Interspecific differences of stridulatory signals in three species of bark beetles from the genus *Polygraphus* Er. (Coleoptera: Curculionidae, Scolytinae) inhabiting the island of Sakhalin

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Abstract

Stridulatory signals are involved in conspecific interactions between bark beetles (Coleoptera: Curculionidae, Scolytinae). In this study, we compared the qualitative profiles of acoustic signals in three species from the genus *Polygraphus* Er. Sympatry can be periodically observed in two of them – *P. proximus* and *P. subopacus*. Sporadically they occur on the same plants. *P. nigrielytris* colonize distinctly different host plant species; however, on the island of Sakhalin it inhabits the same biotopes. The purpose of the study is to identify species-specific parameters and the extent of differences in stridulatory signals of these species. Airborne signals produced during the contact of males of the same species were experimentally recorded. Among tested parameters of stridulatory signals, as the most species-specific were noted: chirp duration, interchirp interval, number of tooth-strikes per chirp, and intertooth-strike interval.

Introduction

Airborne sounds and solid-borne vibrations are widely used by animals as communication signals (Dumortier, 1963; Greenfield, 2002; Cocroft & Rodriguez, 2005). According to one of the latest generalized assessments, the so-called semiophysicals (Mazzoni et al., 2018) are used as a

35 communication channel by 92% of all described insect species (Cocroft & Rodriguez, 2005).

36 Numerous studies on this type of communication analyze variability of inter and intra species

37 signals among grasshoppers, crickets, and cicadas (Gerhardt & Huber, 2002; Greenfield, 2002,

38 2016; Boulard, 2005; Heller, 2005; Henry, 2005; Hoikkala, 2005; Sueur, 2005; Stewart &

39 Sandberg, 2005). It should be noted that the mechanisms of sound production and reception are

40 also widespread among Hymenoptera, Hemiptera, and Coleoptera, which remain poorly studied

41 in this regard despite their predominate species diversity (Kojima et al, 2012; Breidbach, 1986;

42 Wessel, 2006). Insects that live both on the surface and inside plants are of particular interest since

43 plants are good mediators of vibrational signals (Michelsen et al., 1982; McVean & Field, 1996).

44   Bark beetles (Coleoptera: Scolytinae) produce signals using stridulation – a method of

45 producing sounds by rubbing of the sharp cuticular cant (*plectrum)* against a special file (*pars*

46 *stridens)* (Barr, 1969). These signals are used in conspecific interactions (Barr, 1969; Ryker &

47 Rudinsky 1976; Yturalde & Hofstetter, 2015) and for protection against predators (Lewis & Cane

48 1990; Dobai et al., 2017). It is still not clear which of the signals, an airborne signal or a solid-

49 borne one, is perceived by this insects (Fleming et al., 2013; Dobai et al., 2017). Due to dense

50 population of bark beetles, weak signals can be perceived by the receiver via one of the two

51 channels, or both simultaneously (Fleming et al., 2013).

52   Almost all Holarctic representatives of the genus *Polygraphus* Er. occur on Pinaceae

53 (Krivolutskaya 1996; Nobuchi, 1979; Wood and Bright, 1992), for example, the fir bark beetle *P*

54 *subopacus* is specific to Picea spp., and the four-eyed fir bark beetle *Polygraphus proximus* attacks

55 almost exclusively *Abies* Mill. trees (Wood and Bright, 1992). However, there are exceptions, for

56 example, *P*. *nigrielytris* can be found exclusively on *Angiosperms*, *Sorbus* L. and *Alnus* Mill. in

57 particular (Krivolutskaya 1996).

58   In this study, we compared the qualitative profiles of acoustic signals of three species, and

59 two of these, *P. proximus* and *P. subopacus*, can be sporadically found on the same host plant.

60 The third species, *P. nigrielytris*, is distinctly different from the former two species according to host-

61 plant specialization (Krivolutskaya, 1958). The purpose of the study is to reveal the variants and the degree

62 of differences in stridulatory signals required for interspecific differentiation of bark beetles within the

63 genus *Polygraphus*, which are allopatric and sympatric with regard to the host plant.

64

65 ## Materials & Methods

66   **Collection and storage of insects**

67   Overwintered specimens of *P. proximus, P. subopacus* and *P. nigrielytris* were used in the
68   experiment. Imagoes were collected with fir bark from the brood tree in May 2018 on the island
69   of Sakhalin in the territory of Krasnogorsky State Nature Reserve (48°29'22,2" N, 142°1'49,7" W).
70   Species and sexual identification was performed based on morphological characteristics (Stark
71   1952, Krivolutskaya, 1958). Insects were placed individually in separate marked 5 ml glass tubes
72   with a moistened cotton plug and were stored before recording procedure at 4 °C for one day.

73   **Morphological measurements**

74   An image of a longitudinal section of the imago was generated using an X-ray
75   microtomography device XWT 160-TC (X-RAY WorX; Garbsen; Germany) at Tomsk
76   Polytechnic University (Fig. 1a). The images of the elytron-tergite stridulatory apparatus of males
77   were prepared using a Tabletop Hitachi (Tokyo, Japan) 3000 TM scanning electron microscope
78   (Fig. 2 b, c) at Tomsk State University (Kerchev, 2018). Morphological characteristics were
79   measured using Levenhuk ToupView software (release date – 10/15/2015; Levenhuk LabZZ,
80   Tampa, United States).

81

82   **Fig 1.**

83   **Design**

84   Male-male interactions were recorded inside the arena (diameter of 1 cm), a tube with a
85   microphone installed inside (Kerchev, 2018).

86   Audio recording was performed using a Behringer condenser microphone (Willich-
87   Muenchheide II, Germany) (model: ECM 8000; 15–20 000 Hz), and a Zoom R16 digital recorder
88   (Tokyo, Japan); frequency range: 20 Hz – 44.1 kHz; sampling rate: 24-bit). The recorded signals
89   were saved in the VAW format. Recording was carried out in the Krasnogorsk forestry
90   (Krasnogorsk, Sakhalin region) in a 3 L semi-anechoic chamber covered with an echo-absorbing
91   coating (2 cm wave). The recorded signals were analyzed in the Laboratory of Monitoring of Forest
92   Ecosystems, IMCES SB RAS (Tomsk).

93   **Terminology and measurements**

94   For each record, the indicators analyzed were: syllable duration, number of chirps per
95   syllable, chirp rate, chirp duration, interchirp interval, number of tooth-strikes per chirp, and
96   intertooth-strikes interval according to the terminology proposed in previous studies (Ryker and
97   Rudinsky 1976; Pureswaran et al. 2016; Kerchev, 2018). Individual chirps were identified with

98   the band-limited energy detector using Raven Pro 1.5 (Cornell Lab of Ornithology; Ithaca, New

99   York) (Charif et al., 2010). A syllable and the minimum interval between adjacent syllables were

100 empirically found on the sonogram for each recording as a distance between the chirp series

101 exceeding the average interval between the minimal groups of chirps (three intervals were taken

102 for analysis).

103 **Statistical analysis**

104 The listed parameters in each record were measured at 5 points calculated with the

105 RANDBETWEEN function in Microsoft Excel. The mean values taken for each recording were

106 analyzed, and the consistency check of the parameter variations was determined using the Kendall

107 coefficient of concordance (*W*). Signal parameters were compared using the Kruskal-Wallis test;

108 for statistically significant differences, multiple comparisons were performed using a Bonferroni–

109 Dunn post hoc test. All of the statistical analyses were conducted using Statistica 8.0 (StatSoft Inc.;

110 Tulsa, United States).

111

112 # Results

113 For *P. proximus* and *P. subopacus* males selected for recording, the accuracy of sexual

114 separation was 100%. Verification of sexual identification of *P. nigrielytris* carried out after

115 recording of signals and fixation in alcohol was 75% due to less pronounced sexual dimorphism,

116 in contrast to the other two tested species.

117 We obtained sound recordings of the rivalry song of the males of the three tested species.

118 No other type of chirps was recorded. We did not try to record any kind of the female song due to

119 absence of stridulatory apparatus on elytrons as it was noted early (Kerchev, 2018) and checked

120 for *P. nigrielytris* on collection materials of 2015 year.

121 It has been established that *P. nigrielytris* males possess the largest areas of pars stridens. The

122 greatest number of pars stridens is found in the same species (Table 1).

123 **Table 1**

124 The highest density of ridges in pars stridens was noted for *P. subopacus* (Table 1). Simple type

125 of signals was identified in all tested male species. No significant difference was found in the

126 syllable duration and the number of chirps/syllable between species *H* =5.08 (df=2; N= 81; p

127 =0.08).

128 **Table 2**

129   Highly significant differences were identified between the signals of the tested species in the chirp

130   duration parameter H=46.8 (df=2; N= 169; p=0.0000), whereas no significant differences were

131   found between *P. proximus* and *P. nigrielytris* only (Table 1). The value of interchirp intervals in

132   the series is found to be highly differentiated between species H=66.4 (df=2; N=167; p=0.0000),

133   while no significant differences were observed in the pair *P. nigrielytris* and *P. subopacus*. The

134   difference in interval duration can be seen on the sonogram (Fig. 2). The parameter of the number

135   of tooth strikes/chirp H=49.4 (df=2; N=131; p=0.0000) showed high species specificity. In the

136   pairwise comparison of this signal parameter, statistically significant differences were found for

137   all the pairs of species compared (Table 1). The interval duration between tooth strikes did not

138   show significant differences only in the pair of *P. nigrielytris* and *P. proximus*.

139   **Fig. 2.**

140

141   Energy is concentrated between 2000 and 22000 Hz, within the human hearing range, and average

142   dominant frequency is 7–14 kHz (Fig. 2).

143   ## Discussion

144

145   Insects were collected at the beginning of spring dispersion of the four-eyed fir bark beetle.

146   Similar to the secondary range (Kerchev, 2014), this species is one of the earliest among the bark

147   beetles on Sakhalin (Krivolutskaya, 1958). Only young adult beetles were found under the bark of

148   a downed tree inhabited the previous year. Prepupae, pupae, and young beetles with light chitin

149   were mainly observed in the galleries excavated by *P. subopacus* and *P. nigrielytris* in shaded

150   areas of the trunks of infected trees. Mature adult beetles were collected for recording in insolated

151   areas only. Thus, in addition to host-specificity, phenological and phenotypic (Fig. 2) isolation can

152   be considered as one of the factors of interspecific isolation of the test species.

153   Behavioral differences between species can be identified through differences in mating

154   systems. *P. subopacus* is the only harem-poligynous among the three species compared. Sex ratio

155   in its families is about 2–5 females per male (Stark, 1952). The families of the other two species

156   are monoginous. Sexual behavior of the Ussuri polygraph was previously discussed (Kerchev,

157   2014), whereas data on the characteristics of sexual behavior of *P. nigrielytris* are given for the

158   first time. During insect collection, only a pair of parent beetles was always found in nests

159   inhabited by beetles in spite of the fact that the number of egg galleries was 1–4.

160 The morphological characteristics of the stridulatory apparatus of the *P. proximus* were
161 indicated earlier (Sasakawa & Yoshiyasu, 1983), after which they were specified and
162 supplemented (Kerchev 2015). The presence of the stridulatory apparatus in *P. subopacus* was
163 indicated for the first time more than a hundred years ago, but the morphology description was not
164 provided (Witchman 1912; Lial and King, 1996). For *P. nigrielytris*, this study indicates the
165 presence of stridulation and the peculiarities of the structures involved in the sound production for
166 the first time. In general, the species of the genus *Polygraphus Er.* are similar in the morphology
167 of the stridulatory apparatus, but different in morphometric features. Intraspecific comparison
168 shows variations in the area and the number of ridges in pars stridens (Kerchev, 2015), and the
169 density of ridges per unit length of the area can be noted as a more stable feature.

170 Like many other insects, bark beetles are physically limited in the production of sounds
171 due to their small size (Bennet-Clark, 1998). The species studied exhibit noticeable differences in
172 the relative amplitude of signals, which is most likely due to the insect size (Fig. 2). Among cicadas
173 and crickets, the smallest species produce signals with highest frequency compared to those by
174 larger species. A similar dependence was noted earlier for bark beetles of the genus *Dendroctonus*
175 Er. (Bennet-Clark 1998; Pureswaran et al., 2016).

176 The study revealed significant differences between stridulatory signals of the studied
177 species in five of the seven temporal parameters. No differences were found in any of the two
178 parameters associated with the syllables forming a chirp.

179 Signal parameters showed the highest specificity, starting with the level of chirp, which is
180 primarily due to the physiological characteristics of the species and the morphology of the
181 microstructures of their stridulatory apparatus (Yturralde and Hofstetter. 2015; Kerchev, 2018).

182 It was experimentally found that a rather short fragment of the signal consisting of 14 pulses
183 repeated at least once a minute is sufficient for females of the bush-cricket *Metrioptera roeselii*
184 Hagen. to recognize an intraspecific attractive signal (Zhantiev and Korsunovskaya, 2014). In the
185 case of competitive interaction between *P. proximus* males, the contact lasts more than a minute
186 only during the fight for a female boring into the bark. In other cases, the male stays at the entrance
187 to the gallery occupied by a formed family for not more than several seconds (Kerchev, 2018).
188 Consequently, the territorial signal must have the characteristics that would allow it to be
189 recognized in a short period of time, and the chirp as a signal unit has all the necessary
190 characteristics. Under experimental conditions, high duration of this signal is due to the arena used.

191   As already mentioned, interspecific isolation is supported by a number of different
192   ethological and communication features. Species-specificity of stridulatory signals may be an
193   additional parameter that performs the same role for individuals that have started to populate a tree
194   beyond the main dispersal flight period. In interaction of males of different species, the signal
195   receiver may not regard it as a repellent. A clear repellent reaction during conspecific interaction
196   can indicate a crucial role of these signals in reduction of intraspecific competition.

197   To date, a number of research papers (Mankin et al., 2008; Potamitis et al., 2008; Schofield
198   & Chesmore 2010) are devoted to the use of species-specific insect signals for species
199   identification. The possibility of identification of alien species and monitoring of their populations
200   based on detection of their species-specific signals is of particular interest in this regard. Among
201   the parameters tested, the most relevant parameters are syllable duration, the interval between
202   syllables, the number of syllables per unit of time, and the relative amplitude of signals.

203

Conclusions

205   The study showed that temporal parameters of the intraspecific signals of the test species
206   exhibit significant differences in a number of characteristics, not only between sympatric species,
207   but also with the species that has a clear distinction in the host plant.

208   The species-specificity of stridulatory signals may be an additional parameter for
209   interspecific reproductive isolation of species that occasionally occur on the same tree species.
210   Reception and reaction to this type of signals may be present both at the interspecific level of
211   interactions and during intraspecific contacts only. To verify the possibility of interspecific
212   communication at the level of one genus, it is necessary to conduct playback experiments with
213   recording of responses to alternating con- and interspecific signals. Biologically, signals produced
214   by males of one species most likely reduce intraspecific competition at high population density

215   Of particular interest is the possibility of using species-specific characteristics of acoustic
216   signals of bark beetles for identification and detection of alien species. Among the tested
217   parameters of stridulation signals, the following specific characteristics can be distinguished for
218   the genus *Polygraphus*: chirp duration, interchirp interval, number of tooth-strikes per chirp, and
219   intertooth-strike interval. When bark beetles were tested in pairs, they exhibited high
220   reproducibility of stridulation. This method can be used as a universal one to compile libraries of

221 species-specific signals in order to further develop methods for detection and species identification

222 of stem pests.

223

Acknowledgements

228

229

References

231 Barr B.A. 1969. Sound Production in Scolytidae (Coleoptera) with Emphasis on the Genus

232 *Ips*. Canad. Entomol. 101: 636–672.

233 Bennet-Clark HC. 1998. Size and scale effects as constraints in insect sound

234 communication. Philosophical Transactions of the Royal Society of London Series B-Biological

235 Sciences 353(1367): 407–419.

236 Boulard, M. 2005. Acoustic signals, diversity and behaviour of cicadas (Cicadidae,

237 Hemiptera). Insect Sounds and Communication: Physiology, Behaviour, Ecology, and Evolution

238 (ed. by S. Drosopoulos and M.F. Claridge), pp. 331–350. CRC Press, Boca Raton, Florida.

239 Heller, K.G. 2005. Song evolution and speciation in bushcrickets. Insect Sounds and

240 Communication: Physiology, Behaviour, Ecology, and Evolution (ed. by S. Drosopoulos and M.F.

241 Claridge), pp. 137–152. CRC Press, Boca Raton, Florida.

242 Breidbach O. 1986. Studies on the stridulation of *Hylotrupes bajulus* (L.) (Cerambycidae,

243 Coleoptera): communication through support vibrationmorphology and mechanics of the signal.

244 Behav. Processes. 12:169–86.

245 Charif R.A., Waack A.M., and Strickman L.M. 2010. Raven Pro 1.4 User's Manual.

246 Revision 11. pp. 283–287. Cornell Laboratory of Ornithology, Ithaca, NY.

247 Cocroft, R. B., & Rodriguez, R.L. 2005. The behavioral ecology of insect vibrational

248 communication. BioScience, 55, 323–334.

249 Dobai A., Sivalinghem S., Guedes R.N. C., Yack J. 2017. Acoustic communication in the

250 pine engraver bark beetle: do signals vary between behavioral contexts? Physiological

251 Entomology. https://doi.10.1111/phen.12222

252   Dumortier B. 1963. Morphology of sound emission apparatus in Arthropoda. Acoustic
253   Behaviour of Animals (ed. by R.G. Busnel), pp. 277–345. Elsevier Publishing Company, New
254   York, New York.

255   Fleming A.J., Lindeman A.A., Carroll A.L., and Yack J.E. 2013. Acoustics of the Mountain
256   Pine Beetle (*Dendroctonus ponderosae*) (Curculionidae, Scolytinae): Sonic, Ultrasonic, and
257   Vibration Characteristics. Canad. J. Zool. Vol. 91, 4: 235–244.

258   Gerhardt H.C. and Huber F. 2002. Acoustic Communication in Insects and Anurans:
259   Common Problems and Diverse Solutions. University of Chicago Press, Chicago, Illinois.

260   Greenfield M.D. 2002. Signalers and receivers: Mechanisms and evolution of arthropod
261   communication. New York, NY: Oxford University Press.

262   Greenfield M.D. 2016. Evolution of acoustic communication in insects. Insect Hearing (ed.
263   by G.S. Pollack, A.C. Mason, A.N. Popper and R.R Fay), pp. 17–47. Springer International
264   Publishing, Switzerland.

265   Henry C.S. 2005. Acoustic communication in neuropterid insects. Insect Sounds and
266   Communication: Physiology, Behaviour, Ecology, and Evolution (ed. by S. Drosopoulos and M.F.
267   Claridge), pp. 153–167. CRC Press, Boca Raton, Florida.

268   Hoikkala A. 2005. Inheritance of male sound characteristics in Drosophila species. Insect
269   Sounds and Communication: Physiology, Behaviour, Ecology, and Evolution (ed. by S.
270   Drosopoulos and M.F. Claridge), pp. 167–178. CRC Press, Boca Raton, Florida.

271   Potamitis I., Ganchev T., and Fakotakis N. 2008. Automatic Bioacoustic Detection of
272   Rhynchophorus Ferrungineus. In 16th European Signal Processing Conference (EU-SIPCO 2008),
273   Lausanne, Switzerland, August 25–29,

274   Kerchev I.A. 2014. On monogyny of the four-eyed fir bark beetle *Polygraphus proximus*
275   Blandf. (Coleoptera, Curculionidae: Scolytinae) and its reproductive behavior. Entomol. Rev. Vol.
276   94. 8:1059–1066.

277   Kerchev I.A. 2015. Description of the stridulatory apparatus of the Far Eastern bark beetles
278   *Polygraphus proximus* Blandford, 1894 and *P. jezoensis* Niisima, 1909 (Coleoptera,
279   Curculionidae: Scolytinae). Entomol. Rev. Vol. 95. 9:1191–1196.

280   Kerchev I. A. 2018. Context-dependent acoustic signals in the four-eyed fir bark beetle,
281   *Polygraphus proximus* (Coleoptera: Curculionidae: Scolytinae), Environmental Entomology,
282   nvy178, https://doi.org/10.1093/ee/nvy178

283   Kojima W., Ishikawa Y., Takanashi T. 2012. Deceptive vibratory communication: pupae
284   of a beetle exploit the freeze response of larvae to protect themselves. Biol Lett. 8:717–720.

285   Krivolutskaya, G.O. 1958. The Bark Beetles of Sakhalin Island (USSR Acad. Sci., Moscow
286   P. 196 [in Russian].

287   Krivolutskaya, G.O. 1996. 113. Cem. Scolytidae. In: Key to the Insects of the Russian Far
288   East. Vol. 3, Coleoptera, Part 3. Dal'nauka, Vladivostok, pp. 312–373.

289   Lewis, E.E., and J.H. Cane. 1990. Stridulation as a primary antipredator defense of a beetle.
290   Anim. Behav. 40:1003–1004.

291   Lyal C.H.C. and King T. 1996. Elytro-Tergal Stridulation in Weevils (Insecta: Coleoptera:
292   Curculionoidea). J. Natur. Hist. 30:703–773.

293   Mazzoni V., Nieri R., Anfora G., Eeriksson A.E., Polajnar J., Virant-Doblert M., Lucchi
294   A. 2018. Vibrational signals as semiophysicals: a comparison between pheromonal and vibrational
295   mating disruption // Abstract Book Centro Congressi Riva del Garda, Trento, Italy September 4–
296   6. pp. 42

297   McVean A, Field L.H. 1996. Communication by substratum vibration in the New Zealand
298   tree weta, *Hemideina femorata* (Stenopelmatidae: Orthoptera). J Zool. 239:101–22.

299   Michelsen A, Fink F, Gogala M, Traue D. 1982. Plants as transmission channels for insect
300   vibrational songs. Behav Ecol Sociobiol. 11:269–81.

301   Nobuchi, A., 1979. Studies on Scolytidae, XVIII. Bark beetles of tribe Polygraphini in
302   Japan (Coleoptera, Scolytidae). Bull. Forestry and Forest Prod. Res. Inst. 308:1–16.

303   Pureswaran D.S. Pureswaran, R.W. Hofstetter, B.T. Sullivan, and K.A. Potter. 2016. The
304   role of multimodal signals in species recognition between tree-killing bark beetles in a narrow
305   sympatric zone Environ. Entomol. 1–10. doi:10.1093/ee/nvw022

306   Mankin R.W., Smith M.T., Tropp J.M., Atkinson E.B., and Jong D.Y. 2008. Detection of
307   *Anoplophora glabripennis* (Coleoptera: Cerambycidae) Larvae in Di.erent Host Trees and Tissues
308   by Automated Analyses of Sound-Impulse Frequency and Temporal Patterns. Journal of Economic
309   Entomology, 101(3):838–849,

310   Ryker L.C, J.A. Rudinsky. 1976. Sound production in Scolydae: Aggressive and maiting
311   behavior of mountain pine beetle. Ann. Entomol. Soc. Am. Vol. 69. 4: 677–680.

312   Sasakawa M., Yoshiyasu Y. 1983. Stridulatory Organs of Japanese Pine Bark Beetles
313   Coleoptera: Scolytidae). Kontyǔ. Vol. 51. 4: 493–501.

314   Schofield, J. & Chesmore D. (2010) Acoustic detection and monitoring of wood boring
315   beetles. Entomology 2010, Swansea, 26–28 July 2010.

316   Stark V.N. 1952. Bark Beetles, in: Fauna of the USSR. Coleoptera. Vol. 31 (USSR Acad.
317   Sci., [in Russian].

318   Stewart, K.W. & Sandberg, J.B. 2005. Vibratory communication and mate searching
319   behaviour in stoneflies. Insect Sounds and Communication: Physiology, Behaviour, Ecology, and
320   Evolution (ed. by S. Drosopoulos and M.F. Claridge), pp. 179–186. CRC Press, Boca Raton,
321   Florida.

322   Sueur J. 2005. Insect species and their songs. Insect Sounds and Communication:
323   Physiology, Behaviour, Ecology, and Evolution (ed. by S. Drosopoulos and M.F. Claridge), pp.
324   207–219. CRC Press, Boca Raton, Florida.

325   Wessel, A. 2006. Stridulation in the Coleoptera – an overview. In Insect sounds and
326   communication. Edited by S. Drosopoulos and M.F. Claridge. CRC Press, Boca Raton, Fla. pp.
327   397–430.

328   Wichmann H. E. 1912. Beitrag zur Kenntnis des stridulationsapparates der Borkenkäfer,
329   Entomologische Blätter, 8:8–10.

330   Wood, S.L., Bright, D.E. 1992. A catalog of Scolytidae and Platypodidae (Coleoptera),
331   Part 2: Taxonomic Index. Great Basin Nat. Mem. 13, 1–1553.

332   Yturralde, K.M., R.W. Hofstetter. 2015. Characterization of stridulatory structures and
333   sounds of the larger Mexican pine beetle, *Dendroctonus approximatus* (Coleoptera:
334   Curculionidae: Scolytinae). Fla. Entomol. Entomologist 98: 516–527.

335   Zhantiev R. D., Korsunovskaya O. S. 2014. On recognition of sound communication
336   signals in bush crickets (Orthoptera, Tettigoniidae) // Entomological Review 94: 815–819.

Figure 1

Images of *Polygraphus proximus*, *P. nigrielytris* and *P. subopacus* and sonograms of rivalry signals they produce.
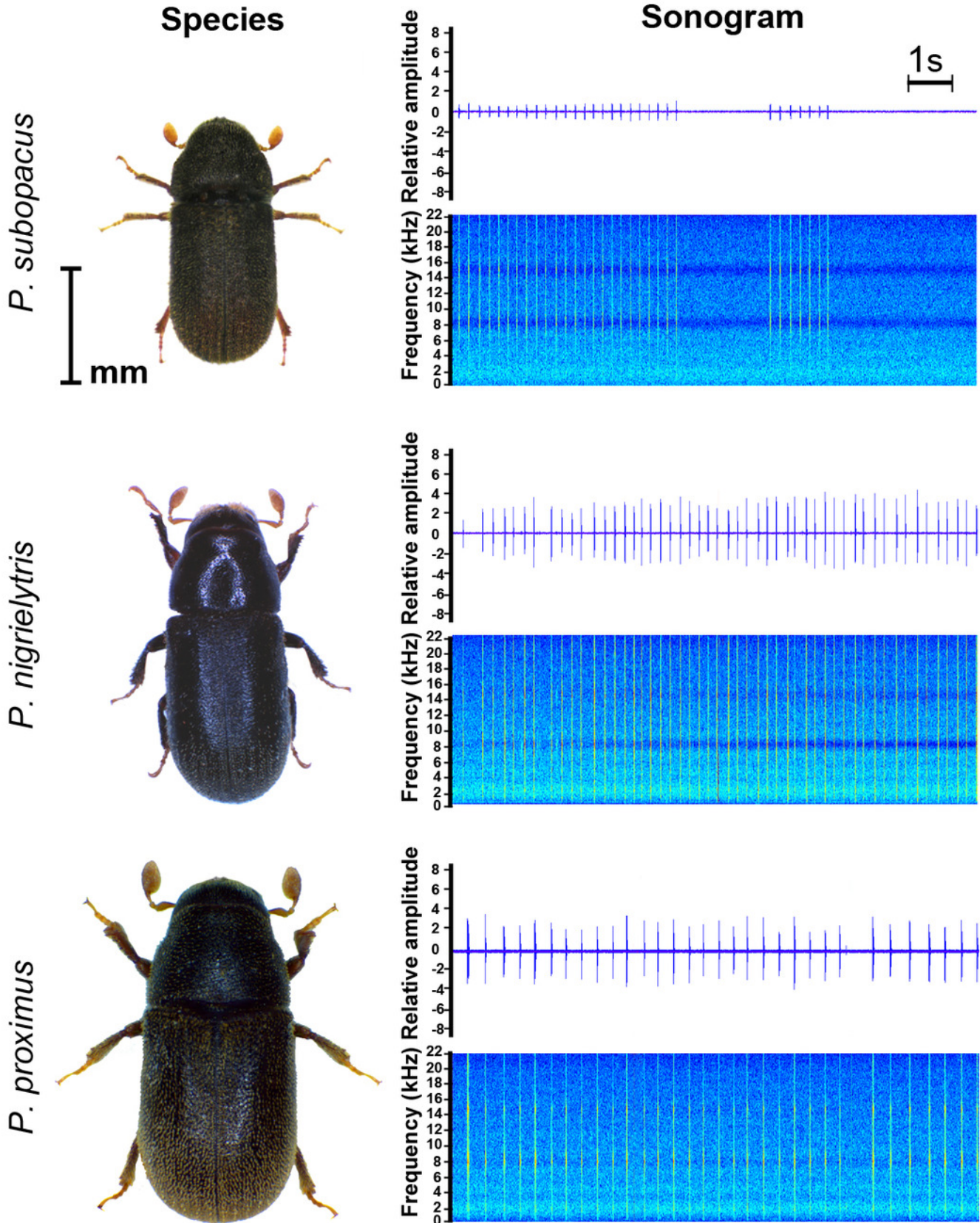
Species

Sonogram

P. subopacus

P. nigrielytris

P. proximus

Figure 2

General view of elytro-tergal stridulatory apparatus morphology.

a – longitudinal section of the imago prepared using an X-ray microtomography device; image of the elytron-tergite stridulatory apparatus of males; **b** – detailed structure of the plectrum; **c** – pars stridens structure
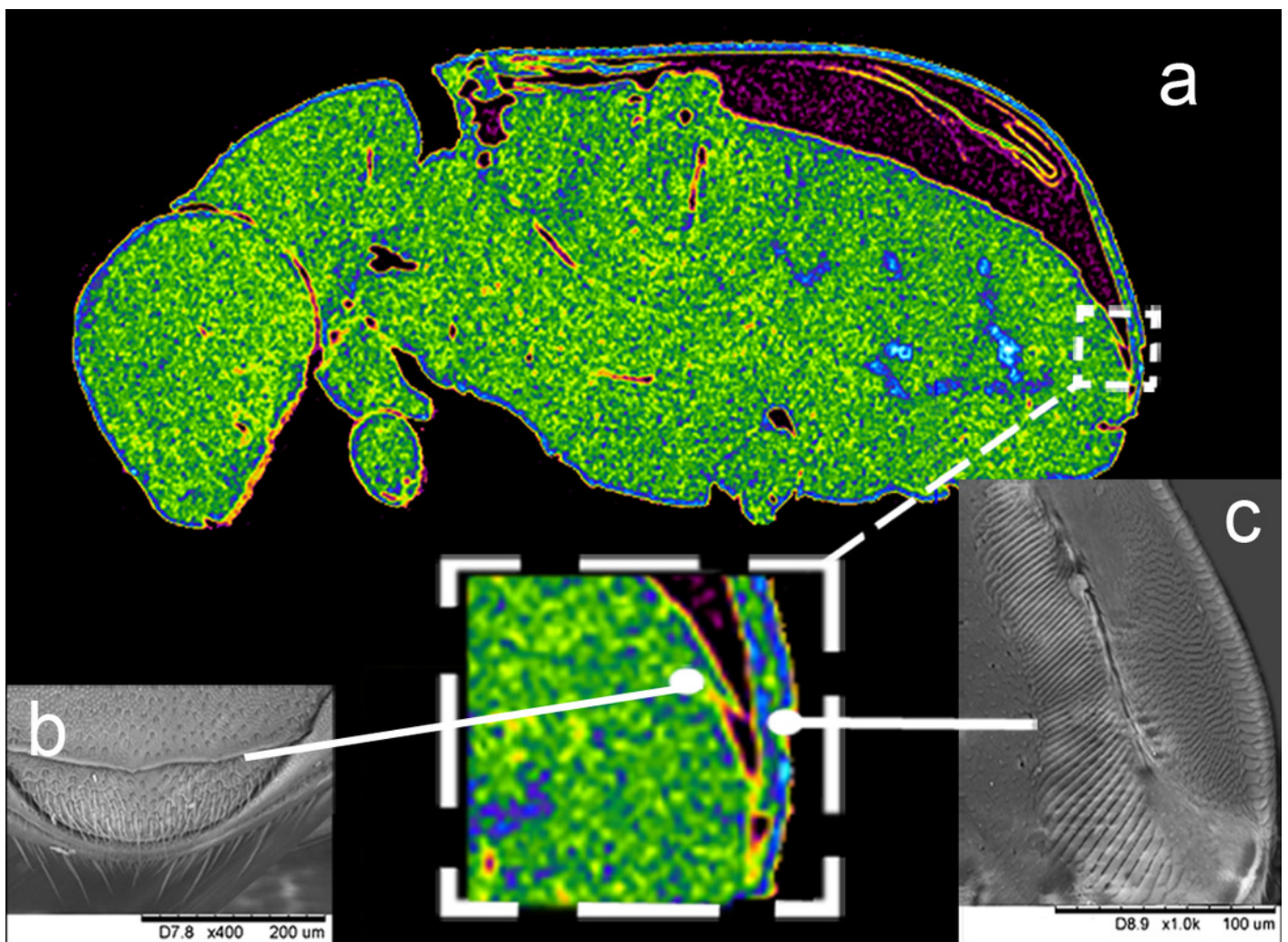
Table 1(on next page)

Table 1. Comparison of the morphological characteristics of the stridulator apparatus and average values of the parameters of competitive signals in males of *Polygraphus proximus*, *P. nigrielytris* and *P. subopacus (Mean ± SD).*

1   Table 1. Comparison of the morphological characteristics of the stridulator apparatus and
2   average values of the parameters of competitive signals in males of *Polygraphus proximus*, *P.*
3   *nigrielytris* and *P. subopacus (Mean ± SD)*.
4

Parameter	*P. proximus*	*P. nigrielytris*	*P. subopacus*
Stridulating sex	male	male	male
Length of pars stridens left/right (μm)	156/193	198/ 213	148/ 152
Number of rows in file	55/53	71/76	65/66
Syllable duration (s)	4.2±3.7	4.3±2.7	7.3±6.2
Number of chirps /syllable	14.8±18.1	19.1±13.3	26.3±21.4
Chirps rate (chirps/s)	5.1±0.9	4.4±0.9	3.9±0.9
Chirps duration (s)	0.025±0.008	0.020±0.007	0.042±0.001
Interchirp interval (s)	0.17±0.4	0.23±0.04	0.26±0.05
Number of tooth-strikes	13.4±4.0	10.5±3.2	7.5±2.2
Intertooth-strikes interval (s)	0.002±0.0006	0.001±0.0005	0.004±0.001

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Table 2(on next page)

Results of pairwise comparison of parameters of competitive signals in males of Polygraphus proximus, P. nigrielytris and P. subopacus.

Z-values in cells, *p<0.05; **p<0.001 with Bonferroni correction

1   Table 2 Results of pairwise comparison of parameters of competitive signals in males of
2   *Polygraphus proximus*, *P. nigrielytris* and *P. subopacus*.
3

Parameter	Species	*P. subopacus*	*P. nigrielytris*
Syllable duration (s)	*P. proximus*	2.3	0.9
	P. subopacus		1.3
Chirps /syllable	*P. proximus*	2.7	2.2
	P. subopacus		0.5
Chirp rate (s)	*P. proximus*	4.4**	2.5
	P. subopacus		1.8
Chirp duration (s)	*P. proximus*	6.01**	2.2
	P. subopacus		6.0**
Interchirp interval	*P. proximus*	7.4**	5.0**
	P. subopacus		1.9
Tooth strikes /chirp	*P. proximus*	7.0**	3.2*
	P. subopacus		3.3*
Intertooth strike interval (s)	*P. proximus*	6.0**	2.7
	P. subopacus		7.1**

4   Z-values in cells, *p<0.05; **p<0.001 with Bonferroni correction

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