

**Acoustic communication in the subtroglophile planthopper
Trigonocranus emmeae Fieber, 1876
(Hemiptera: Fulgoromorpha: Cixiidae: Oecleini)**

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HOCH H., MÜHLETHALER R. & WESSEL A. 2013: Acoustic communication in the subtroglophile planthopper *Trigonocranus emmeae* Fieber, 1876 (Hemiptera: Fulgoromorpha: Cixiidae: Oecleini). In: KMENT P., MALENOVSKÝ I. & KOLIBÁČ J. (eds.): Studies in Hemiptera in honour of Pavel Lauterer and Jaroslav L. Stehlík. *Acta Musei Moraviae, Scientiae biologicae* (Brno) **98(2): 155–162**. – A recently discovered, and apparently autochthonous, population of *Trigonocranus emmeae* Fieber, 1876 in Germany (Rhineland-Palatinate: Bernkastel) confirmed the large degree of intraspecific variation with regard to the size of the compound eyes, length of tegmina and bodily pigmentation reported in the literature. For the first time, intraspecific communication signals for the species could be recorded. *T. emmeae* is identified to be at least subtroglophile, and its potential as a suitable model to study the evolution of cave adaptation in a natural system is discussed.

Keywords. Auchenorrhyncha, phenotypic variation, behaviour, vibrational communication, troglomorphy, cave adaptation, climatic relict hypothesis, adaptive shift hypothesis, western Palearctic

Introduction

Trigonocranus emmeae was originally described by FIEBER (1876) from Switzerland. It is widely distributed in the southern half of continental Europe and Great Britain (for detailed information on its geographic distribution see HOLZINGER *et al.* 2003, NICKEL 2003, SELJAK 2004, MALENOVSKY & LAUTERER 2010, and MUSIK *et al.* 2013). Despite its comparatively large geographic range, *Trigonocranus emmeae* is regarded as a locally rare species; usually only a few specimens are collected, mostly from pitfall traps. Consequently, information on its ecology is sparse, but the species is assumed to “live in the top soil and leaf litter in at least moderately warm sites with incomplete vegetation cover, feeding on roots of shrubs” (NICKEL 2003: 27). In Germany, hitherto only three autochthonous populations (from Warburg, Hildesheim and Herne: NICKEL 2003) have been reported, “all from sun-exposed embankments or hillsides with scattered shrubs on damp to moderately dry soils” (NICKEL 2003: 27).

Adults have been reported to display a conspicuous polymorphism concerning the size of the compound eyes, length of tegmina and bodily pigmentation (NICKEL 2003, HOLZINGER *et al.* 2003). A recent discovery of an apparently autochthonous *Trigonocranus emmeae* population in southern Germany (Rhineland-Palatinate: Mosel valley, Bernkastel) allowed us to document nymphal and varying adult phenotypes and – for the first time – a recording of their intraspecific communication signals.

Material and methods

Material examined. 6 males (all brachypterous), 18 females (16 macropterous, 2 brachypterous), 5 nymphs (1 IV. instar; 4 V. instar), Germany, Rhineland-Palatinate, Bernkastel/Mosel, from roots of *Convolvulus arvensis* L. (Convolvulaceae), M. Maixner leg., in coll. Museum für Naturkunde, Berlin. Subsequent to behavioural experiments, specimens were preserved dry on card mounts or in vials containing 96% ethanol.

Scanning electron microscopy. For scanning electron microscopy, specimens were dehydrated with ascending ethanol series and transferred into absolute ethanol, then dried at the critical point (BAL-TEC CPD 030, BAL-TEC AG, Balzers, FL) and sputter-coated (gold/palladium, Polaron Shutter Coater SC7640); micrographs were taken with a Zeiss EVO LS10 (Carl Zeiss, Jena, DE; tungsten cathode, manufacturer's software) at the Museum für Naturkunde, Berlin. Figures were edited with Adobe® Photoshop® CS4 and Adobe® Illustrator® CS4 (Adobe Systems Incorporated, San Jose, USA).

Recording and analysis of vibrational signals. Experiments were carried out at the Museum für Naturkunde, Berlin, between June 12th–14th, 2012 (Fig. 3). Fresh roots of the host plant, *Convolvulus arvensis*, were placed on moist filter paper lining the floor of a 10 x 7 x 4 cm translucent plastic box with a lid. The roots were partially covered by a black plastic tube in order to imitate natural soil cavities. A small piece of reflecting foil (ca. 2 x 2 mm) was placed on the root part outside the black plastic tube. Vibrational signals emitted by *Trigonocranus* specimens were detected with a portable digital laser vibrometer PDV-100 (Polytec GmbH, Waldbronn, Germany) and registered directly with a Roland Edirol R-4 Pro recorder at a sampling rate of 16 bits and 44.1 kHz. Recordings were made at room temperature (22–33°C). Signal analysis was carried out using Raven Pro 1.4 (Bioacoustics Research Program, 2011). The sound files obtained are deposited at the Animal Sound Archive (TSA: Tierstimmenarchiv), Museum für Naturkunde, Berlin, Germany; accession number TSA *Trigonocranus emmeae*_DIG0168_02.

Results

Presumed host. Nymphs and adults of *Trigonocranus emmeae* were found in the top soil layer of a temporarily uncultivated patch in a private garden, apparently feeding on roots (and stems close to the soil) of *Convolvulus arvensis* (M. Maixner, personal communication), and were collected on June 10, 2012. By this time, females had apparently already mated and were ready to oviposit as their abdomina were swollen with eggs.

Phenotypic variation (Figs 1–2). Adults of *Trigonocranus emmeae* display remarkable intraspecific variation in regard to the overall size of the compound eyes, the number of ommatidia, length of tegmina, and bodily pigmentation. The observed variation is accentuated by sexual dimorphism, as “reductive” characters appear to be more strongly expressed in males. In the sample studied – which did not contain macropterous males – the number of ommatidia varied between 87 (in a brachypterous male) and 194 (in a macropterous female).



Fig. 1. Habitus of *Trigonocranus emmeae*: a – brachypterous male; b – macropterous female; c – fifth instar nymph (photographs by J. Deckert, Berlin).

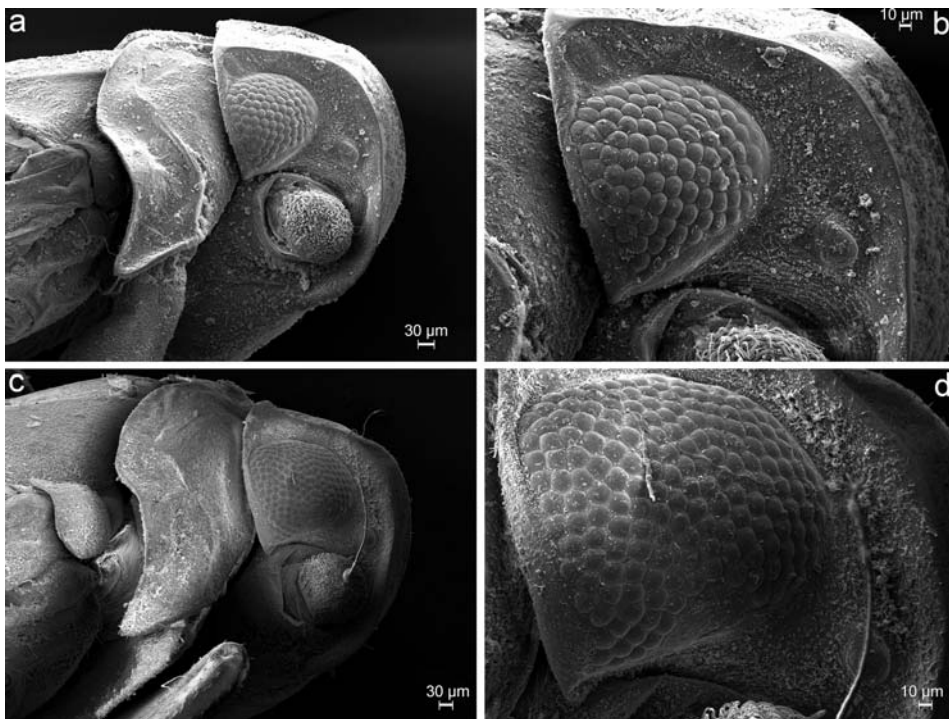


Fig. 2. Variation in the size of the compound eyes in *Trigonocranus emmeae* (SEM): a – brachypterous male; b – same, at higher magnification; c – macropterous female; d – same, at higher magnification.

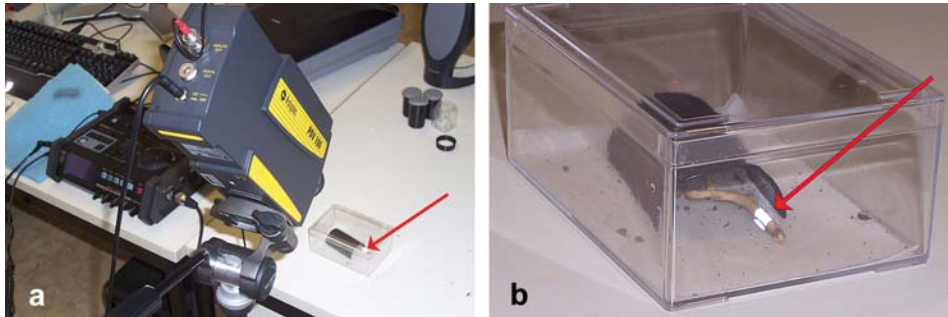


Fig. 3. Experimental set-up for recording of vibrational signals, Museum für Naturkunde: a – digital laser vibrometer and recording chamber; b – close-up of the recording chamber with root and dark zone. Arrows: reflecting foil (photographs by M. Kretzschmar, Berlin).

Phototaxis. Due to the small sample size this observation must be regarded as preliminary, however all brachypterous males tested displayed a distinct negative phototactic behaviour. Once placed inside the recording box, the brachypterous males immediately moved into the part covered by the black plastic vial (Fig. 3). On the contrary females, most of which were macropterous, were observed most frequently sitting on the underside of the translucent lid of the box, perhaps orientating towards the ceiling light.

Acoustic communication. For recording experiments, one to several males were placed together with up to three females into the recording box. Within a few minutes, males were observed to initiate calling. We obtained calls from three males; females did not emit any calls, and under no constellation was active courtship leading to copulation observed.

Male calls were emitted at varying intervals (less than one minute to several minutes). Single calls consisted of more or less homogenous pulse trains (Fig. 4). Total length of single calls varied from 9.88 to 27.5 s (mean: 16.7 s; SD: 5.36; n=10; N=3). The average centre frequency was 662 Hz (SD: 140; n=10; N=3). The number of pulses within a single call varies from 19 to 161 (mean: 98; SD: 32.44; n=10; N=3). The length of a single pulse is 92 ms and is very consistent (SD: 10 ms; n=20; N=3).

Discussion

The large range of phenotypic variation in *Trigonocranus emmeae* is exceptional among Cixiidae and raises a number of questions. Reduction of compound eyes, tegmina and bodily pigmentation is usually found in species adapted to subterranean environments. Although such troglomorphies are not *a priori* adaptive, they are indicative of a cryptic way of life, usually associated with habitats characterized by high humidity and reduced light, such as leaf litter, crevices inside the soil, or caves. It can

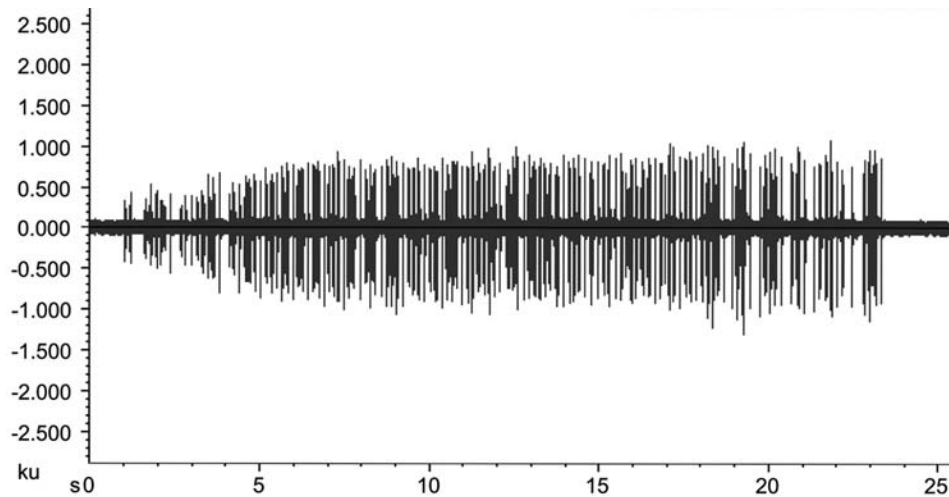


Fig. 4. Oscillogramm illustrating the time-amplitude pattern of a single male call of *Trigonocranus emmeae* (brachypterous male; in coll. Museum für Naturkunde, Tierstimmenarchiv, Berlin).

therefore be assumed that the range of morphological variation within the species is paralleled by variation of ecological parameters characterizing the species' habitat.

With nymphs living underground while adults either complete their life cycle in the top layer of the soil, or live and disperse in epigeal environments, *T. emmeae* is – according to the classification of subterranean animals proposed by SKET (2008: 1560) – a *subtroglophile* (= “species inclined to perpetually or temporarily inhabit a subterranean habitat but is intimately associated with epigeal habitats for some biological function (daily, e.g., feeding, seasonally, or during the life history, e.g., reproduction)”) or a *eutroglophile* (= “essentially epigeal species able to maintain a permanent subterranean population (which may become troglotic)”). Among the Fulgoromorpha, independent evolutionary lineages have colonized subterranean environments in many parts of the world (for a review see HOCH 2002, HOCH & WESSEL 2006, and references therein).

The question as to which factors drive an epigeal species to colonize underground environments has long intrigued evolutionary biologists. However, in order to study the process of cave adaptation in a natural system suitable model systems to test existing hypotheses need to be identified.

The evolution of obligate cave species (troglobites) has traditionally been explained by the so-called climatic relict hypothesis (CRH) (e.g., BARR 1968). Under this hypothesis severe climatic oscillations, such as glaciation, are assumed to cause epigeal populations to become extinct or extirpated, eventually resulting in the isolation of troglitic populations in underground environments which subsequently evolve into obligate cave dwellers characterized by reduction and even loss of eyes, bodily

pigmentation, and – in the case of insects – wings. This hypothesis was supported by the seeming absence of troglobites from the tropics (e.g., BARR 1968). The discovery of rich and diverse cave faunas on young oceanic islands comprising many terrestrial obligate cave-dwellers has, however, challenged this view. HOWARTH (1986) provided an alternative hypothesis on the evolution of terrestrial troglobites, which has since become known as the adaptive shift hypothesis (ASH).

While the CRH essentially postulates allopatric speciation between epigeal and cave-dwelling species, the ASH assumes parapatric speciation, consistent with the observed occurrence of closely related species in close geographic vicinity, e.g., on the same island. It is possible, though, that even many temperate-zone troglobites also evolved in parapatry through adaptive shifts, and that their current isolation occurred only after cave adaptation (HOWARTH & HOCH 2005, HOCH *in press*).

HOWARTH & HOCH (2005) identified a number of intrinsic and extrinsic factors underlying adaptive shifts into cave habitats. Among the intrinsic factors are preadaptation (exaptation, i.e., ability to survive in dark, damp microhabitats), genetic repertoire (i.e., variability, adaptability to changing environments), and mating behaviour (i.e., the ability to locate and recognize potential mating partners in absolute darkness). Among extrinsic factors favouring adaptive shifts are the presence of cavernicolous habitat and exploitable food resources. The newly discovered population of *Trigonocranus emmeae* in Bernkastel largely fulfils the postulated requirements: the nymphs and brachypterous adults live in dark, damp soil crevices, the observed phenotypic variability suggests underlying genetic variability, and vibrational signals are a well-known communication channel in (epigeal and) obligately cavernicolous Cixiidae (HOCH & HOWARTH 1993, HOCH & WESSEL 2006). Potentially suitable cavernicolous habitats are probably available, as in the Mosel valley, adjacent mountain slopes consist of loose slate (MEYER 1988), such that the existence of an extended superficial underground compartment or MSS (*milieu souterrain superficiel*, as described by JUBERTHIE *et al.* 1980) can be assumed.

Under an assumed scenario of disruptive selection (either through the availability of a novel habitat or food resources, or by ecological/climatic deterioration on the surface) *Trigonocranus emmeae* is a promising candidate for giving rise to obligately cavernicolous species, equally conceivable in either allopatry or sympatry.

The discovery of a permanent and accessible population of *Trigonocranus emmeae* is the first step towards establishing a new model system to study the process of cave-adaptation on the genetic, behavioural and evolutionary-developmental level in a natural system. Further research is needed to address questions of behavioural differentiation among brachypterous and macropterous individuals, symmetry of mating success among similar and different phenotypes, as well as the deciphering of the genetic and developmental mechanisms underlying phenotypic variation.

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Dedication

This contribution is dedicated to Pavel Lauterer on the occasion of his 80th birthday in recognition of his outstanding contribution to the taxonomy and zoogeography of the Hemiptera in Europe.

Zusammenfassung

Eine kürzlich entdeckte und offenbar autochthone Population von *Trigonocranus emmeae* Fieber, 1876 in Deutschland (Rheinland-Pfalz: Bernkastel) bestätigte die in der Literatur erwähnte breite Spanne intraspezifischer Variabilität hinsichtlich der Größe der Komplexaugen, der Flügellänge und der Körperpigmentierung. Erstmals konnten die intraspezifischen Kommunikationssignale dieser Art aufgezeichnet werden. *T. emmeae* wird als mindestens subtroglöphil eingeschätzt; die Eignung der Art als möglicher Modellorganismus zur Untersuchung des evolutiven Übergangs zum Höhlenleben in einem natürlichen System wird diskutiert.

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