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Comments on the Malaysian Katydid *Ancylecha fenestrata* (Fabricius, 1793) (Orthoptera: Tettigoniidae)

Bemerkungen zur Malayischen Laubschrecke *Ancylecha fenestrata* (Fabricius, 1793) (Orthoptera: Tettigoniidae)

Hartmut Greven, Sabrina Braatz & Dieter Schulten

Summary: *Ancylecha fenestrata* is a rather large phaneropterine tettigoniid from Malaysia with leaf-like tegmina that are characterized by two crescent-like markings. This species is often raised in captivity, but publications about its biology are rare. Searching the internet we found several plants accepted for oviposition, but not for feeding. These plants have relatively fleshy and leathery leaves and contain various substances (e. g. saponins, oxalic acid, specific glucosides etc.) often harmful at least to vertebrates. Only a few plants appear to be used for both, egg deposition and feeding. Whether this is a strategy pursued by *A. fenestrata* in the wild, is unkown. Females oserved by us inserted up to 13 large kidney-shaped eggs (per leaf) in the leaf parenchyma of the Spotted Dracaena *Dracaena surculosa* often used for breeding. The chorion of the egg is composed of a thin, delicate outer layer that apparently forms a close association with the walls of the parenchyma cells of the leaf, followed by a broader spongy layer, a relatively thick and solid layer with dilatations (air spaces) connected by fine pore canals that also open out in the large spaces of the spongy layer, and a very thin basal layer. At temperatures of 22 to 25 °C and relatively high humidities, nymphs hatch within 70 days on average. The first nymphal instars are strikingly multicoloured. In the resting position, in which the forelegs are extended forwards, the hind legs backwards, and the long antennae are hidden under the abdomen, they resemble spiders. Males and females of *A. fenestrata* produce sounds by tegminal stridulation. Stridulatory organs are sexually dimorphic. As typical for many tettigoniids, males possess a strongly sclerotized file with "teeth" (*pars stridens*) on the underside of the left tegmen base and on the upper surface a scraper (*plectrum*) near to the so-called mirror. Females lack a mirror possessing several small files with laterally cuspidate teeth on the upper surface of the right tegmen, whereas the underside of the left tegmen is not conspicuously modified. When disturbed, both sexes produce alarm or defence sounds.

Key words: *Ancylecha fenestrata*, stridulatory apparatus, reproduction, chorion structure, site of oviposition, aposematism

Zusammenfassung: *Ancylecha fenestrata* ist eine relativ große Tettigoniide (Phaneropterinae) aus Malaysia mit grünen, blattähnlichen Tegmina, auf denen sich je zwei bunte, halbmondförmige Muster finden. Die Art wird zwar mittlerweile häufig in menschlicher Obhut gehalten und gezüchtet, über ihre Biologie ist aber offenbar bisher nur wenig publiziert worden. Eine Internetrecherche ergab, dass *A. fenestrata* in Insektarien eine Reihe von Pflanzen zur Eiablage nutzt, diese aber nicht frisst. Diese Pflanzen haben relativ dicke und ledrige Blätter und enthalten verschiedene Substanzen (z. B. Saponine, spezifische Glucoside, Oxalsäuren etc.), von denen viele zumindest für Wirbeltiere nicht bekömmlich sind. Nur wenige Pflanzen scheinen gleichzeitig zur Eiablage und als Futter genutzt zu werden. Ob es sich dabei um eine Strategie handelt, die *A. fenestrata* im Freiland verfolgt, ist unbekannt. Die von uns beobachteten Weibchen legten pro Blatt bis zu 13 große, leicht nierenförmige Eier in Blätter der buntgefleckten Drachenlilie, *Dracaena surculosa*, die häufig zur Zucht von *A. fenestrata* benutzt wird. Das Chorion der Eier besteht außen aus einer dünnen, homogenen Lage, die offenbar eine enge Verbindung mit den Zellwänden des Blattparenchyms eingeht; ihr folgen eine breitere, schwammartige Lage, eine dicke, kompakte Schicht, deren Hohlräume (Lufträume) durch feine Kanäle miteinander verbunden, sich auch in die Hohlräume der schwammigen Schicht öffnen, sowie eine sehr dünne Basallage. Die Nymphen schlüpfen bei Temperaturen von 22-25 °C nach durchschnittlich 70 Tagen. Die ersten Nymphenstadien unterscheiden sich in Färbung und Ruheposition auffällig von späteren Stadien; sie sind durch gelbe Punkte auf dem Abdomen sowie einen größeren gelben bis grünen Fleck an der Seite gekennzeichnet. In Ruhestellung (die Vorderextremitäten sind nach vorn, die beiden Hinterextremitäten nach hinten gestreckt, die langen Fühler liegen unter dem Abdomen) erinnern sie ein wenig an Spinnen. Bei *A. fenestrata* stridulieren beide Geschlechter, doch ist der Stridulationsapparat geschlechtsdimorph. Männchen besitzen, wie typisch für viele Tettigoniidae, eine kräftige, stark sklerotisierte Pars stridens mit kräftigen Zähnen auf der Unterseite der linken Flügelbasis und auf der Oberseite des rechten Flügels das Plectrum sowie den sogenannten Spiegel. Weibchen besitzen keinen Spiegel auf der Oberseite der rechten Flügelbasis, sondern Reihen von Flügeladern mit seitlich zugespitzten Zähnchen, die offenbar als Schrillleisten fungieren, während die Unterseite des linken Flügels nicht auffällig modifiziert ist. Wenn die Tiere massiv gestört werden, produzieren sie Alarm- oder Verteidigungslaute.

Schlüsselwörter: *Ancylecha fenestrata*, Stridulationsapparat, Fortpflanzung, Chorion-Struktur, Eiablage, Aposematismus

1. Introduction

The Malaysian leaf katydid *Ancylecha fenestrata* was described as *Locusta fenestrata* by Johann Christian Fabricius (1745-1808) already in 1793 (s. Fabricius 1793). He wrote (in Latin as usual at that time and very condensed): fenestrata. *4. L. thorace laevi, elytris viridibus: macula ocellari baseos fenestrata, pedibus spinosissimus. Habit in India orientali … Magna. Antennae longissimae, fuscae. Caput nigro fuscoque varium. Thorax deflexus, laevis, viridis, postice rotundatus, niger. Elytra concava longitudine alarum, viridia lobo baseos ocello magno, fenestrato. In medio maculae duae e lunula fusca, atra, alba exterioreque flavescente. Margo posticus lineolis nigris, abbreviatis notatus, praeterea maculae tres ocellares ejusdem coloris at multo minores. Alae albae. Corpus virescens, dente dorsali, elevato, acuto. Pedes valde spinosi spinis quibusdam pedum anteriorum & posteriorum compressis, membranaceis, nigris.*" (*fenestrata*. 4. L. with smooth thorax, green elytra with eye-like fenestrated spot on <their> base, very spiny legs, lives in India orientalis (= used in reference to some or all of Southeast Asia; authors) … Large. Very long and brown antennae; head variably black and brown; thorax curved, smooth, green posteriorly rounded, black. Elytra concave as long as the wings, but more green with a large fenestrated eye on the cover of the base. In the midst <of elytra> two spots each consisting of a brown, black, white and more outside yellowish, small crescent. The posterior margin characterized by small, black and short lines; further three eye-like spots of the same colour, but much smaller. Wings white. Body greenish with a dorsally elevated acute cusp. Legs with many spines, with some flattened spines of the forelegs and hindlegs membrane-like and black) (Fabricius 1793; pp. 34-35).

This is a quite exact description of a male emphasizing the large "fenestrated ocellus" that represents the so-called mirror of the stridulatory apparatus of many tettigoniids (see below) and the two striking crescent-shaped markings of the tegmina. Later, Serville (1839) created the genus *Ancylecha* (from Greek ankýlos = curved; echein = to have) with a single female from Java stressing the numerous curved spines on the legs. He named his specimen *Ancylecha lunuligera*, i.e. the small crescent bearing *Ancylecha*, but did not forget to add to his careful description: „Je ne connais pas le mâle; serait-ce lui Fabricius a décrit sous le nom de *Locusta fenestrata*, Ent. Syst. Tom. 2, pag. 34, n° 4?" (Serville 1839, p. 413) (I do not know the male; it seems Fabricius has described it under the name *Locusta fenestrata*). In his monograph of the Phanopteridae summarizing the older literature Brunner von Wattenwyl (1878) used the name *Ancylecha fenestrata* (still valid to date) giving a good drawing of a male (Fig. 1). *A. lunuligera* is a synonym of *A. fenestrata*; the genus *Ancylecha* is monospecific to date.

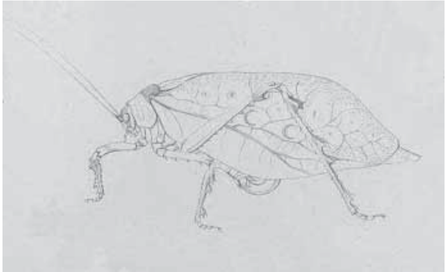


Fig. 1: Male of *Ancylecha fenestrata* (from Table III in Brunner von Wattenwyl 1878).
Abb. 1: Männchen von *Ancylecha fenstrata* (aus Tafel III in Brunner von Wattenwyl 1878).

Due to its size and colouring, *A. fenestrata* is an attractive katydid held and bred by many insect-keeping hobbyists. Thus, the internet is full of more or less serious information about this species (good data are presented in http://lemondedesphasmes.free.fr./spip.php?article137). Generally, however, data available from insectaries and from the field are insufficient. Our literature research concerning field studies was unsuccessful.

Summarizing the information available to us, the following picture emerges: *A. fenestrata* is a moderately sexually dimorphic (regarding size and colouring), leaf-mimicking, nocturnal katydid (or bush-cricket). During the day animals stay between leaves sitting or hanging more or less immobile on the twigs. Males and females are able to stridulate when disturbed; an oscillogram of several consecutive sounds with a relatively fast rise in amplitude, but not further specified, is published in the internet (http://lemondedesphasmes.free.fr./spip.php?article137). *A. fenestrata* feed on various plants and, like some other katydids (see Leroy 1969; Ingrisch & Köhler 1998; Gwynne 2001), females insert their eggs into leaves of plants that they often do not eat. The incubation lasts two to three months; the final moult takes place approximately five months later. Males seem to mature in five, females in six moults. The first three or four nymphal instars are noticeably coloured (http://lemondedesphasmes.free.fr./spip.php?article137). Recently it was shown that adults show a strong IR-reflection comparable to that of green leaves (see Mielewcik et al. 2012).

The Aquazoo/Löbbecke-Museum (Düsseldorf) breeds *A. fenestrata* since many years. Here, specimens feed on leaves of blackberry (*Rubus fruticosus* agg.), but females deposit their eggs into the leaves of *Dracaena surculosa*, a plant, they do not eat. We carried out the present study to learn something about (i) the spectrum of plants suitable for *A. fenestra* to lay eggs and to feed (internet search) and, based on specimens of the population of the Aquazoo, to learn something about (ii) the number of eggs deposited in *D. surculosa* leaves; (iii) the exact position of the eggs in the leaves; (iv) the structure of the egg chorion; and (v) the organization of the stridulatory apparatus of both sexes. Finally, we hypothesize that colourfulness and specific resting position of younger instars could be aposematic traits.

2. Material and methods

2.1. Keeping and breeding

For observations several specimens of *Ancylecha fenestrata* were kept in two insectaries (I: 60 x 33 x 95 cm; 10 cm soil substrate, twelve adults, eight older nymphs and one plant of *Dracaena surculosa* already containing eggs; II: 60 x 30 x 70 cm, 3 cm soil substrate, four adult males and two adult females; one plant of *D. surculosa* without eggs). All katydids were fed with fresh blackberry leaves. Temperature varied between 20 and 25 °C; during night it occasionally dropped slightly below 20 °C; relative air humidity was high.

Every three days the plant in insectary II was checked for newly deposited eggs and eggs were consecutively numbered to evaluate incubation time. In addition, we counted the distribution of eggs in 184 leaves of varying size of two *D. surculosa* plants from the insectary of the Aquazoo/Löbbecke-Museum. Leaf-sizes were derived by first approximation from the length and width of the leaves.

2.2. Sounds

When taken out of the insectary and held in the hand, males and females of *Ancylecha fenestrata* produce sounds that were tentatively recorded with a mobile phone (Samsung Wave GT-S8500). The phone was held about 10 cm in front of the animals (male and female). Sounds were shown as sonagrams using the program Raven Lite 1.0.

2.3. Histology (LM)

Pieces of *Dracaena surculosa*-leaves containing eggs were fixed in 2.5% glutaraldehyde in 0.1 mol/l cacodylate buffer for several hours, were postfixed in 2% osmium tetroxide and embedded in plastic (SPURR 1969). Semi-thin sections (approx. 1 µm thick) were stained with toluidinblue blue/borax.

2.4. Scanning electron microscopy (SEM)

For SEM, the stridulatory apparatuses were cut from dry or ethanol-preserved specimens and glued to metal stubs. Further, pieces of egg-containing leaves were fixed and postfixed as described, transferred in liquid nitrogen, split with a razor blade, critical-point dried, glued on metal stubs, sputtered with gold, and viewed in a SEM Leo 1430 (Fa. Zeiss).

2.5. Photographic documentation

The animals were photographed with a Canon EOS 5 D using a ring flash (Canon Macro Ring Lite MR-14EX) and macro-lenses (Canon MP-E 65mm 1:2.8; Sigma 70 mm 1:2.8). The stridulating apparatuses and leaves with eggs were photographed using a dissecting microscope (Olympus SZH); semi-thin sections were photographed using a microscope (Olympus, Vanox-T AH -2) with a digital camera (Olympus C-3030-Z).

3. Results

3.1. Plants for feeding and oviposition

Ancylecha fenestrata feeds on leaves of several plants (see Tab. 1) and even on blackberries, raspberries and apple slices. With the exception of privet (*Ligustrum vulgare*), none of these plants is used for oviposition, probably due to their relatively thin leaves. On the other hand, we found several plants used for oviposition only. These plants are characterized by relatively thick and leathery leaves and

Tab. 1: Food plants of *Ancylecha fenestrata* recommended by breeders. Exponents refer to internet adresses in the appendix; *poisonous, see text.

Tab. 1: Von Züchtern empfohlene Futterpflanzen für *Ancylecha fenestrata*. Hochzahlen verweisen auf Internetadressen im Anhang; *giftig, s. Text.

Family	Species
Rosaceae	*Rubus fruticosus* agg.[1-6] *Rubus idaeus* [2,7]
Oleaceae	*Ligustrum vulgare*[8,9] *Forsythia* sp.[9]
Hypericaceae	*Hypericum* sp.[7,9]
Scrophulariacae	*Buddleja* sp.[7,9]
Anacardiaceae	*Cotinus coggygria*[9] *Toxicodendron* (*Rhus*) sp.[9*]

most of them contain (secondary plant) substances more or less harmful to men (Tab. 2). *Toxicodendron* spp. is toxic, but has recommended as food plant (Tab. 1), and *Ligustrum vulgare*, also toxic, is used for both, feeding and oviposition (Tab. 2).

3.2. Habitus and wing markings

Adult *Ancylecha fenestrata* do not reveal a very pronounced sexual dimorphism in size. Males reach a body length of approx. 7.0 cm (head to the tip of the forewings); with approx. 7.5 cm length females are slightly larger (Fig. 2 A, C). Females are characterized by a strong and flattened ovipositor bent upward (Fig. 2 D).

The leaf-like tegmina exhibit green shades that are slightly different in the various individuals, but all show the same markings, i.e. two crescent-shaped markings lying in row more or less centrally in the tegmen followed by a fragmentary crescent markings (Fig. 2 E). The crescent-like markings are formed by four crescent-shaped lines or areas that, starting from the outermost layer, are brown, whitish, black and dark-brown. Three to four smaller coloured markings are present above the crescent-shaped areas, from which at least two show from proximal to distal five coloured areas (brown, white, black, white, brown, Fig. 2 E). Posteriorly, each tegmen shows six to eight variable black dots; the upper region of the tegmen reveals delicate, black broken lines.

The antennae, approximately as long as the body, are brown-black (Fig. 2 B). The compound eyes are light green with brownish stripes. The head is coloured light green to whitish and contains black areas (Fig. 2 B). The front legs are brown and have rear-facing, pointed thorns. They are significantly smaller than on the strongly developed third pair of legs. The green femora are thickened; tibiae are green and tarsi grey.

3.3. Sounds and stridulatory apparatus

Males and females produce sounds, when held in the hand. Our very preliminary sonagrams show that these sounds last up to approx. 1 s and are interrupted by breaks of various length. Sounds of males consist of rather regular syllables, each of which contains two elements. Number of syllables

Tab. 2: Plants recommended from breeders as oviposition sites for *Ancylecha fenestrata*, some of their secondary substances, and their impact on humans. *Largely after Wink et al. (2008); for saponins in Asparagaceae see Sparg et al. (2004). Exponents refer to internet addresses in the appendix.

Tab. 2: Von Züchtern als Eiablageorte für *Ancylecha fenestrata* empfohlene Pflanzen, einige ihrer Inhaltstoffe und deren Wirkung auf den Menschen *Weitgehend nach Wink et al. (2008); Saponine in Asparagaceae s. auch Sparg et al. (2004). Hochzahlen verweisen auf Internetadressen im Anhang.

Family	Species	Plant substances*	Symptoms of toxicity*
Asparagaceae	*Dracaena surculosa*[1,3,6,10] *Yucca* sp.[10]	saponins saponins	stomach trouble, vomiting, diarrhoea, kidney damage, caridiac arrhythmia
Oleaceae	*Ligustrum* sp.[4,8]	secoiridoidglucosides	nausea, vomiting, diarrhoea etc.
Araliacaea	*Hedera helix*[2,5,4,6]	saponins (α- and β-hederin), falcarinol etc.	nausea, vomiting, respiratory arrest etc.
Araceae	*Epipremnun aureum*[10,11, 5]	calcium oxalate crystals, toxic peptides	painful irritations of skin, mucosae and digestive tract
Moraceae	*Ficus elastica*[11]	furocumarines etc.	latex causes photodermatosis

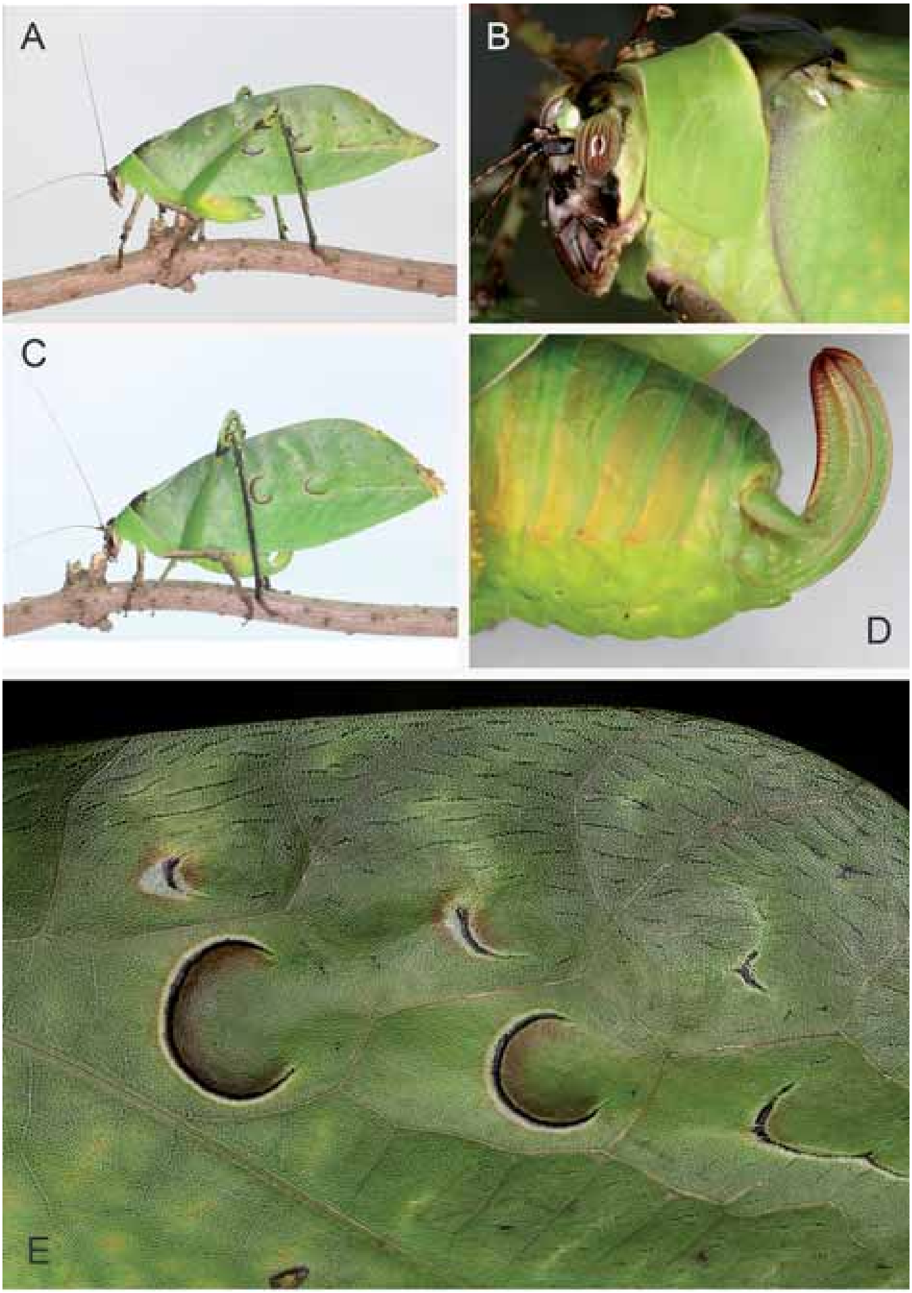


Fig. 2: Habitus (**A**) and head region (**B**) of a male. Note the spot in the compound eye (pseudopupil); habitus (**C**) and ovipositor (**D**) of a female of *Ancylecha fenestrata* and the colour pattern of the tegmen (**E**).

Abb. 2: Habitus (**A**) und Ansicht des Vorderkörpers (**B**) eines Männchens. Man beachte die Pseudopupille im Auge; Habitus (**C**) und Ovipositor (**D**) eines Weibchens von *Ancylecha fenestrata* und Musterung des Tegmen (**E**).

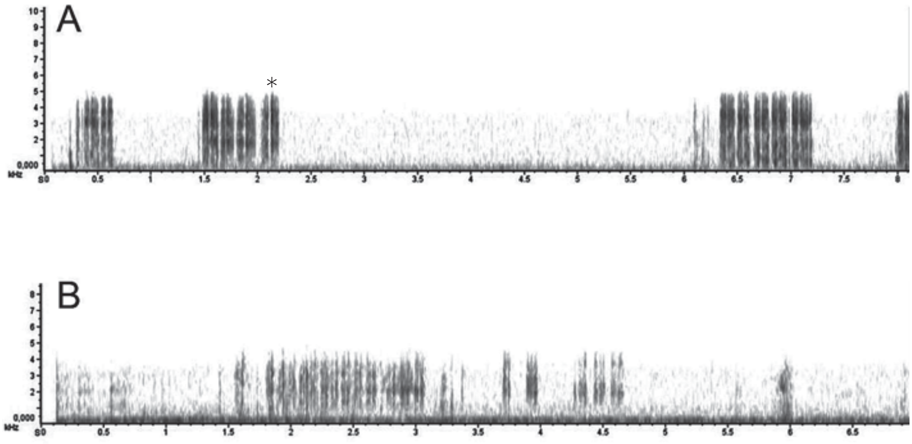


Fig. 3: Sonagram of the sounds produced by a male (**A**) and a female (**B**) of *Ancylecha fenestrata*. Each sound consists of several syllables and each syllable contains two elements (*discernable especially in A).

Abb. 3: Sonagramm der Laute von Männchen (**A**) und Weibchen (**B**) von *Ancylecha fenestrata*. Jeder Laut besteht aus mehreren Silben, von denen jede aus zwei Elementen besteht (*zu sehen vor allem in A).

may vary (Fig. 3 A). In females the sounds are noisier and syllables are less regular over time (Fig. 3 B). Sounds are broadband reaching < 500 Hz to about 4.5 kHz in the male (Fig. 3 A) and < 500 Hz to approx. 4.0 kHz in the female (Fig. 3 B).

The stridulatory apparatus is located at the bases of the overlapping tegmina (Fig. 4 A). Sounds are produced by rubbing a file of teeth (*pars stridens*) on a scraper (*plectrum*). These elements differ considerably in males and females.

In males the *pars stridens* – clearly visible already at low magnification (Fig. 4 B) – is a modified vein on the underside of the left tegmen base. Teeth of the file look like small lamellae, are very similar to each other, but become smaller towards the ends of the file (Fig. 4 D, E). The highly sclerotized scraper (*plectrum*) is located on the upper surface

Tab. 3: Distribution of 60 eggs of *Ancylecha fenestrata* in 184 *Dracaena surculosa*-leaves of different sizes (expressed as leaf length and width).

Tab. 3: Verteilung von 60 Eiern von *Ancylecha fenestrata* in 184 unterschiedlich großen Blättern (angegeben als Länge und Breite) von *Dracaena surculosa*.

Eggs per leaf	Number of leaves	Length of leaves Range in cm (mean plus SD)	Width of leaves Range in cm (mean plus SD)
0	73	3.0 -13.1 (8.75 ± 2.7)	1.0 - 4.3 (2.84 ± 0.9)
1	18	4.6 -14.2 (9.35 ± 2.6)	1.1 - 4.3 (3.14 ± 0.8)
2	27	4.5 -11.7 (9.02 ± 1.9)	1.0 - 4.0 (3.08 ± 0.7)
3	20	6.9 -11.7 (9.13 ± 1.4)	2.1 - 4.0 (3.17 ± 0.5)
4	22	6.2 -14.0 (9.22 ± 2.1)	1.9 - 4.5 (3.15 ± 0.7)
5	10	8.3-13.6 (10.87 ±1.8)	2.8 - 4.4 (3.53 ± 0.6)
6	3	9.6 -11.1 (10.23 ± 0.8)	2.3 - 3.9 (3.17 ± 0.8)
7	7	6.2 -11.6 (9.81 ± 1.9)	2.0 - 3.7 (2.92 ± 0.6)
8	2	6.5 -10.9 (8.7 ± 3.1)	2.2 - 3.7 (2.95 ± 1.19
11	1		
13	1		

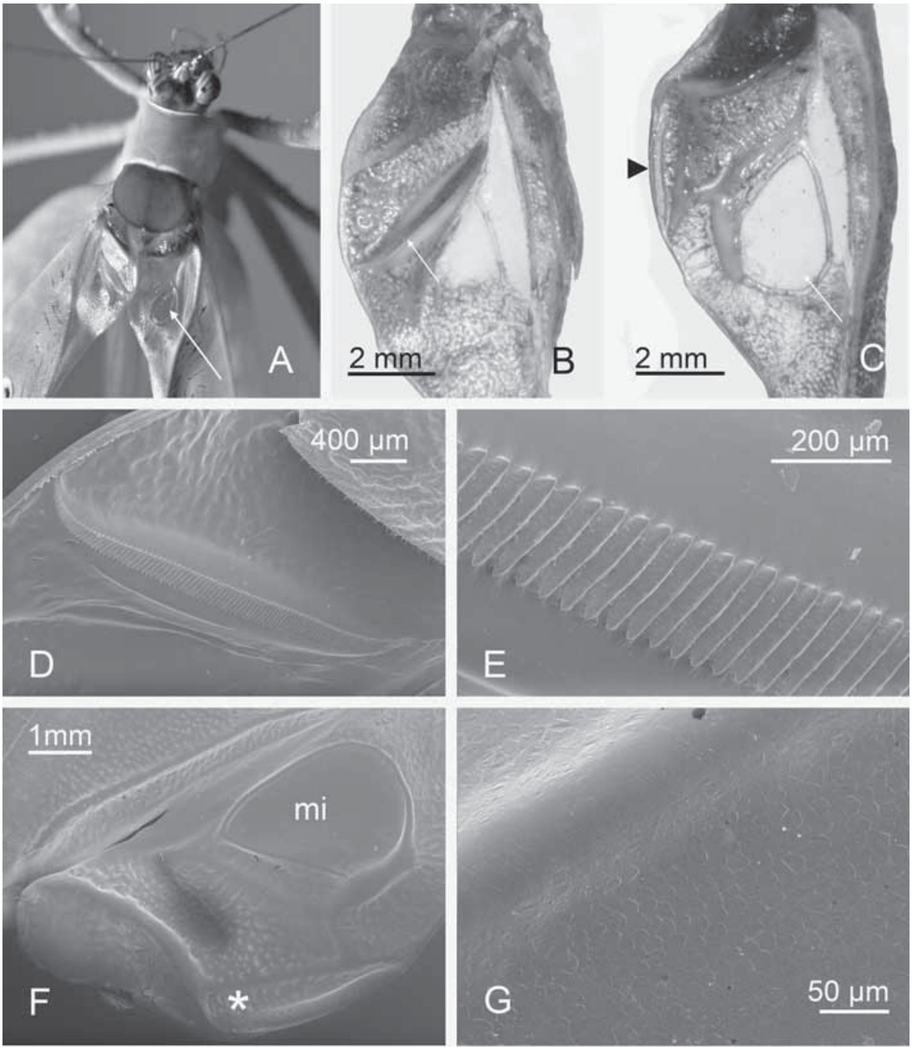


Fig. 4: Stridulatory apparatus of the male *Ancylecha fenestrata* (LM: A-C; SEM: D-G) **A** Dorsal view with opened forewings. Note the mirror (arrow). **B** Underside of the left tegmen showing the file (*pars stridens*) (arrow). **C** Upper surface of the right tegmen with mirror (arrow) and scraper (*plectrum*) (arrowhead). **D** Curvature of the file. Note smaller teeth at the ends. **E** Detail of teeth from the mid portion of the file. **F** Upper surface of the right wing base with mirror (mi) and mirror frame; scraper (asterisk). **G** Veins of the frame are not toothed. The tegmen articulation is on the top (B, C).
Abb. 4: Stridulationsapparat des Männchens von *Ancylecha fenestrata* (LM: A-C; REM: D-G). **A** Dorsalansicht mit geöffneten Flügeln. Man beachte den Spiegel (Pfeil). **B** Unterseite der linken Flügelbasis mit Schrilleiste (*pars stridens*) (Pfeil). **C** Oberfläche des rechten Flügels mit Spiegel (Pfeil) und Plectrum (Pfeilkopf). **D** Krümmung der Schrillleiste. Man beachte die kleineren Zähne an den Enden. **E** Detail aus dem mittleren Abschnitt der Schrillleiste. **F** Oberseite der rechten Flügelbasis mit Spiegel (mi) und Spiegelrahmen; Plectrum (Stern). **G** Die Adern des Spiegelrahmens sind glatt. Artikulation des Tegmens oben (B, C).

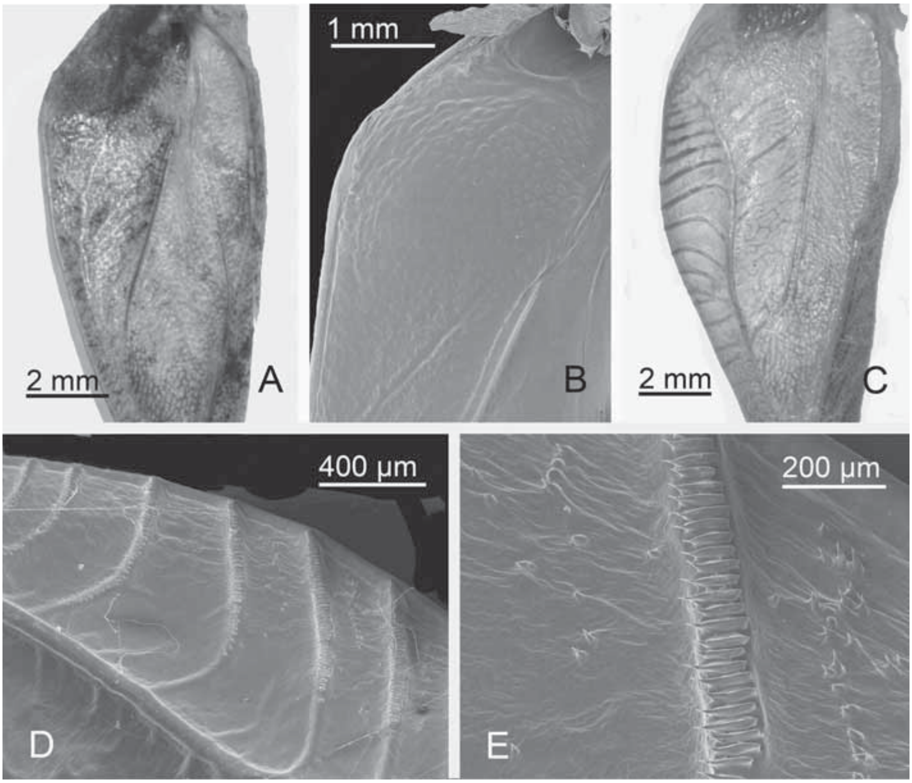


Fig. 5: Stridulatory apparatus of a female of *Ancylecha fenestrata* (LM: A, C; SEM: B, D, E). **A** Underside of the left tegmen with a thickened vein. **B** Ditto. **C** Upper surface of the right tegmen with many toothed lateral veins (left) acting as files. **D** Lateral veins; the distal region is left. **E** Detail of teeth from the mid portion of a file. The tegmen articulation is on the top (A, B, C).

Abb. 5: Stridulationsapparat des Weibchens von *Ancylecha fenestrata*. (LM: A,C; SEM: B, D, E). **A** Unterseite des linken Tegmen mit verdickter Ader. **B** Dito. **C** Oberseite der rechten Flügelbasis mit mehreren bezahnten Adern (Schrillleisten). **D** Seitliche Adern; distal ist rechts. **E** Detail aus dem mittleren Abschnitt einer Schrillleiste. Artikulation des Tegmen oben (A, B).

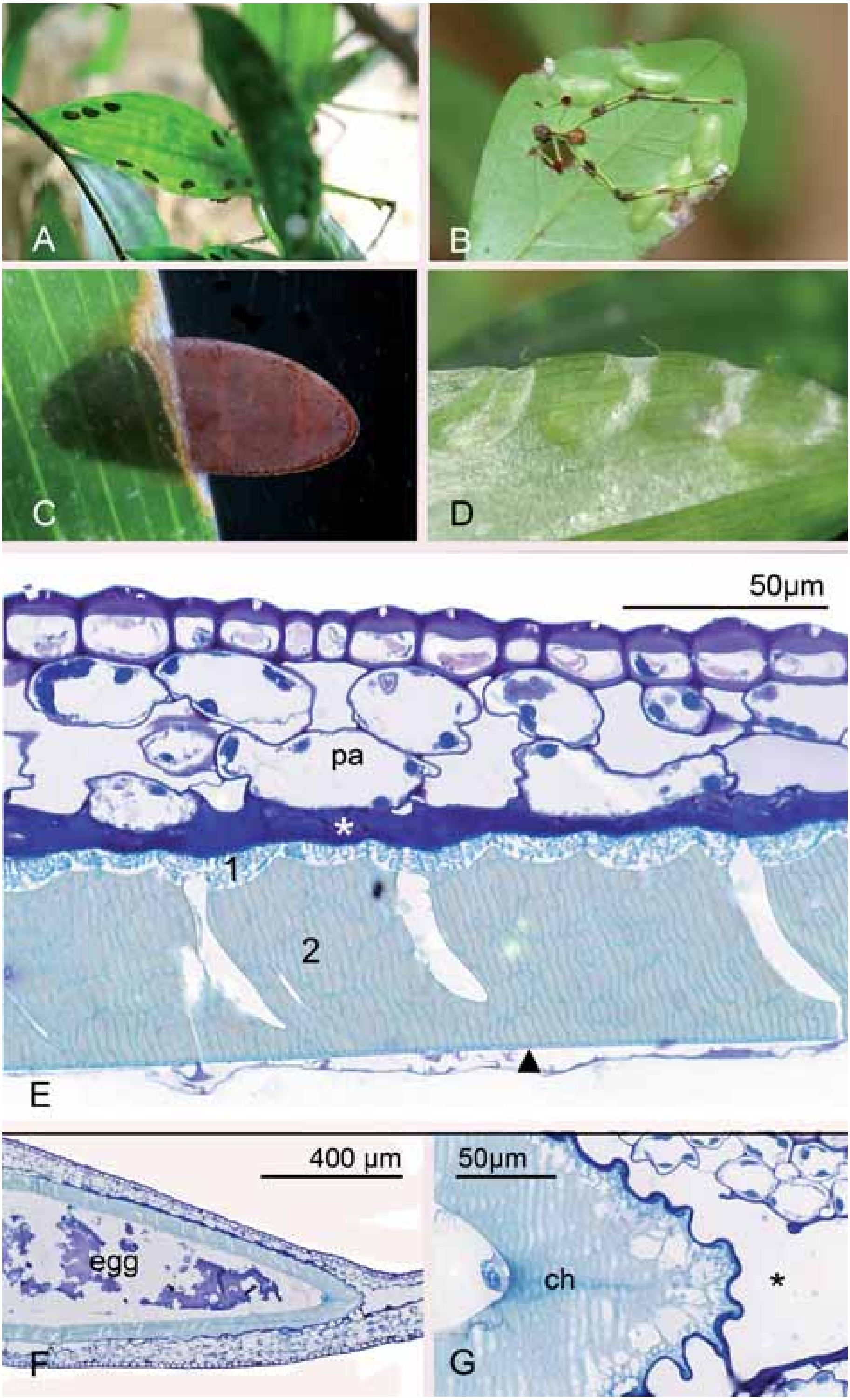
of the right tegmen close to the so-called mirror, i. e. an area, approximately 3 mm long and 2 wide with a thin and clear cuticle surrounded by a framework of thickened, smooth veins (Fig. 4 C, F, G).

In the female the upper surface of the right tegmen bears several transversal veins branching off from a longitudinal vein. The transversal veins bear rather uniform “teeth”; each tooth has an acute spine pointing distally (Fig. 5 C-E). The underside of the left tegmen is inconspicuously shaped showing a prominent, sclerotized vein (Fig. 5 A, B).

3.4. Site of oviposition and first instars

Oviposition was never observed either on the day or in the night during our observations. The two females housed in the insectary II laid 123 eggs within a period of 56 days. We found up to 13 eggs per leaf (see Tab. 3; Fig. 6 A). A preference for a certain leaf-size cannot be derived from our data.

The ovipositor of the female makes a longitudinal wound on the edge of the leaf, which becomes necrotic during incubation, but generally those leaves stay alive (Fig. 6 B). Further alterations due to oviposition are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not visible with the naked eye. Occasionally we noticed eggs that were not completely pushed into the leaf (Fig. 6 C).

Development (temperature 22-25°C) took 66.9 ± 1.49 days. After hatching of the nymphs the chorion remains in the leaf. Therefore it may be difficult in some cases to distinguish between eggs with and without embryos, but the latter yield under slight pressure. To leave the parenchyma, hatchlings apparently use the channel the female ovipositor has made during oviposition. After hatching the epidermal tissue of the plant appears unaffected (Fig. 6 D).

Hatchlings are of considerable size (body length approx. 1 cm) and nicely coloured (see Fig. 6 B, 8 A). Even more colourful are the following instars (Fig. 8 B). This pattern begins to change conspicuously during further growth, probably with the fourth moult. When resting, forlegs are angled, whereas the second and third pair of legs are stretched backwards and the antennae are positioned under the abdomen (Fig. 6 B, 8 A, B).

3.5. Structure of the chorion and its association with plant tissue

Eggs are formed like a kidney tapering slightly to rounded ends; at the beginning of their development they are about 7 mm long, 2.5 mm wide and 1 mm thick. Near hatching thickness increases to about 2 mm. Deposited eggs lie in the parenchyma of the leaves that seems to be largely unaffected; the same holds for the ab- and adaxial epidermal cells (Fig. 6 E-G, 7 A).

LM and SEM of deposited eggs reveal the organisation of the chorion. The thickest layer resting on a very thin basal layer is more or less solid and is traversed by fine pore canals that terminate in large dilatations (air spaces) near the basal layer (Fig. 6 E, G, 7 B, C) . Neither the dilatations nor the pore canals penetrate the basal layer. At their outer ends, pores open out into a spongy layer (Fig. 7 C, D), whose outer boundary is thin, homogeneous and stains heavily with toluidine blue; it is closely attached to the parenchyma cells (Fig. 6 E, 7 G). The surface of the egg shows a basically hexagonal to polygonal pattern, clearly seen on eggs not entirely pushed into the leaf, and on the edges of deposited eggs not associated with the parenchyma (Fig. 6 G, 7 E, F). At the bottom of the hexa- or polygons small pores seem to be present (Fig. 7 F).

4. Discussion

4.1. Food plants and plants used for oviposition

Considering some basic requirements such as high temperatures, high relative air humidity and large terraria, rearing of *An-*

Fig. 6: Position of eggs of *Ancylecha fenestrata* in the leaves of *Dracaena surculosa*. **A** Several eggs within a leaf. **B** Necroses (brown) at the sites of oviposition. Note the multi-coloured young nymph (first instar). **C** Egg not entirely inserted into the leaf. **D** After hatching the epidermal tissue of the plant appears unaffected. **E** Main layers of the chorion (1: spongy; 2: compact; the outer boundary of the spongy layer closely associated with the walls (asterisk) of parenchyma cells (pa) (arrowhead: basal layer). **F** Developing egg in the leaf parenchyma. **G** The free edge of the egg is not associated with parenchyma cells (asterisk).

Abb. 6: Lager der Eier von *Ancylecha fenestrata* in Blättern von *Dracaena surculosa*. **A** Mehrerer Eier in einem Blatt. **B** Nekrosen (braun) an den Einstichstellen des Ovipositors. Man beachte die bunte junge Nymphe (erstes Stadium). **C** Ein nicht vollständig in das Blatt gelegtes Ei. **D** Auch nach dem Schlupf erscheint das Deckgewebe des Blattes intakt. **E** Schichten des Chorions (1: schwammig; 2: kompakt; 3: Pfeilkopf: Basallage; Stern: Deckschicht der schwammigen Lage, eng mit den Wänden der Parenchymzellen (pa) assoziiert. **F** Sich entwickelndes Ei im Parenchym des Blattes. **G** Der seitliche Rand der Eier ist nicht mit den Parenchymzellen assoziiert (Stern).

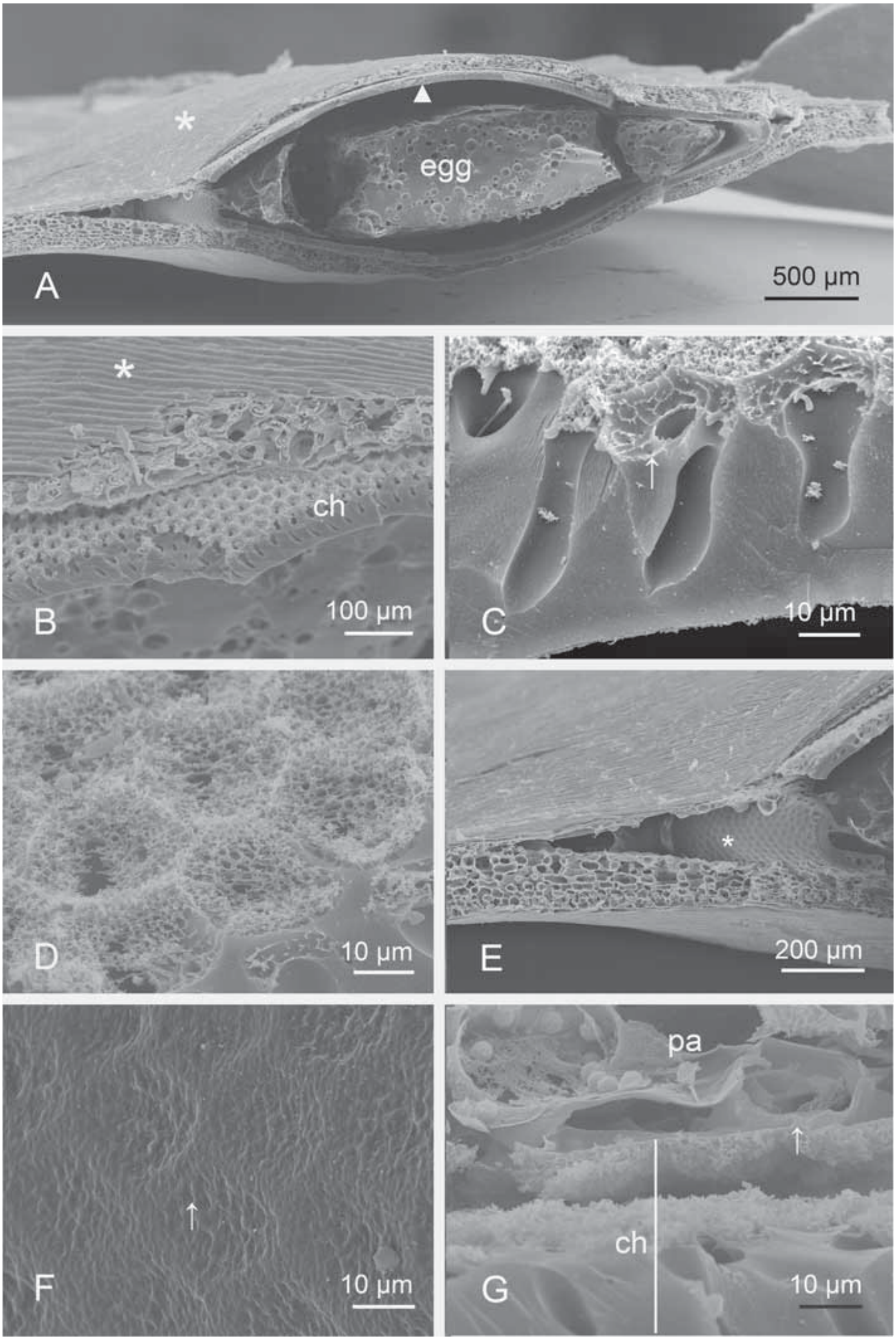


Fig. 7: SEM of the eggs of *Ancylecha fenestrata* inside a leaf of *Dracaena surculosa*. **A** Overview (see Fig. 6 F). Surface of the leaf (asterisk); chorion (arrowhead). **B** Chorion (ch); surface of the leaf (asterisk). **C** Compact layer with cavities and small canals, which open into the spongy layer (arrow). **D** Spongy layer. **E** Detail from A; edge of the egg with intact outer boundary of the spongy layer

cylecha fenestrata might not be problematic in captivity (see also the various internet fora in the appendix). Regarding the diet, *A. fenestrata* appears to be a generalist that feeds on various plants including toxic ones such as *Ligustrum* spp. and *Toxicodendron* spp. (see Wink et al. 2008). The number of plants accepted for feeding might be even larger as known today. We do not know the natural food plants of *A. fenestrata*, but *Buddleja* spp. and *Cotinus* spp., both occurring in South Asia, may be part of the natural diet of this katydid.

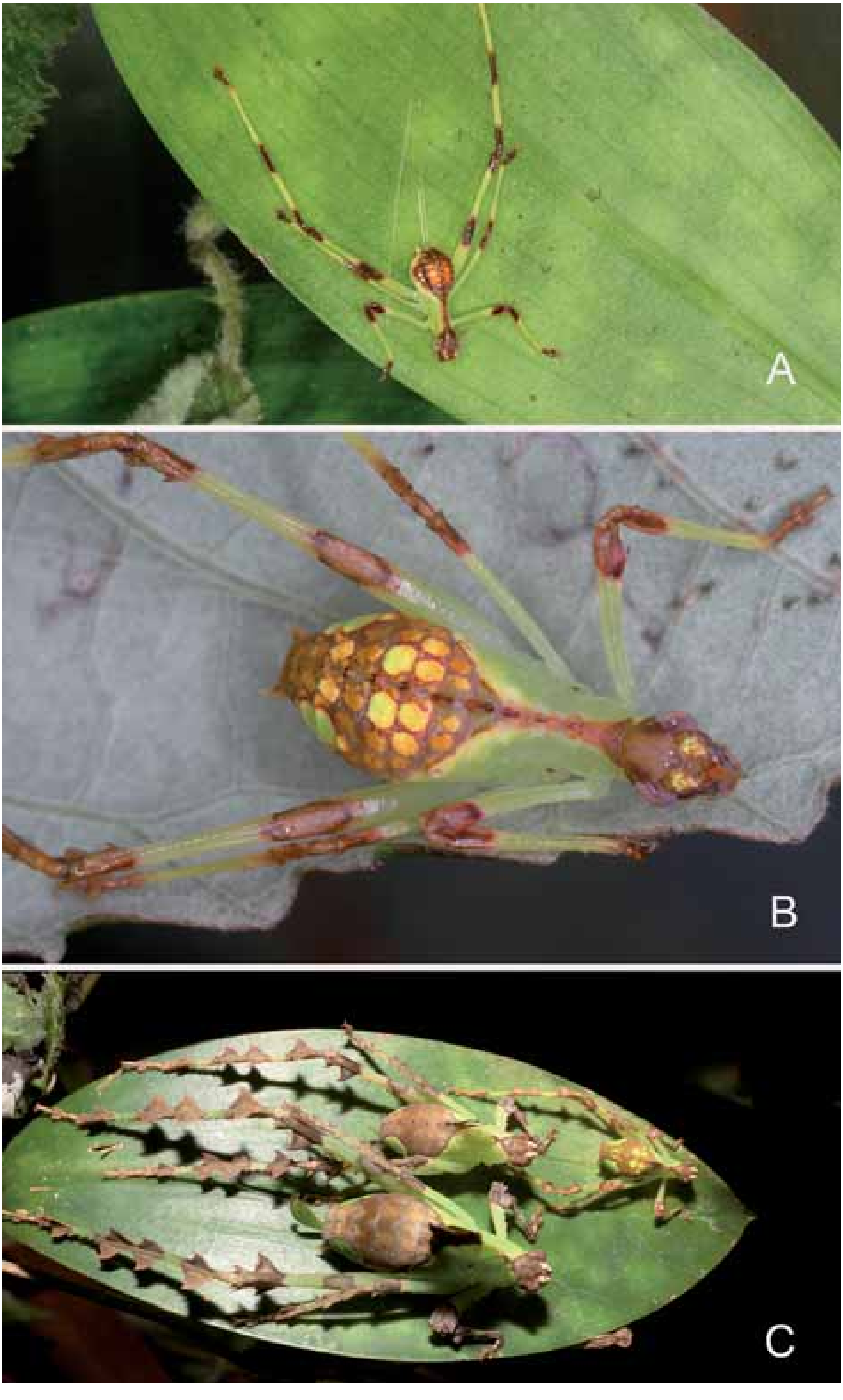
With the exception of *Ligustrum* spp. the food plants listed in table 1 are not used for oviposition. This may be ascribed to the relatively thin leaves of these plants that do not allow females to insert their flat and serrated ovipositor into the leaf-parenchyma. We also do not know which criteria *A. fenestrata* females use to select plants for oviposition, but certainly the thickness of leaves will play a decisive role. As expected, the various plants used for ovipostions in insectaries including *Ligustrum* spp. have relatively thick and leathery leaves. However, excepting *Ligustrum* spp., *A. fenestrata* does not feed on these plants, from which only *Epipremnum aureum* and *Ficus elastica* occur in the tropical forests of Malaysia and Indonesia. Why katydids do not eat them, perhaps because of their thickness, is unclear. However, it is noticeable that these plants (including *Ligustrum* spp.) contain substances that are more or less harmful at least to men (see Tab. 2) and, thus, may provide protection from herbivores. For example, saponins, widely distributed natural detergents, have haemolytic, antifungal, antibacterial and many more activities (for review see Sparg et al. 2004) and protect plants from phythopathogenic microorganims, phytophagous mammalians and insects (e. g. Harmatha 2000). Whether oviposition in "poisonous" plants is a strategy pursued by *A. fenestrata* in the field, is unknown. In addition, *A. fenestrata* does not seem to feed on edible leaves containing eggs (http://lemondedesphasmes.free.fr./spip.php?article137), a matter that deserves closer attention.

4.2. Number of eggs and oviposition sites

Oviposition was not observed by us, but is described and pictured in the internet. The female hangs on the leaf holding its edge along her abdomen. Then she bends her abdomen until the ovipositor is approximately perpendicular to the leaf edge, inserts the ovipositor into the leaf and lays the egg. Then, the female moves on a few centimeters to lay another egg. This is repeated three to four times (http://lemondedesphasmes.free.fr./spip.php?article137). Thus, *A. fenestrata* females deposit more than one egg in the same leaf. As indicated by our still provisional data based on the measurement of length and width of leaves (used as rough measure of size) size and position of *Dracaena surculosa*-leaves do not seem to be a significant criterion for oviposition.

(asterisk). **F** Detail from E; surface pattern of the outer boundary of the chorion possibly with small pores (arrow). **G** Close association (arrow) of the outer boundary of the chorion (ch) with the walls of the parenchyma cells (pa).

Abb. 7: REM der Eier von *Ancylecha fenestrata* im Blatt von *Dracaena surculosa*. **A** Übersicht (vgl. Fig. 6 F). Oberfläche des Blattes (Stern); Chorion (Pfeilkopf). **B** Chorion (ch); Oberfläche des Blattes. **C** Kompakte Lage mit Höhlungen und feinen Kanälen (Pfeil), die in die schwammige Lage münden. **D** Schwammige Lage. **E** Ausschnitt aus A; Rand des Eies mit intakter Grenzschicht der äußeren Lage des Chorions (Stern). **F** Ausschnitt aus E; Oberfläche des intakten Chorions , wahrscheinlich mit winzigen Poren (Pfeil). **G** Enge Assoziation (Pfeil) der äußeren Begrenzung des Chorions (ch) mit den Wänden der Parenchymzellen (pa).


A
B
C

We counted a maximal number of 13 eggs in a single leaf. However, we do not know whether such large numbers come from a single female or from several females. Number of deposited eggs should be limited to retain the viability of leaves, which is vital for the successful development of eggs. Reduction of the egg numbers might be achieved by chemical signals (known as oviposition deterrence and common in many leaf mining insects to reduce subsequent larval competition; summarized in ANDERSON 2002). Leaves of *D. surculosa* punctured by the female ovipositor show necroses at the puncture site, but survive for a while. This does not exclude impairment of punctured leaves and leaves used for incubation, which may be direct by wounding and consumption of the tissue or indirect by the reduction of photosynthetic rate in adjacent undamaged tissue (e. g. WELTER 1989; ZANGERL et al. 2002; SCHRÖDER et al. 2005). In addition, development of defensive responses of the plant may by induced by the mechanical wounding or feeding. This matter has been intensely studied in insects laying their eggs on leaves and mining species (for more recent summaries see HILKER et al. 2002; HILKER & MEINERS 2006).

Although no detailed information is available, the eggs of *A. fenestrata* may directly and indirectly benefit from this kind of oviposition, and this in a similar way as "leaf-mining" insects (see CONNOR & TAVERNER 1997 for review). To be in a leaf may protect the developing eggs of *A. fenestrata* from harmful influences of the physical environment, from desiccation, from direct and indirect effects of UV radiation, and from attacks by natural enemies (see CONNOR & TAVERNER 1997) and herbivores (see above).

4.3. Developmental stages and anti-predator defence

Under the conditions mentioned above, the incubation period was 66.9 days on average, but this time may vary considerably depending on the external conditions. Males of *Ancylecha fenestrata* are said to undergo one fewer moult than do females maturing in five instars (e.g. http://lemonddesphasmes.free.fr./spip.php?article137). However, contrary to the source quoted, we are currently not clear about the exact number of instars, which in insects may vary intra- and interspecifically (RAMSAY 1964; ESPERK et al. 2007), and the colour changes coupled with the moults.

Katydids possess various indirect (primary) and direct (secondary) anti-predator defences. Indirect defences are crypsis, aposematism and Batesian mimicry (reviewed in BELWOOD 1990; NICKLE & CASTNER 1995). The green adults of *A. fenestrata* clearly mimic leaves (as do many other Phanopterinae) and their colour match the environment even in the NIR-range (MIELEWZIK et al. 2012). In this context, the significance of the crescent markings (mimics of necrotic leaf tissue or bird droppings (?), as suggested for other Phanerpterinae and Pseudophyllinae, see BELWOOD 1990) is unknown, but these markings should not be confused with eyespots that are considered as secondary defences and are present on the hindwings of several Pseudophyllinae. These katydids actively expose their eyespots when disturbed (e. g. COTT 1957; BELWOOD 1990). To our knowledge the only example of Batesian mimicry and aposematic colouration in katydids are the rare species that mimic wasps (Pompiliidae) (WICKLER 1968; BELWOOD 1990).

Fig. 8: Instars of *Ancylecha fenestrata* in resting position. **A** First instar. **B** Second or third instar**. C** The same as in B (right side) and two older and less colourful nymphs (left side).

Abb. 8: Nymphen von *Ancylechea fenestrata*. **A** Erstes Nymphenstadium. **B** Zweites oder drittes Nymphenstadium. **C** Nymphenstadium wie in B (rechts) und zwei weniger farbige ältere Nymphen (links).

Especially the first instars of *A. fenestrata* differ considerably from later instars and adults. They are extremely colourful and when roosting on green leaves their bodies contrast with the environment. Although nothing is known about the biology of *A. fenestrata* and the diurnal resting places of subadults (and adults), we hypothesize that the first instars of *A. fenestrata* may be aposematic, either being distasteful (less probable) or mimicking certain spiders. We will not deepen this aspect here, but when allowing 190 students of biology to have a short (approx. 4 s) look on a slide that showed a second instar of *A. fenestrata* sitting on a leave, slightly more than the half (approx. 55%) identified an insect (grasshopper, cricket or beetle), approx. 35% a spider, 7% a froglet, and the rest a crayfish and some other obscure animals. Certainly, this does not prove the imitation of spiders with aposematic colours, but the results of our questioning are suggestive and deserve attention.

4.4. Plant tissue and chorion structure

The cuticle structures of *Dracaena* spp. varies between species and in some species also between the adaxial and abaxial surfaces. In *D. surculosa* the adaxial cuticle appears undulated due to elongated protuberances, whereas the abaxial surface appears verrucously (Klimko & Wiland-Szymanska 2008). In addition, epidermal cells appear larger adaxially than abaxially. Therefore the layer covering the eggs is adaxially slightly thicker. In the region, in which the chorion touches the parenchyma cells the outer layer of the chorion is closely associated with their walls.

The structure of the chorion in tettigoniid eggs was studied by Hartley (1964, 1971), who assumed that respiration occurs only through the pore system. Chorions of species depositing their eggs in leaves were not examined (for gaseous exchange in insect eggs see also Hinton 1969; for detailed overviews of insect eggs see Margaritis 1985 and Trougakos & Margaritis 2002). More recently, Yilmaz et al. (2012) examined the ultastructure (SEM and TEM) of the egg chorion in the tettigoniid *Poecilimon cervus*. Authors describe the polygonal surface pattern, fine pores that opens to the exterior (aeropyles) and call the layer homologous to our spongy layer as exochorion, and the compact layer as endochorion. Principally this organisation resembles the chorion structure described herein for *A. fenestrata*, but the latter has remarkable air spaces (dilatations) in the solid layer, perhaps facilitating a better gas exchange in the leaf (see also Hinton 1969). Possible modifications in certain regions such as the micropyle etc. were not considered in the present study. The delimitation of the spongy layer may be of special interest as it becomes very closely associated with the walls of the parenchyma cells as seen in TEM (unpublished).

4.5. Stridulatory apparatus

The structure of the stridulatory apparatus of males of *Ancylecha fenestrata* is in accordance with that known from other tettigoniids with tegminal stridulation (e. g. Schumacher 1978; Robinson 1990; Desutter-Grandcolas 2003, and others). The tegmina overlap and there is a file of teeth (*pars stridens*) on the underside of the left tegmen that is struck by a plectrum (a sclerotizised edge of the right fore wing) on the upper surface of the right tegmen during wing movement. The vein that forms the plectrum is attached to a cuticular frame surrounding the so-called mirror (for details of the venation and their modifications see see Desutter-Grandcolas 2003). The mirror frame and the surrounding cells and veins are specialized structures for sound radiation (Bailey 1970; Bailey & Broughton 1970; for more recent details of the functioning of the stridulatory apparatus see Montealegre-Z & Mason 2005).

Sound producing females are common in the Phaneropterinae (and two other unrelated taxa of the Tettigoniidae), but the stridulatory apparatus of the sexes is not homologous. Nickle & Carlysle (1975) described the stridulatory field of female Phaneropterinae as a complex of stout spines on the upper surface of the anal area of the right tegmen; the mirror and its cuticular frame are missing. The plectrum is said to be the “sharpened anal margin of the left tegmen … thickened and curved downward, especially at the area overlapping the posterior field of spines” (Nickle & Carlysle 1975, p. 161), whereas Heller & Helversen (1985) consider a thickened vein on the underside of the left wing to serve as plectrum. Generally, the tegmen underside of female *A. fenstrata* appears rather unspectacular.

Although our sonagrams are preliminary at best due to our inadaequate equipment, they reveal regular sounds in males and rather noisy sounds in females reaching 4.5 and 4.0 kHz, respectively. Sounds of tettigoniids are commonly involved in intraspecific (e. g. attraction of females, male-male interactions, male-female interactions, duetting) and interspecific communication (e. g. predator deterrence) (for reviews see Robinson 1990; Robinson & Hall 2002) and frequency of sounds may range from below 1 kHz to > 100 kHz (Robinson & Hall 2002). There is no evidence that the sounds we heared from *A. fenestrata* as yet play any role in reproduction. We think that these calls primarily are disturbance (alarm or defence) sounds that are ubiquitous in insects and may startle a predator (e. g. Alexander 1967; Masters 1979; Robinson & Hall 2002).

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Prof. Dr. Hartmut Greven (corresponding author)
BSc Sabrina Braatz
Zoologie II der Heinrich-Heine-Universität
Universitätsstr. 1
D-40225 Düsseldorf
E-Mail: Grevenh@uni-duesseldorf.de

Dieter Schulten
Aquazoo/Löbbecke-Museum
Kaiserswerther Straße 380
D-40474 Düsseldorf
E-Mail: dieter.schulten@duesseldorf.de

Appendix

Some internet sources about feeding and breeding *Ancylecha fenestrata* (numbers correspond to the numbers in the tables 1 and 2)

[1] Aquazoo/Löbbecke-Museum Düsseldorf
[2] http://braunjork.npage.de/ancylecha_fenestrata_blattschrecke_68030284.html
[3] http://www.chitin-monsters.de/index.php/schrecken1/ancylecha-fenestrata
[4] http://wirbellosenzentrum.de/index.php/insekten/heuschrecken/660.html
[5] http://terra-mantodea.jimdo.com/haltungsberichte/orthoptera/ancylecha-fenestrata/
[6] http://www.saltatoria.info/deutsch/arten%C3%BCbersicht-a-z/ancylecha-fenestrata
[7] http://carnivorousockhom.blogspot.com/2010/11/katydid-ancylecha-fenestrata.html
[8] http://reptilienseite.net/index.php?option=com_content&view=article&id=71&Itemid=100
[9] http://lemondedesphasmes.free.fr/spip.php?article137
[10] http://www.phasmiden-forum.de/index.php?page=Thread&postID=19481&l=2
[11] http://andres-krabbelviecher.npage.de/ancylecha_fenestrata_65661553.html

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