Allometric effect of body size and tegmen mirror area on sound generator characters in *Euconocephalus pallidus* (Orthoptera, Tettigoniidae, Copiphorini) from Singapore

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Abstract

Acoustic communication, including allometry of secondary sexual traits and body size, can differ among katydid species from different parts of the world. However, Neotropical species tend to be better studied than their Southeast Asian relatives. This is true for the tribe Copiphorini (Orthoptera, Tettigoniidae). To allow for future comparative studies of Neotropical and Palaeotropical Copiphorini, the allometric relationships between sound generator characters and body size of *Euconocephalus pallidus* from Singapore were examined. Five sound generator characters–tegmen length, stridulatory file length, tooth width, teeth density, and mirror area–were correlated with pronotum length as the proxy for body size. Stridulatory file length, tooth width, and teeth density were also correlated with the mirror area. The relationships were subsequently tested for difference between scaling slope and isometry based on 29 male adults from a single population. All sound generator characters except teeth density exhibited significant positive correlations with pronotum length, whereas teeth density exhibited significant negative correlation with pronotum length. Among them, only tooth width and teeth density scaled hyperallometrically, while the other characters scaled isometrically. As males produce a continuous buzzing call over long durations, larger teeth (i.e., larger tooth width and lower teeth density to accommodate larger teeth) are probably more resistant to age-related abrasion. This may imply that males with larger teeth can produce calls recognized and/or favored by the females over a longer part of the males' adult lifespan. File length and mirror area exhibited isometric scaling. This suggests a stabilizing selection driven by their function in dictating carrier frequency, which females tend to rely on to recognize conspecific males.

Keywords

acoustic communication, cone-headed katydid, mirror, Southeast Asia, stridulatory structure, tegmen morphology

Introduction

Studying the allometric relationships between morphological traits and body size is important to understand the evolutionary patterns of within-species variations in morphology (Shingleton et al. 2007, 2008). Many morphological characters are phenotypically plastic and correlate with body size, often owing to the influence of environmental conditions (Shingleton et al. 2009). Some of the morphological characters under the influence of selection can become disproportionately larger or smaller with increasing body size (i.e., hyperallometry) (Shingleton et al. 2007, 2008, Rodríguez and Eberhard 2019). For example, sexual selection tends to favor the hyperallometry of secondary sexual traits (Bonduriansky and Day 2003; Bonduriansky 2007). Studying the allometric relationships between these traits and body size can offer insights into patterns of sexual selection.

For animals that communicate using sound to find and attract mates, the acoustic signals produced by males can sometimes reveal information about the male condition and/or quality to the female (Bennet-Clark 1998, Bentsen et al. 2006, Brown et al. 2006). The sound generator characters responsible for producing the acoustic signals can thus be subjected to female preference, male–male competition, and sexual selection, and consequently exhibit hyperallometry (Anichini et al. 2017, Rebrina et al. 2020). In some instances, larger sound generator characters are an indication of better body condition, because developing and maintaining these structures can be energetically costly (Del Castillo and Gwynne 2007). Hence, females can exhibit a preference for acoustic signals produced by larger sound generator characters. Furthermore, larger sound generator characters can also be more resistant to wear and tear, conferring males with larger sound generator characters to be more competitive in producing sound to locate and attract mates than males with smaller ones (Ritchie et al. 1995, Anichini et al. 2017).

In many species of katydids (Tettigonioidea Krauss, 1902), males also produce sound to attract females, and the sound generator characters are found on their asymmetrical tegmina (Montealegre-Z 2009, Montealegre-Z et al. 2017). These include the stridulatory file, a specialized serrated vein on the left tegmen that produces sound when the teeth hit against the scraper on the right tegmen, as well as the mirror, a specialized cell membrane on the right tegmen that helps amplify the sound and dictate resonance and frequency (e.g., Morris and Pipher 1967, Bailey 1970, Montealegre-Z and Postles 2010). The biophysical mechanics of sound production, allometry of sound generator characters in katydids, and how they play a role in attracting mates and avoiding predators have been well studied (e.g., Bailey 1967, 1970, Sales and Pye 1974, Heller 1995, Ritchie et al. 1995, Bennet-Clark 1998, Morris

1999). These enabled more recent works that examined allometry of sound generator characters in a broad range of species while accounting for phylogenetic relatedness (e.g., Montealegre-Z 2009) and that focused on targeted species to build on studies of sexual selection in katydids (e.g., Anichini et al. 2017, Rebrina et al. 2020). The comparative study by Montealegre-Z (2009) also demonstrated that many sound generator characters exhibited hyperallometry with body size, but Anichini et al. (2017) and Rebrina et al. (2020) showed that this is not necessarily the case in *Poecilimon* Fischer, 1853 (subfamily Phaneropterinae).

While Anichini et al. (2017) and Rebrina et al. (2020) based their investigation on temperate model species, Montealegre-Z (2009) provided a comparative study of 58 tropical species–most of which are from the Neotropics. Heller (1995) previously demonstrated that the acoustic signaling in Neotropical and Palaeotropical Pseudophyllinae is highly variable owing to different predation pressures in different parts of the world. Likewise, it is also plausible that allometric relationships between sound generator characters and body size can differ among taxonomically related but geographically distant species. Therefore, expanding the investigation of allometry in sound generator characters to lesser-known species may reveal new insights and, consequently, provide a more comprehensive understanding of the evolutionary patterns related to these sound generator characters.

Here, the allometric relationships between sound generator characters and body size of a Palaeotropical katydid species from the tribe Copiphorini Karny, 1912 is examined, specifically from the genus *Euconocephalus* Karny, 1907. Very little is known, apart from a few anecdotal observations, about the katydids from this region (e.g., Tan 2011, 2020, Tiwari and Diwakar 2019). In comparison, Neotropical Copiphorini have been used extensively as study subjects in various studies on acoustic communication (e.g., Montealegre-Z and Mason 2005, Montealegre-Z and Postles 2010, Sarria-S et al. 2016, Celiker et al. 2020). These also include *Neoconocephalus* Karny, 1907, a genus very similar morphologically to *Euconocephalus* (e.g., Counter Jr 1977, Schul and Patterson 2003, Deily and Schul 2004). Building up information about acoustic communication in *Euconocephalus*, including examining their allometry, may eventually allow for comparative inference between species from the Neotropics and Palaeotropics.

For this study, *Euconocephalus pallidus* (Redtenbacher, 1891) was collected, as the species is a relatively large katydid with well-developed sound generator characters suitable for studying allometry with body size. Being the most abundant and widely distributed *Euconocephalus* from Singapore and highly adaptable to both urban and peri-urban habitats (Tan 2011, 2020), *E. pallidus* has the potential to be an important model species to examine acoustic communication of katydids in the context of urbanization. The following questions were investigated: (1) What is the relationship between body size and sound generator characters (both stridulatory structures and mirror)? (2) What is the relationship between the different sound generator characters on different tegmina (e.g., stridulatory file length on the left tegmen *vs.* mirror area on the right tegmen)? And if, as predicted, these relationships are significant, (3) can their isometric or hyperallometric relationships allow for inference about the selection pressures acting on these sound generator organs? By using a similar methodology and addressing similar questions as previous species-targeted studies (see Anichini et al. 2017, Rebrina et al. 2020), the aim was to also examine how generalizable the patterns observed in *Poecilimon* are in the taxonomically more distant *E. pallidus*.

Materials and methods

Study subject.—*Euconocephalus pallidus* inhabits open grassland and is among the largest orthopterans and best fliers from this habitat (Tan 2011, 2020, Tiwari and Diwakar 2019). At night, males produce a distinct loud buzz for a substantially long duration. The dominant frequency of the calls is around 12 kHz (Tan 2020). Multiple males have been observed to call concurrently (Tan 2011).

Sampling.—Between 6 February and 2 April 2019, 29 adult males were collected from an open grassland in Singapore (1.34279N, 103.87751E) known formerly as Bidadari Cemetery. The site has since been cleared for residential development. The katydids were identified using a key in Tan (2011). The katydids were euthanized by freezing, dried and pinned, and subsequently deposited in the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, Singapore. Collections were carried out from this single site within a short period of time, which minimizes potential confounding effects of population, generational, and temporal differences.

Measurement of body size and sound generator characters.—All measurements were done using ImageJ 1.51j8 (Wayne Rasband, Research Services Branch, National Institute of Mental Health, Bethesda, MD, USA) following the approach in Tan et al. (2020).

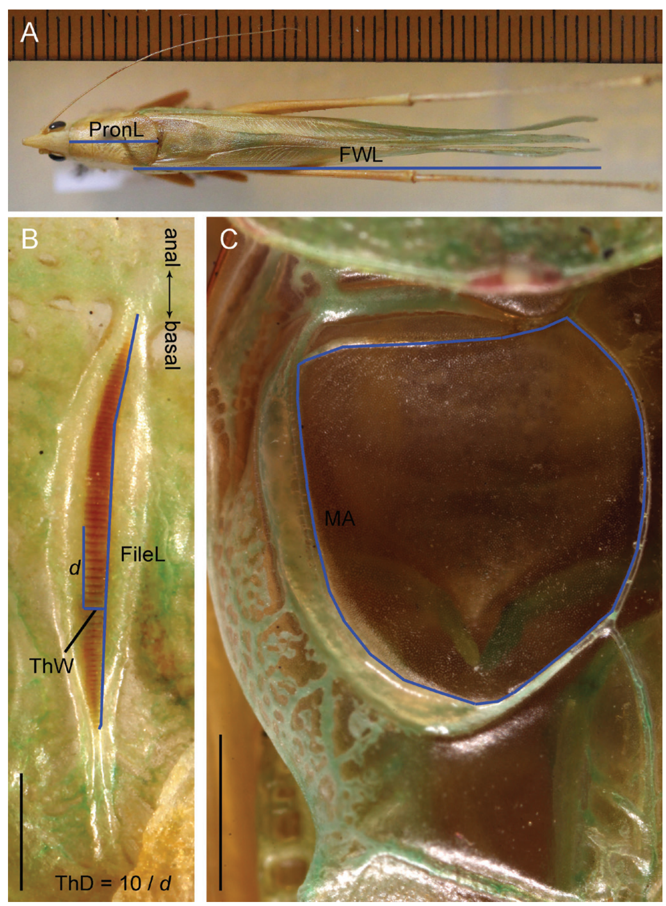

Fig. 1. Measurements of body size and sound generator characters. **A.** Male habitus in dorsal view; **B.** Stridulatory file on the left tegmen in ventral view, scale bar = 0.5 mm; **C.** Mirror area on the right tegmen in dorsal view, scale bar = 1.0 mm. PronL = pronotum length, TL = tegmen length, FileL = file length, ThD = teeth density, ThW = tooth width, *d* = length of 10 teeth in the middle region of the file.

Pronotum length (PronL), measured between the middle of the anterior margin and that of the posterior margin (Fig. 1A), was used as a proxy for body size (Montealegre-Z 2009). To measure the PronL and tegmen length (TL), the dried-pinned specimens were photographed using a Canon EOS 700D digital SLR camera with a Canon EF 100 mm f/2.8 Macro USM lens (Fig. 1A).

Five sound generator characters were examined: TL; stridulatory file length (FileL), tooth width (ThW), and teeth density (ThD) on the left tegmen; and mirror area (MA) on the right tegmen. Measurements of these traits follow those of Rebrina et al. (2020). To measure the sound generator characters, the tegmina were dissected and the stridulatory areas on both left and right tegmen were photographed using the dSLR camera with a Canon MP-E 65 mm f/2.8 USM (1–5×) lens. The FileL was measured as the total length of the stridulatory file on the ventral side of the left tegmen (Fig. 1B). This was done by connecting the posterior ends of the cusp of each tooth of all the visible teeth using the 'segmented line' function in ImageJ. The ThW was determined by obtaining the average tooth width of the teeth in the middle region of the file. The middle region of the file was defined as the central tooth on the file plus five teeth to the basal end and four to the anal end (Fig. 1B). Tooth width was measured between the posterior ends of the cusp of the tooth. The ThD was calculated as the ratio of the 10 teeth previously chosen to the length of the middle region of the file (measured along the edge of the tooth) (Fig. 1B). The MA on the right tegmen was measured using the 'polygon selection' function in ImageJ to connect the inner margin of the vein surrounding the membrane making up the mirror (Fig. 1C).

Analysis

All statistical analyses were done using R software version 4.1.0 (R Core Team 2019). Prior to modeling, all traits were $\log_{10}$-transformed to normalize the distribution and reduce heteroscedasticity (Packard et al. 2011). To examine the allometric scaling of sound generator characters with body size, the approach used by Anichini et al. (2017) and Rebrina et al. (2020) was adopted: a standardized major axis (SMA) regression was fitted for each sound generator character using the 'smatr' R package (Warton et al. 2012), with the PronL as a fixed effect. SMA regression is preferred over ordinary least square (OLS) regressions owing to the lower expected error of the former (Warton et al. 2006, Smith 2009). Moreover, SMA is preferred because both the sound generator characters and body size have similar levels of error as a result of the measurements being collected using the same method and having similar magnitudes (Warton et al. 2006, Smith 009).

The coefficient of determination, R^2, was reported as a measure of the strength of regressions (Kasuya 2019). Effect sizes were interpreted as high ($R^2 > 0.25$), medium ($R^2 > 0.09$), or low ($R^2 > 0.01$) (Cohen 1992). To test for significant difference between the scaling slope and isometry for each sound generator character, the 'slope. test' function of the 'smatr' package was used. 'Slope = 1' was used when a one-dimensional character (e.g., TL, FileL, ThW, and ThD) was scaled with body size (PronL, also one-dimensional). For MA, 'slope = 2' was used since the (two-dimensional) surface area of the mirror increases as a square of body length. This is to account for the assumption that a body grows equally in all three dimensions, i.e., that structure surface area should grow as a square of body length (Hirst et al. 2017, Rebrina et al. 2020).

Results

The average and range (minimum to maximum) of each sound generator character of the 29 males were as follows: PronL = 7.8 mm (7.0–8.7 mm); TL = 40.3 mm (35.4–44.5 mm); FileL = 1.8 mm (1.6–2.0 mm); ThW = 0.12 mm (0.07–0.14 mm); ThD = 39.4 mm^{-1} (29.7–49.0 mm^{-1}); MA = 4.4 mm^2 (3.7–5.0 mm^2).

All sound generator characters exhibited significant correlations with PronL (Fig. 2), with strong effect sizes (i.e., R^2 of the SMA models ranging from 0.3 to 0.5, except for ThD) (Table 1). With the exception of ThD, the remaining sound generator

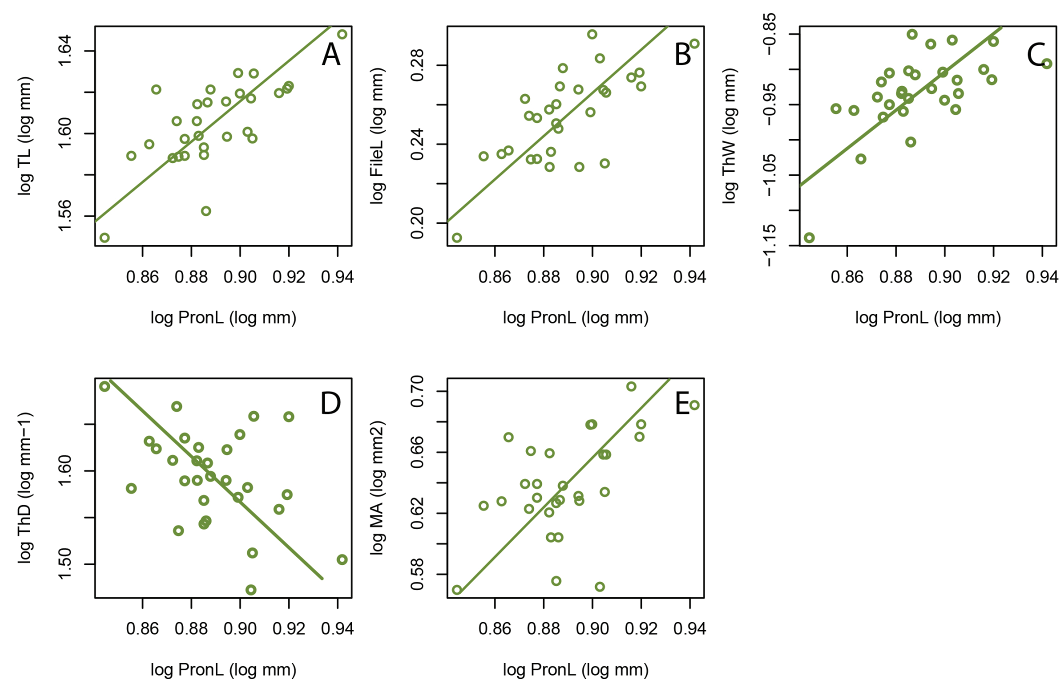

Fig. 2. Relationships between the five sound generator characters with pronotum length (PronL) as body size based on SMA **A.** Tegmen length; **B.** Stridulatory file length; **C.** Tooth width; **D.** Teeth density; **E.** Mirror area. All traits were $\log_{10}$-transformed. The thicker lines indicate hyperallometric relationships, and the thinner lines indicate isometric relationships.

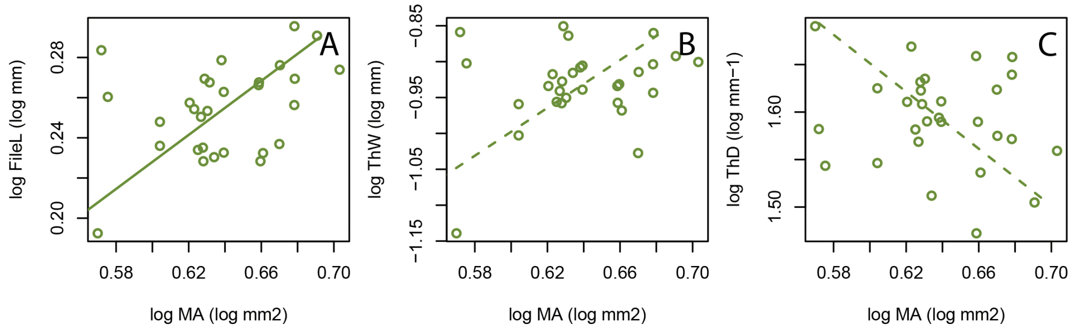

Fig. 3. Relationships between the sound generator characters on the left tegmen with mirror area (MA) on the right tegmen based on SMA **A.** Stridulatory file length; **B.** Tooth width; **C.** Teeth density. All traits were log_{10}-transformed. The dotted lines indicate non-significant relationships, and the thinner lines indicate isometric relationships.

Table 1. Summary of the allometric analysis using SMA of the sound generator characters with pronotum length (PronL) as a proxy for body size and of the sound generator characters on the left tegmen with mirror area (MA). All traits were log_{10}-transformed. Slope $_{SMA}$ refers to the estimate of the SMA model. CI = confidence interval of the slope; R^2 = coefficient of determination of the model. P refers to the p-value of the correlation; P $_{SMA}$ refers to the p-value from the slope test. Asterisks represent significant effects: *P < 0.05; **P < 0.01; ***P < 0.001.

log_{10}-Trait	Slope $_{SMA}$	95% CI	R^2	P	Slope test	P_{SMA}
PronL as a proxy for body size						
TL	0.98	[0.74, 1.29]	0.50	<0.001 ***	1	0.878
FileL	1.10	[0.83, 1.44]	0.50	<0.001 ***	1	0.509
ThW	2.71	[2.00, 3.68]	0.39	<0.001 ***	1	<0.001 ***
ThD	–2.44	[–3.47, –1.72]	0.18	0.022 *	–1	<0.001 ***
MA	1.63	[1.18, 2.26]	0.29	0.002 **	2	0.211
Mirror area (MA)						
FileL	0.67	[0.47, 0.96]	0.15	0.036 *	½	0.101
ThW	1.67	[1.15, 2.42]	0.07	0.17		
ThD	–1.50	[–2.19, –1.03]	0.04	0.31		

characters correlated positively with PronL. Furthermore, there was strong evidence of ThW and ThD scaling hyperallometrically with PronL: ThW increased hyperallometrically about 2.7 times faster than PronL, whereas ThD decreased hyperallometrically about 2.4 times faster than PronL (Table 1). There was very little evidence of TL and FileL scaling more than slope = 1 with PronL, indicating that these characters scale isometrically (Table 1). Likewise, there was also very little evidence of MA scaling more than slope = 2 with PronL, indicating that MA also scales isometrically (Table 1).

FileL exhibited significant correlation with MA (Fig. 3), with moderate effect size (i.e., R^2 of the SMA models = 0.15) (Table 1). However, there was very little evidence of FileL scaling more than slope = ½ with MA. ThW and ThD did not correlate significantly with MA (Fig. 3, Table 1).

Discussion

In the investigated paleotropical katydid, there was significant hyperallometric scaling of tooth width and teeth density with pronotum length. Mainly, larger males of *E. pallidus* bear disproportionately broader teeth and have disproportionately less densely arranged teeth. The rest of the sound-producing characters scaled isometrically with body size. Specifically, larger *E. pallidus* males were found to bear significantly longer tegmina and stridulatory file and larger mirror than smaller males. These results corroborate previous studies showing the influence of male body size on sound generator characters in other katydids, including a comparative study of 38 species by Montealegre-Z (2009) and species-based studies of *Poecilimon* (Anichini et al. 2017, Rebrina et al. 2020).

ThW and ThD exhibited hyperallometric scaling with body size, which has also been reported in *Poecilimon* (Anichini et al. 2017, Rebrina et al. 2020). One possible explanation is that these traits are subjected to positive sexual selection (Bonduriansky 2007) and may be crucial for aggressive male–male competition or as an exhibition of male quality (Eberhard et al. 2018, Rodríguez and Eberhard 2019). The striking of teeth against the scrape can cause wear and tear to the teeth (damage or loss) (Hartley and Stephen 1989). A possible hypothesis is that, since larger teeth are probably more resistant to age-related abrasion, males with larger teeth (i.e., larger ThW and lower ThD to accommodate larger teeth) are more likely to produce calls with signal properties that are recognized and/or preferred by the females over a longer period of their adult life span (Ritchie et al. 1995, Anichini et al. 2017). This could be true for *Euconocephalus* because males produce a continuous buzzing call over long durations. The continuous striking of teeth in such call types can lead to the teeth being more susceptible to wear and tear than katydids that produce shorter echemes.

The sound generator characters FileL and MA exhibited isometric scaling. This is perhaps indicative of stabilizing selection driven by their functions (Bennet-Clark 1998, Anichini et al. 2017). Specifically, FileL and MA are important morphological determinants of the carrier frequency that females tend to rely on for recognizing conspecific males, in which longer FileL and larger MA tend to scale negatively with carrier frequency in katydids (Morris et al. 1994, Montealegre-Z 2009, Montealegre-Z et al. 2017, Rodríguez and Eberhard 2019). This also implies that the variations in FileL and MA within a species should correlate with the normal distribution of wing resonance and carrier frequency to ensure conspecific recognition. Therefore, FileL and MA are probably less likely to be subjected to positive sexual selection.

However, in *Poecilimon*, MA scaled hyperallometrically with body size and was postulated to be under positive sexual selection facilitated by female preference for louder signals (Rebrina et al. 2020), the mirror structure also being important for the amplification of sound (Morris and Pipher 1967, Bailey 1970, Chivers et al. 2017). The same cannot be said for *E. pallidus,* because whether the mirror structure is under sexual selection would be out of the scope of this paper when data on the acoustics and female preference of *E. pallidus* were not available. Nonetheless, this illustrates how the scaling of sound generator characters with body size is not always generalizable.

Lastly, TL scaled isometrically with body size in the macropterous *E. pallidus* because the wings of this species are likely to be more important for flight. This species was observed in Singapore to call on tree canopies along streets, suggesting that they can fly and disperse over long distances along green corridors (Tan 2011). A plausible explanation for the positive coupling of TL and body size may be associated with the correlated growth of TL and body size during development, and consequently, the TL becoming fixed in the adult after the final molt (Rebrina et al. 2020). A larger male, therefore, probably has longer wings to facilitate effective flight.

Unfortunately, the examination of the relationships between the sound generator characters, body size, and acoustic signal properties (see Montealegre-Z 2009, Montealegre-Z et al. 2017) was not possible in this study, as acoustic data were unavailable. As a result, inferences about female preference in *E. pallidus* are only speculative and require further testing. Nonetheless, this study provides the basis for further studies into acoustic communication in *E. pallidus* and Southeast Asia Copiphorini. Future studies examining the allometric relationships between sound generator characters and body size among different populations of *E. pallidus*–from urban and peri-urban habitats–can provide insights into the microevolution of these characters. It may also be worth looking into comparative studies by including syntopic congeners [e.g., *E. mucro* (Haan, 1843)] and/or relatives (e.g., *Xestophrys horvathi* Bolívar, 1905) (see Tan 2011).

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