Ocnerosthenus*) and without (*Acinipe*) specialized structures on hind femurs. Overall, these specialization structures were found on hind femurs in 18 of 69 winged or squamipterous genera with the Krauss's plate. In the 20 genera without a Krauss's plate, this stridulation mechanism cannot be used.

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