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Bioacoustics and systematics of the *Poecilimon hamatus* group (Tettigonioidea: Phaneropteridae: *Poecilimon: Hamatopoecilimon* n. subg.)

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Abstract

The genus *Poecilimon*, with more than 150 species, is the largest genus of the family Phaneropteridae. According to DNA data (Ullrich *et al.* 2010) the most basal branch of the genus is formed by the *P. hamatus* group (*Hamatopoecilimon* n. subgen.). The coloration and a male calling song composed of series of short syllables, which follow each other at a relatively high frequency (9 - 26 Hz at 25°C), are important characteristics of this group. For all species of the subgenus, male calling songs, stridulatory movements (except for one species), and diagnostic genital morphology are described and figured. The females respond acoustically to the male song with a delay of about 30 ms. In four of six species the males have been observed to use two types of calling song, obviously connected to the female response behavior. The reasons for this behavior are discussed, as well as the phylogeny of the group, considering also its biogeography.

Key words

calling song, taxonomy, Aegean sea, Greece, Turkey

Introduction

Bushcrickets (katydids) of the family Phaneropteridae are well known for their complicated male calling songs (*e.g.*, Walker & Dew 1972, Walker *et al.* 2003, Hemp *et al.* 2010). In this family typically not only do the males produce sounds, but the females also respond acoustically to the male song.

By far the largest genus of the family is *Poecilimon* Fischer, 1853. All of its more than 150 named species and subspecies occur nearly exclusively in a relatively small area, the East Mediterranean. Within the genus, two different types of acoustical communication systems and a large variety of different song patterns are found (Heller 1990). The genus thus offers excellent opportunities to study the evolution of song patterns and possible factors responsible for divergence. While within subgroups this approach has been successfully applied (*e.g.*, Lehmann 1998; Heller *et al.* 2006, 2008; Chobanov & Heller 2010), for the genus as a whole, the evolution of the song patterns could not be traced and understood properly, partly because of a lack of information about the songs of some groups and partly because of missing knowledge about relationships between different subgroups and species.

After some initial phylogenetic studies (Ramme 1933, Heller 1984), the situation has been greatly improved by a recent molecular study by Ullrich *et al.* (2010). One important result of this study was that a group of species, the *Poecilimon hamatus* group, seems to be the sister group to all other *Poecilimon* (including some related small genera). The members of the group had already previously been identified as closely related, but the relationship to their congeners remained unsolved (see phylogenetic scheme in Warchalowska-Sliwa *et al.* 2000).

In this paper we review morphology and distribution and present new data on the acoustical behavior of all species of the *P. hamatus* group. Both males and females are acoustically active and communicate with each other using very short time intervals (< 100 ms) for reaction (responding and recognition time-windows). While the songs are quite short, they are surprisingly complicated. Without registration of the wing movement their structure would be hard to understand. The song patterns of all species (except of two sister forms) are distinct, but share some important characters.

Methods

Depositories of material are abbreviated as follows: CH - Collectio Heller, Magdeburg; ITZ - Instituut voor taxonomische Zoologie, Amsterdam; NHM - The Natural History Museum, London; NMW - Naturhistorisches Museum, Vienna; ZMB - Museum für Naturkunde der Humboldt-Universität, Berlin.

All described species are mentioned in the databanks of the Orthoptera Species File (OSF, Eades *et al.* 2010), mostly with quite incomplete reference lists; they are also in Fauna Europaea (http://www.faunaeur.org/) and The Orthoptera of Europe (http://www.ortheur.org/); selected species are also at http://members.tripod.com/Cesa88/orthtr.htm (*hamatus*, *unispinosus*) and DORSA/SYSTAX (http://www.biologie.uni-ulm.de/systax/daten/index.html).

The stridulatory files of the males were studied after removal of the left tegmen using a scanning electron microscope (SEM HITACHI S-450, Bielefeld).

The songs were recorded with a Uher tape recorder 4200 IC ,with microphone Uher M 645 (frequency response flat up to 20 kHz) or a Sony WM-3D Walkman with microphone Sony ECM-121 or a Sony WM-GX688 Walkman with a stereo microphone (flat up to 18 kHz) (distance to microphone 5 to 10 cm). Additional sound recordings were made with a Racal store 4-D tape recorder, with microphones Brüel & Kjær 4133 and 4135 (frequency response flat up to 40 and 70 kHz respectively; all frequency measurements were made on animals without reflective tape; see below) and a Pettersson D240 bat-detector (*P. klausgerhardi*). After digitizing the songs on a PC or an Apple computer, oscillograms (after filtering) and sound analyses were made using the programs Turbolab, Amadeus and Canary (Apple).

Wing movements were registered by an opto-electronic device (Helversen & Elsner 1977, modified as in Heller 1988). Due to the heating effect of the registration lamp, only a lower limit for body temperature can be given [see Heller 1988; in the oscillogram figures which follow these measurements are marked by ">"; for correction

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Table 1. Bioacoustical data.

	Song				Stridulatory file			
Species	Syllable repetition rate [Hz] for 25°C Q_{10}=2 mean±S.E.	Syllable repetition rate [Hz] for 26°C ANCOVA	Number of syllables per echeme (range (mean); short echeme)	Number of recording sessions / males	Length of file (mm)	Number of file teeth (SEM data)	Distance between two teeth (middle of file) [µm]	No. files analyzed
hamatus	8.7±1.6	7.7	1-2	13/13	1.49±0,06	115±8	17±1	5
paros	17.3±1.9	20.5	5-14 (x=9.3)	8/4	1.79	128	17	1
klausgerhardi	25.9	16.9	10-14 (x=12.2)	1/1	1.58	103	20	1
deplanatus	23.9±1.5	20,0	(2-)3-6(-7)*	10/7	1.73	91	23	1
ikariensis	22.8±3.7	24.5	2(-3)	11/8	1.06	97	18	1
unispinosus	18.1±0,9	18.3	(6-)7-9(-11)*	15/9	1.28	83	17	1

* Echeme with only simple syllables

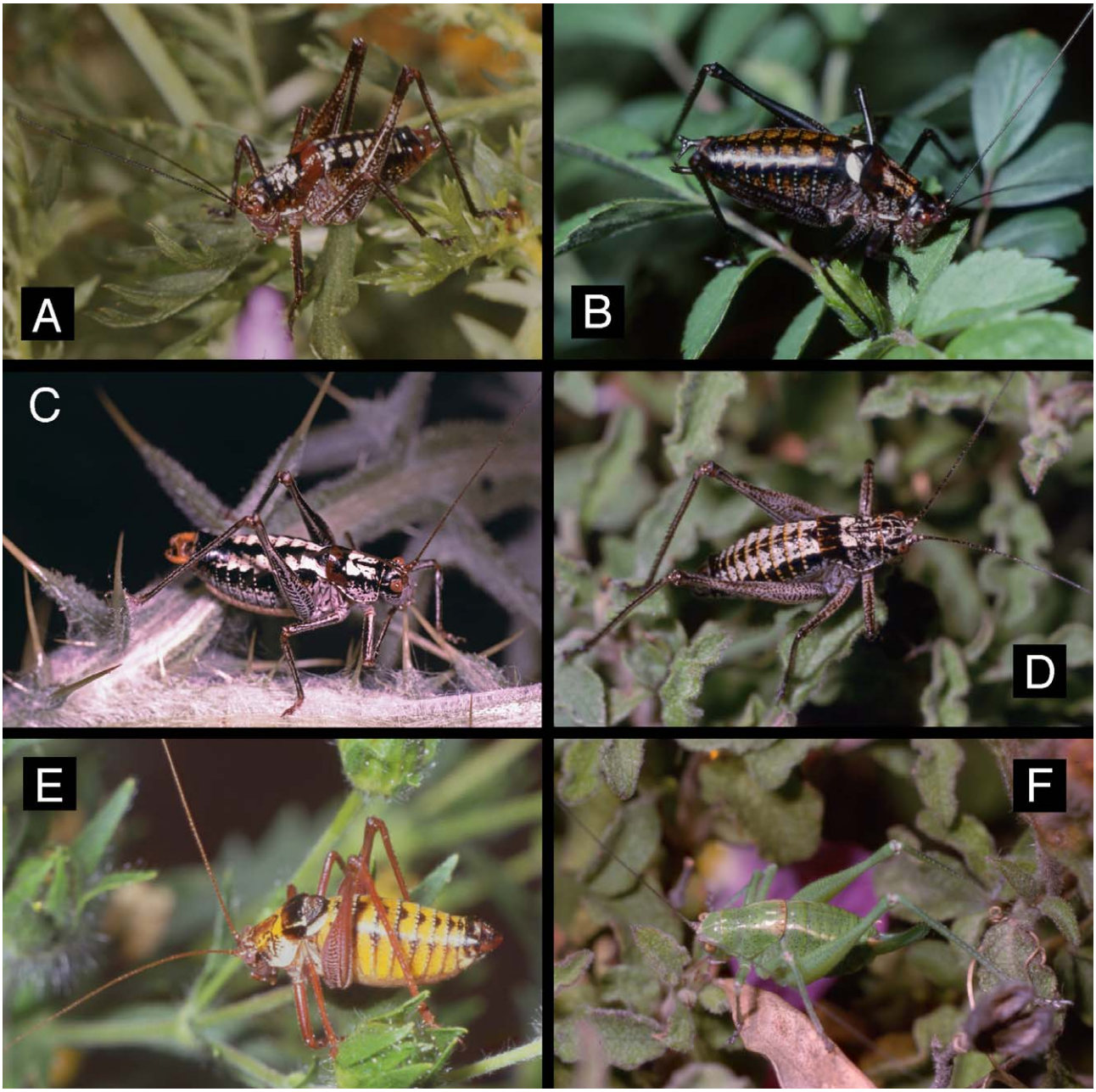


Fig. 1. A. *Poecilimon hamatus*, male (Rhodos). B. *P. paros*, male (Paros, paratype). C. *P. unispinosus*, male (Chios). D. *P. ikariensis*, male (Ikaria). E. *P. deplanatus*, male (Karpathos). F. *P. ikariensis*, female (Ikaria). For color version, see Plate V.

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of temperature effects [see below] degrees have been added to the measurements of air temperature].

To get song data comparable between different species, the influence of temperature had to be eliminated. This has been done (1) using a van't Hoff temperature coefficient (Q10) of 2 (despite some limitations as discussed by Walker 1975). As a second independent estimate (2) we ran an analysis of variance with temperature as linear covariate (ANCOVA; SPSS v 16.0, Chicago, Illinois). The data from both approaches were similar (see Table 1), although some species slightly differed.

The maps were produced using the program Versamap (http://www.versamap.com/). Localities with sound records are characterized by 'SR' in the text.

Song terminology.— Calling song: song produced by an isolated male. Syllable: the sound produced by one complete up (opening) and down (closing) stroke of the wing. For "simple" and "complex" syllables see Results. Echeme: a first-order assemblage of syllables. Impulse: a simple, undivided, transient train of sound waves (here: the highly damped sound impulse arising as the impact of one tooth of the stridulatory file; see Elsner 1974). Recording session: all sound files of one animal obtained at the same date and the same temperature.

Results

Hamatopoecilimon Heller n. subgenus

Type species.— *P. hamatus* Brunner von Wattenwyl, 1878

Included species.— *P. hamatus*, *P. paros*, *P. klausgerhardi*, *P. deplanatus*, *P. ikariensis*, *P. unispinosus* (see below).

Characteristics

Molecular results.—Molecular analyses (Ullrich 2007, Ullrich *et al.* 2010) clearly show that *Hamatopoecilimon* has to be placed close to the root of the genus *Poecilimon*, separated from all congeners. Both the sequences of mitochondrial DNA and that of nuclear DNA indicate the same pattern. In the nuclear data the placement as a sister group to all other *Poecilimon* species was statistically well supported, but in the faster evolving mt-DNA this old bifurcation could not be traced with the same certainty (Ullrich *et al.* 2010). There is only one unexplained point in the nuclear dataset at the moment: that is the inclusion of *P. ersisi* within the group. Regarding its morphology, bioacoustics and mt-DNA (and in a combined DNA-tree, Ullrich 2007) this species belongs to the *P. syriacus*-group (Heller *et al.* 2008) and is also geographically quite distant from the species discussed here. Considering the fact that species of several small genera like *Parapoecilimon*, *Phonochorion* and even *Polysarcus* are grouped together with *Poecilimon*, the basal position of *Hamatopoecilimon* becomes even more striking.

Morphology

Coloration.— The members of the *P. hamatus* group are easily recognised by their coloration, a feature already used by Ramme (1933) as the most important character to consider as closely related the three species known at that time. Typically the body color is not green, but yellowish-white to light brown (yellow in *P. deplanatus*) with many dark brown and black markings (Fig. 1. See also *e.g.*, jacket picture of Heller 1988, Willemse & Willemse 2008: 55; Kleukers in http://www.ortheur.org/). Male tegmina are largely covered by the pronotum, the free parts black, distolaterally bordered with an ivory-white band. The metazona of the pronotum is always reddish-brown to black and the eyes are typically red. These data refer mainly to males. In many populations, besides varicolored females (like males), more or less green ones are also found (Fig. 1), quite rarely also yellow-green males (*e.g.*, Willemse & Willemse 2008: 56). Nymphs are also quite often green. Black and white tegmina are found in other *Poecilimon* species (*e.g.*, *P. thoracicus*), but not in combination with an unusual body coloration. Body colors other than green are, to our knowledge, not mentioned for other *Poecilimon* species. However, at high densities individuals with many black markings, as described above, can sometimes be found (see *e.g.*, Chobanov & Heller 2010). In *Hamatopoecilimon* the coloration seems not to be correlated with population density, since in localities where a species was rare, nearly exclusively non-green individuals were also found.

Cerci.— Three of the six species of the group have cerci with a quite unusual bifurcate shape (Fig. 2). From the other three, however, only *P. unispinosus* might be considered as a prestage to the bifid type: the other two show no similarities.

Stridulatory file.— The species differ only slightly concerning shape (Fig. 3), number of teeth (range 83-128), intervals between teeth (range 16-23 µm in the middle of the file) and file length (range 1.06-1.79 mm; Table 1).

Other characters.— Ramme (1933) mentioned unusually short hind legs as typical for the group, but did not present any quantification. According to our data (Table 2) and in comparison to the measurements given by Harz (1969), neither absolute nor relative dimensions (in relation to pronotum length) are strikingly different from other species of the genus.

Song.— In all species of the group the male calling song consists

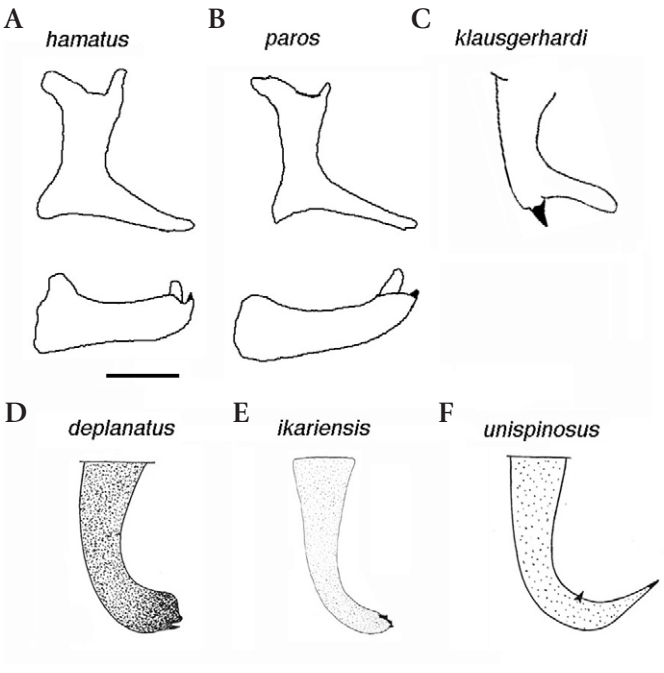


Fig. 2. Left male cercus. A, B according to Heller & Reinhold 1992, C Fontana 2004, D, F Ramme 1933, E Willemse 1982.

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Table 2. Body dimensions [length in mm; using data from Brunner von Wattenwyl 1878, Fontana 2004, Harz 1969 (all outgroup data), Heller & Reinhold 1992, Willemse 1982, own data] of the species of *Hamatopoecilimon* and some representatives from other *Poecilimon* groups.

Species	Pronotum	Hind femur	Ratio hind femur/pronotum	Ovipositor
	m/f	m/f	m/f (from middle of range)	
hamatus	5-6/6-6.5	12.5-15/15-15.5	2.5/2.44	7-8.5
paros	4.7-5.5/5.7-6.2	14.0-14.7/14.7-15.6	2.8/2.55	7-7.5
klausgerhardi	4.6/4.9	12.5/13	2.72/2.65	6.4
deplanatus	5.3-5.8/5.2-6.1	12/13-14	2.16/2.39	7.5-8
ikariensis	4.5-4.9/5.2-5.9	12.1-13/14.5-16	2.67/2.75	7-8
unispinosus	4.3-4.5/4.8-5.4	12.7-13.3/12-14.7	2.95/2.62	8
jonicus superbus	4-5.5/5-5.5	9.6-17/13.5-21	2.8/3.29	8-9.5
ornatus	6.3-8/7.5-10	19-24/19-24	3.01/2.46	13-21
heroicus	8-9/7.2-9	18.5-24/20-25	2.5/2.78	12-15
sanctipauli	7-8/7.5-10.5	20-21/20-28	2.73/2.67	9-12.5
propinquus	4.5-7/5.5-7	13-17.5/15-19.5	2.65/2.76	7-8.5
ampliatus	3.5-5/3.5-6	12-13.5/15-17	3/3.37	8.5-9.5
syriacus	5-6.5/5.2-7	14-15.5/15-17	2.56/2.62	7.2-9.5

of small groups of short syllables (echemes), which are repeated at intervals of about one to several seconds. The number of syllables per echeme differs between species. Except for *P. bilgeri* (see Discussion) such song types have not been found in any other *Poecilimon* species with responding females (see Heller 1984, Heller 2004, Heller & Sevgili 2005, Heller *et al.* 2006, Chobanov & Heller 2010). In all species of the group, syllables are known which are produced by a continuous closing movement of the tegmina ("simple syllables"). Except for the closely related *P. paros* and *P. klausgerhardi*, the other species also produce echemes partly or entirely containing more complex acoustical signals, in addition to echemes consisting of only simple syllables. Here the closing movement shows steps (changes in closing speed) that result in isolated impulses (Figs 4, 6, 8). Often these impulses are followed by similar ones, produced by stridulatory movement cycles with small amplitude. These units might therefore also be called microsyllables. Since there is a continuous transition by partial wing openings (see *e.g.* Fig. 8) and since the exact state can only be determined by simultaneous recording of the tegmen movement, for simplicity we will call all these elements 'complex syllables' (normal syllable together with following impulses).

In frequency composition the songs of all species are quite similar (Table 3) with the maximum of sound energy at about 30 kHz, in the females perhaps slightly higher.

Taxonomic remarks

The other previously described subgenus of *Poecilimon*, *Eupoecilimon* Tarbinsky 1932, seems to refer to a group at the top of the tree (see Ullrich *et al.* 2010). It was redefined and elevated to genus

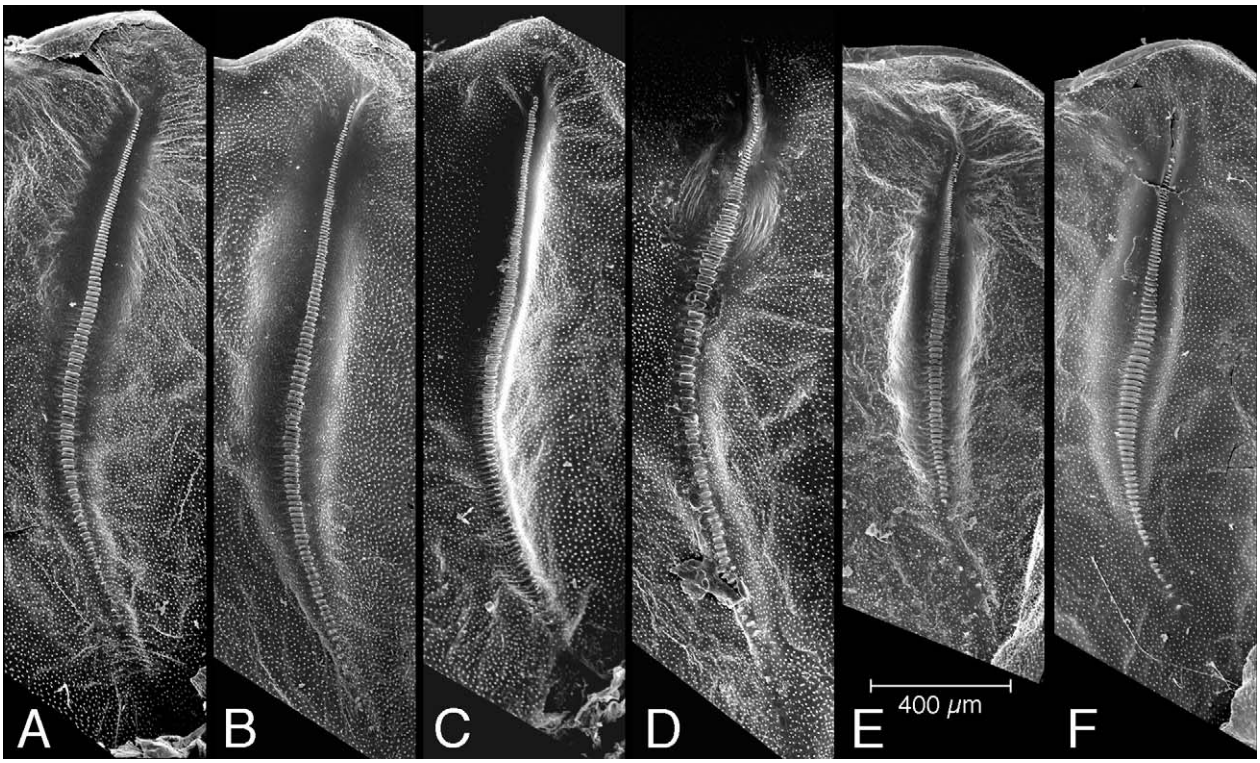


Fig. 3. Male stridulatory file, tegmen articulation at the bottom. A. *P. hamatus*. B. *P. paros*. C. *P. klausgerhardi*. D. *P. deplanatus*. E. *P. ikariensis*. F. *P. unispinosus*.

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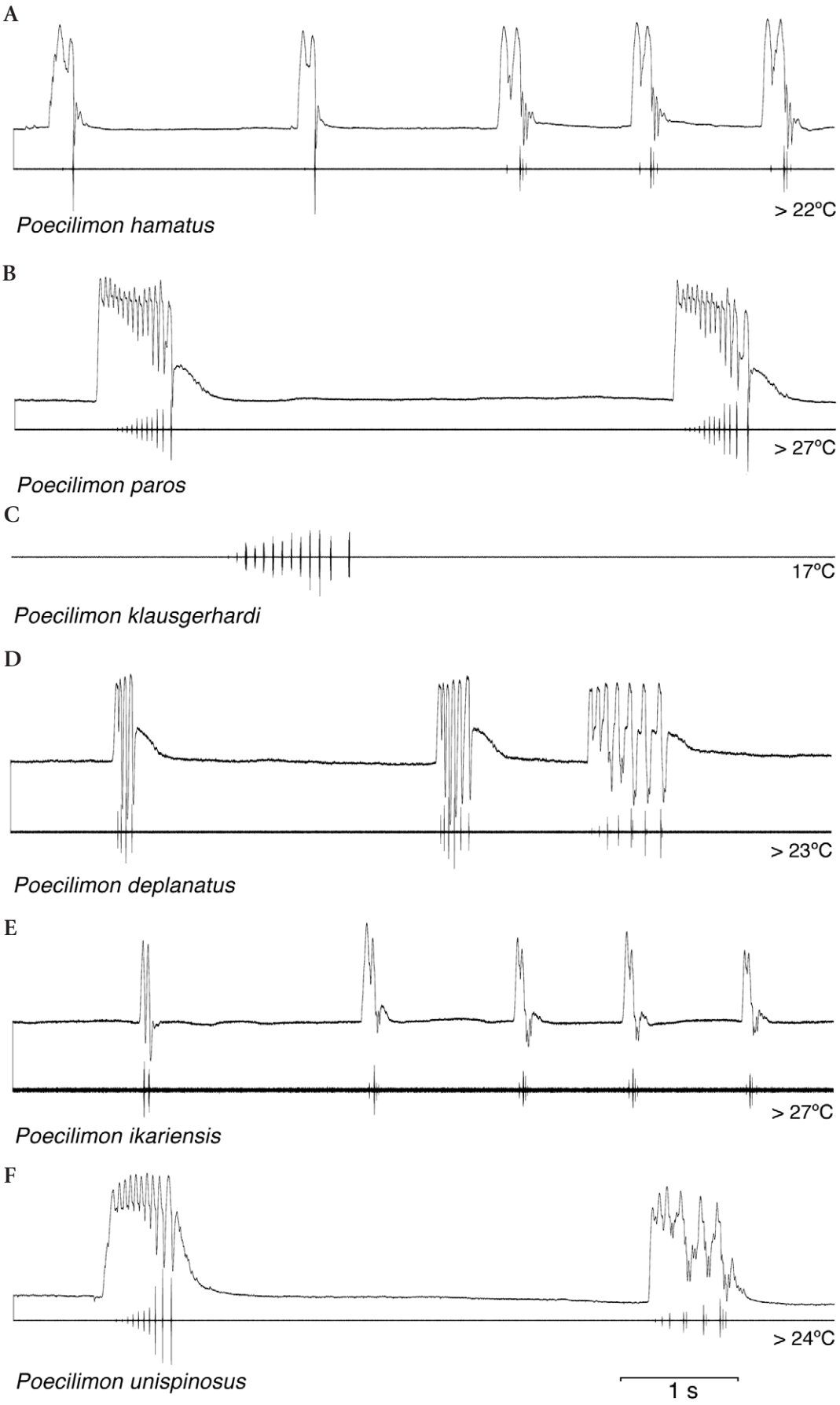


Fig. 4. Overview of calling songs. Oscillograms of stridulatory movements and song [synchronous registration of left tegmen movement (upward deflection represents opening, downward closing) and sound]. A. *P. hamatus*. B. *P. paros*. C. *P. klausgerhardi* (sound only). D. *P. deplanatus*. E. *P. ikariensis*. F. *P. unispinosus*.

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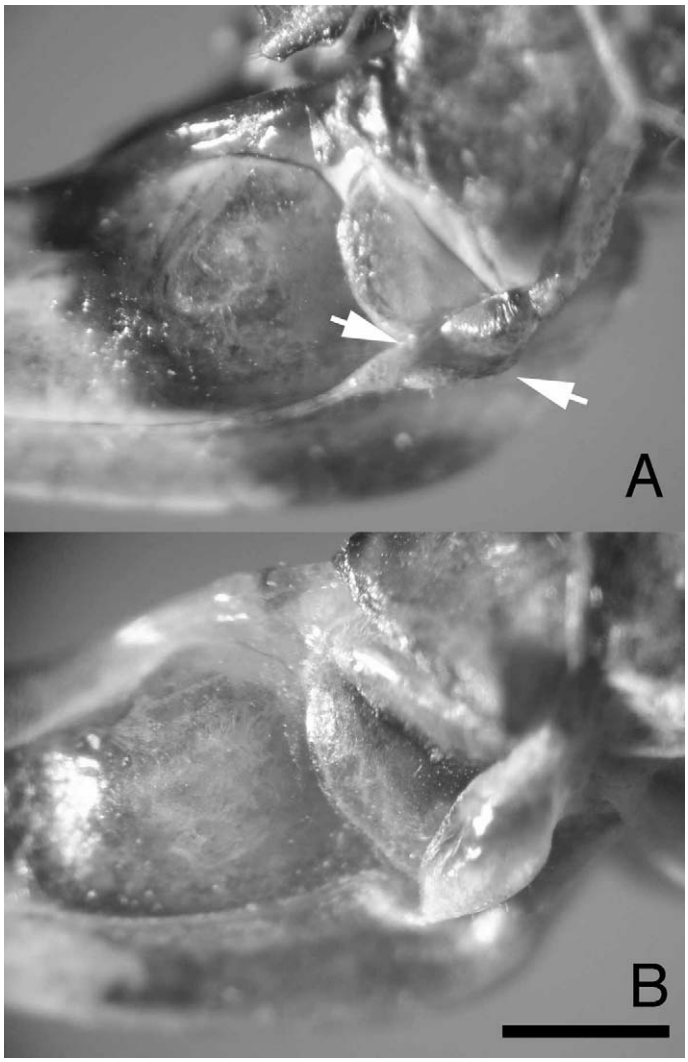


Fig. 5. Lateral view of the basal fold of the dorsal margin of the lower ovipositor valve. A. *P. hamatus*. B. *P. unispinosus*. Scale 1 mm. Arrows indicate the notch in *P. hamatus*.

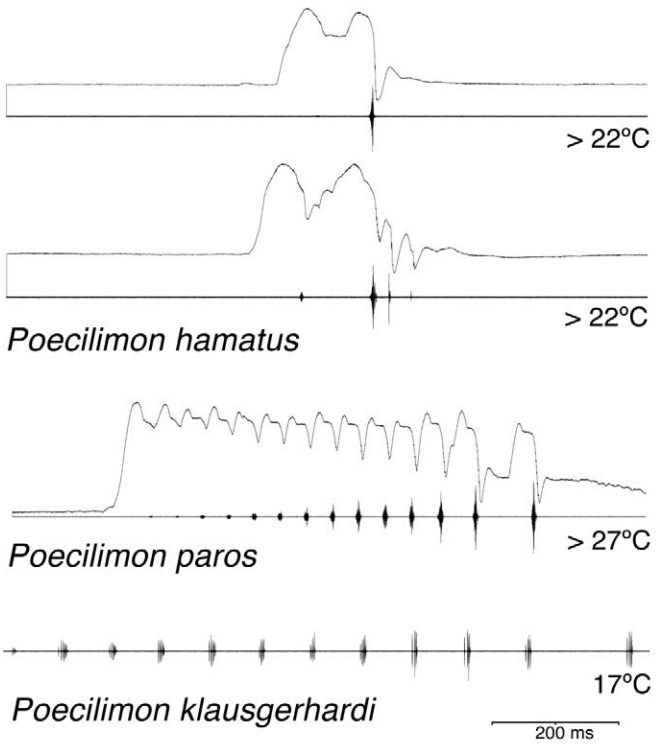


Fig. 6. Expanded oscillograms of stridulatory movements and song [synchronous registration of left tegmen movement (upward deflection represents opening, downward closing) and sound]. Two types of echemes in *P. hamatus*; in *P. paros* and *P. klausgerhardi* (sound only) only one type observed.

rank by Ramme (1951), but considered as a synonym by Bey-Bienko (1954) and most later authors. Other genera later synonymized with *Poecilimon* never included a member of *Hamatopoecilimon* (see also Ünal 2010). According to present knowledge, all other species of *Poecilimon* thus belong to the nominal subgenus *Poecilimon*, with the type species *P. jonicus* (containing as subspecies *P. superbus*, the taxon *Poecilimon* is based on; Fischer 1853).

Identification of species

Males of the six species can easily be identified by the shape of their cerci (Fig. 2), except for *P. hamatus* and *P. paros*. These two species are separated easily only by song. Females are more difficult to discriminate. However, the species are by and large allopatric — only the ranges of the *P. hamatus* and *P. unispinosus* overlap. Females of these two species can be differentiated by the deep notch in the basal fold of the ovipositor of *P. hamatus* (see Fig. 5).

Species account

Poecilimon hamatus Brunner von Wattenwyl, 1878
Syn. *Isophya kattabica* Giglio-Tos, 1914; Heller 1984:75

Type locality.— GREECE, Rhodes & TURKEY, Tireh near Izmir ("Smyrna"), restricted to Rhodes by Karabag (1950) and Ünal (2010).

Depository.— Lectotype male [nr 6493 Brunner von Wattenwyl 1878), NHW, (Ünal 2010, pers. comm.)]. Of the two syntypes mentioned by Brunner von Wattenwyl (1878), only one topotypic male (now lectotype) remained after restriction of the type locality by Karabag (1950). The "co-typic specimens" (Karabag 1950) in London may be topotypes, but not syntypes. The information in SYSTAX about specimens in Berlin as "collected with the types" is obviously not correct, since the species was described in 1878 and the Berlin specimens were collected by v. Oertzen not before 1887.

P. hamatus: Brunner von Wattenwyl 1878: 41 description; Brunner von Wattenwyl 1891: 25 key; Werner 1901: 286 quotation; Jacobson 1905: 330, 356: key, description; Kirby 1906: 376 taxonomic list; Giglio-Tos 1914: 3 faunistics; Werner 1933:190 faunistics; Ramme 1933: 507, 509 (arrangement), 510 (checklist), 538 (description); Werner 1936:11 faunistics; Jannone 1936: 73-76 biology, 144 faunistics; Karabag 1950: 154-5 comparison with *P. cervus*; Bey-Bienko 1954: 317f description; Karabag 1958: 25 faunistic list; Karabag 1964: 45 faunistics; Harz 1969: 140 description; Karabag 1971:77 faunistics; Willemse 1982: 190 description; Willemse 1984: 42 faunistic list; Heller 1984: 75 description; Willemse 1985a: 37 key; Heller & Helversen 1986: bioacoustics; Heller 1988: cover + 59f bioacoustics; Heller 1990: 141 song; Baccetti 1992: 250 faunistics (nymphs); Ciplak 1993: 18 (as *hammatus*): faunistics; Otte 1997: 123 taxonomic list; Naskrecki & Otte 1999: CD-ROM taxonomic list; Önder *et al.* 1999: 246 faunistics; Ciplak *et al.* 1999: 752 fau-

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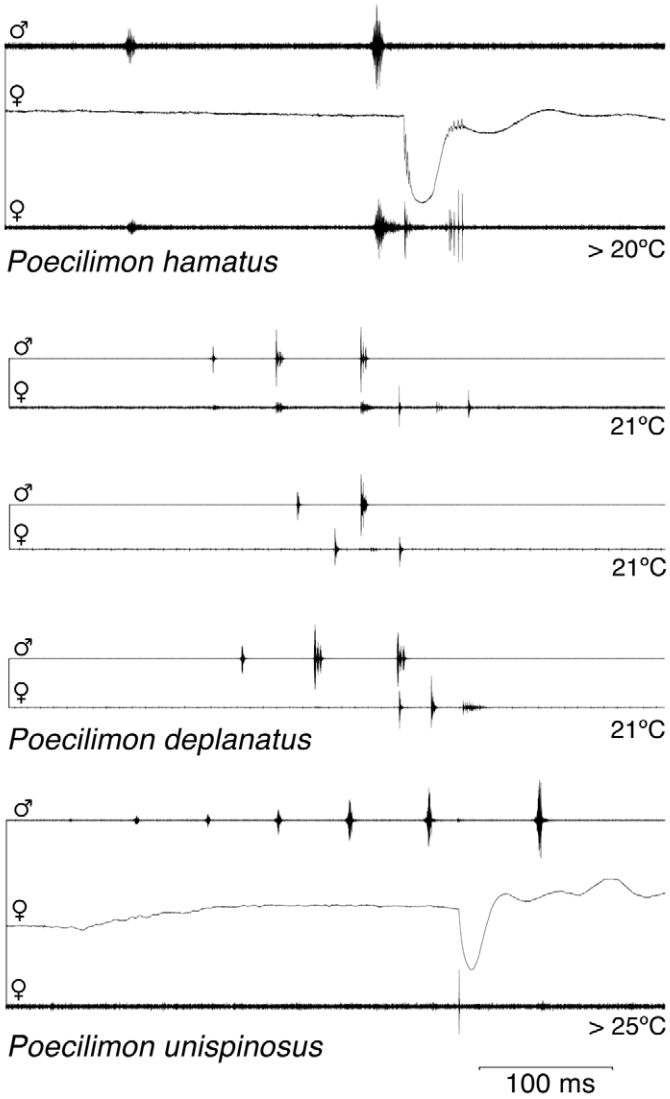


Fig. 7. Oscillograms of female response song [in *P. hamatus* and *P. unispinosus* synchronous registration of left tegmen movement (upward deflection represents opening, downward closing) and sound; middle and lower track] with the simultaneously recorded male song (upper line). In the female sound track often the male sound can also be seen.

nistic list; Ciplak *et al.* 2002: 685 faunistic list; Fontana 2004: 49 faunistics, description; Ünal 2005: 437 faunistics; Heller 2006: 143 song evolution; Willemse & Willemse 2008: 4 faunistic list; Kenyeres *et al.* 2009: 192 biodiversity; McCartney *et al.* 2009: spermatophore size; Ullrich *et al.* 2010: phylogeny, DNA data; Ünal 2010: 141 lectotype designation.

Isophya kattabica: Giglio-Tos 1914: 4 description; Ramme 1951: 137 not member of genus *Isophya*, probably *Poecilimon*; Passerin d'Entreves 1981: types in Turin; Heller 1984: 75 synonym of *P. hamatus*; Willemse 1984: 30 faunistics; Willemse 1985b: 9 synonymy; Heller 1988: 59 synonymy; Otte 1997: 123 taxonomic list; Heller et al. 1998: 29 faunistic list; Naskrecki & Otte 1999: CD-ROM taxonomic list; Willemse & Willemse 2008: 4, 18 synonymy (erroneously *Poecilimon hamatus* / *P. sanctipauli* respectively *Isophya kattabica* / *I. isidori* exchanged)

The note of Werner (1934: 323f faunistics) refers to *P. unispinosus* (Ünal 2010).

Material examined.—GREECE: Southern Sporadhes, N. Dodekanissa, island of Rhodes: 8 MM, 4 FF, 2 km north of Dimilia (36°16'N, 28°0'E), 14 v 2005, coll. K.-G. Heller & M. Heller (SR); 1 F, Eleoussa (36°15'N, 28°0'E), 14 v 2005, coll. K.-G. Heller & M. Volleth; 1 M, above Salakos (36°16'N, 27°56'E), 21 v 2005, coll. K.-G. Heller & M. Volleth; 1 M, Dimilia (36°16'N, 28°0'E), 30 m, 14-15 iv 1983, coll. Heller (SR); 10 MM, 4 FF, Lindos (36°5'N, 28°4'E), 30 m, 18-19 iv 1983, coll. Heller (SR); 1 M, 1 F, Lindos (36°5'N, 28°4'E), 30 m, 20 iv 1987, coll. A. Stumpner; 2 M nymphs, 1 F nymph, Umg. Kattavia (36°0'N, 27°45'E), 5 m, 22 iv 1983, coll. Heller; island of Nisyros: 1 M, coll v. Oertzen (ZMB). N. Samos, island of Samos: 3 MM, 3 km nordöstl. Mytilinioi (37°44'N, 26°54'E), 19 v 1998, coll. Heller & Volleth; 5 MM, 3 FF, Umg. Kallithea (37°44'N, 26°34'E), 21 v 1998, coll. Heller & Volleth (SR); 1 M, 1 F, 3 km südlich Pirgos (37°41'N, 26°47'E), 20 v 1998, coll. Heller & Volleth; 1 F, Rasierstelle (surroundings Pirgos) (37°43'N, 26°46'E), 19-20 v 1998, coll. Heller & Volleth; 1 M, 1 km westl. Kokkarion (37°47'N, 26°52'E), 22 v 1998, coll. Heller & Volleth; 1 M, Umg. Poseidonion (37°43'N, 27°3'E), 19 v 1998, coll. Jay McCartney; 2 MM, 19-20 v 1998, coll. Jay McCartney; TURKEY: **Aydin:** 1 M, Dilek Yarimadasi Milli Parki (ca 20 km wsw Söke) (37°42'N, 27°12'E), 5 m, 11 vi 2000, coll. K.-G. Heller (SR); 1 F nymph, westl. Söke (Dilek Yarimadasi Milli Parki) (37°40'N, 27°5'E), 3 v 1985, coll. Heller; **Mugla:** 1 F, unterhalb Bayir(koy) (ca 17 km sw Marmaris) (36°43'N, 28°8'E), 8 vi 2000, coll. K.-G. Heller; 4 MM, 1 F, oberhalb Bayir(koy) (ca 17 km sw Marmaris) (36°43'N, 28°11'E), 450 m, 8 vi 2000, coll. K.-G. Heller (SR).

Other published localities.—GREECE: Southern Sporadhes, N. Dodekanissa, island of Rhodes: Rhodos (Brunner von Wattenwyl 1878), Mt Attaviro (Werner 1936), Lindos (Jannone 1936, Willemse 1982), Aghios Isidoros (Giglio-Tos 1914, as *I. kattabica*); island of (C)Halki near Rhodes (Baccetti 1992, nymphs); island of Nisyros (Ramme 1933); N. Samos, island of Samos: Marathokampos 1400 m (Werner 1933); Samos (Ramme 1933); TURKEY: **Aydin:** Bölüntü (Karabag 1958), Didim Ziraat Adasi (Ünal 2005), Çine yolu (Ünal 2005), Efes Martyemana (Fontana 2004); Söke (Ünal 2010); **Bursa:** Armutlu Elma köyü Gözsu (Karabag 1964); **Canakkale**: Ezine (Karabag 1964); **Izmir:** "Tireh bei Smyrna" (Brunner von Wattenwyl 1878; Ünal 2010), Gümüldür (Karabag 1971), Menderes (Önder *et al.* 1999), Tire (Önder *et al.* 1999); **Mugla:** Cebiskiri (Karabag 1964), Datca (Önder *et al.* 1999), Marmaris (Ünal 2005). Distribution Fig. 11.

Morphology.— The differences of *P. unispinosus* in color of antennae and shape of fastigium verticis, mentioned by Brunner von Wattenwyl (1878), are not diagnostic. Males of this species can easily be discriminated by the shape of the cerci, females by that of the ovipositor (Fig. 5; see also *P. unispinosus*). For details of the stridulatory file see Fig. 3. and Table 1.

Song.— The male calling song is composed of series of single syllables or disyllabic echemes. The stridulatory movement consisted "as a rule of two opening and closing movements; the first closing movement is extremely variable and often entirely soundless" (Heller & Helversen 1983). The syllable repetition rate in these disyllabic echemes was distinctly lower than in the echemes of all other species of the group (Table 1). Sometimes single opening-closing movement cycles were also registered. In audio recordings it is difficult to decide if and how, regularly disyllabic echemes are produced. Typically single (or several) simple syllables (or disyllabic echemes with a simple second syllable) alternate with series

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of complex syllables (or disyllabic echemes with a complex second syllable: Fig. 4). In the complex syllables the first isolated impulse followed about 30 ms after the beginning of the main part (Fig. 6). At about the same interval (see Fig. 10), after the main part of the male syllable, the female responded. She also produced a single impulse by a rapid closing movement of her tegmina (Fig. 7, female stridulatory organs see Heller & Helversen 1983). Sometimes a series of impulses followed, produced during the wing opening (Fig. 7). The frequency spectrum of the male song had its peak at 32 kHz, that of a female at 33 kHz (see Table 3).

Poecilimon paros Heller & Reinhold, 1992

Type locality.— GREECE, Kiklades, island of Paros, above the village of Lefkes, leg. K. Reinhold.

Depository.— Holotype male, Collectio Heller (CH2333).

P. paros: Willemse 1982: faunistics (as *P. hamatus*); Heller & Reinhold 1992: description; Otte 1997: 125 taxonomic list; Heller *et al.* 1998: 29 faunistic list; Naskrecki & Otte 1999: CD-ROM taxonomic list; Heller 2006: 143 song evolution; Willemse & Willemse 2008: 4, 22 faunistic list, 56 photo; Ullrich *et al.* 2010: phylogeny, DNA data.

Material examined.—GREECE: Kikladhes, N. Kiklades, island of Paros: 8 MM, 6 FF, oberh. Lefkes (37°3'N, 25°11'E), 550 m, 17 v 1991, leg. K. Reinhold. (SR).

Other published localities.—GREECE: Kiklades, Island of Naxos: Sifones (abandoned village near the village of Moni), Moutsouna (Heller & Reinhold 1992); Island of Ios (Willemse & Willemse 2008: 56). Distribution Fig. 11.

Morphology.— In the female the tegmina are clearly visible (part not covered by pronotum, about 1 mm; Heller & Reinhold 1992), while in the other species they are often completely concealed. For details of stridulatory file see Fig. 3. and Table 1.

Song.—The male calling song consists of polysyllabic echemes, which are repeated at intervals of several seconds. Each echeme contained 9.3 syllables (mean of 8 recording sessions of 4 males; 26-32°C) produced with a rate of 17 to 22 Hz respectively (Table 1, calculated for 25°C, range observed 23-28 Hz). Only the last syllable is separated from the others by a distinctly larger interval corresponding to a rate of 10-14 Hz. The number of movement cycles differed between both individual males and circumstances (range 6-15) (see Heller & Reinhold 1992). The number of syllables was always slightly lower, since during the first movements no sound could be detected. Up to now only songs consisting of simple syllables with 7-10 impulses each were observed.

In a quantitative one-day observation of the acoustic behavior, *P. paros* was found to be active mainly in the late afternoon and more weakly, at night (Fig. 8), differing clearly from the other *Poecilimon* species studied with the same method (Heller & Helversen 1993). The male produced 5000 echemes during 24 h, most often at intervals of 3 to 5 s (minimum temperature at night 14°C, maximum 29°C during the day).

The frequency spectrum of the song had its peak at 26.5 kHz (see Table. 3).

Poecilimon klausgerhardi Fontana, 2004

Type locality.— GREECE, Kyklades, island of Andros. Apikia, 30 v 1973.

Depository.— Holotype male, Collectio Fontana.

P. klausgerhardi: Fontana 2004: description; Willemse & Willemse 2008: 4, 21 faunistics; Ünal 2010: 141 faunistics.

Material examined.— GREECE: Kikladhes, N. Kiklades, Island of Andros: 1 M, 1 F, 1 km S Andros (Ormos turnoff) (37°46'N, 24°53'E), 350 m, 16 v 2004, coll. L. Willemse; 1 M, 1 F, hills SE of Ormos (37°45'N, 24°58'E), 150-250 m, 18 v 2004, coll. L. Willemse (+3 M, same data, in Collectio Willemse, from one of these sound records).

Other published localities.— Greece, Kikladhes: Island of Andros, Apikia (Fontana 2004; Ünal 2010); Exo Vouni, at Stavros turnoff; Livadhia at Vrakhnos turnoff; 3.5km S of Palaiopoli: Island of Tinos: Aetofolia-Koris Pirgos Mt.Tsiknias; Moni Katopolianis; Tinos-Pirgos above Kardiani; Tinos-Steni, 0.5 km S of Kedhros; 1 km W of Mamadhos (Willemse & Willemse 2008). Distribution Fig. 11.

The male calling song (Figs 4, 6) is quite similar to that of *P. paros*. In the single recorded male the number of syllables per echeme (x=12.2; range 10-14; n=18) was slightly higher than in most *P. paros*, but within the range of that species. The syllables contained 4-8 impulses and had a duration of 8.3±1.7 ms (n=103; 17°C).

For details of the stridulatory file see Fig. 3 and Table 1.

Poecilimon deplanatus Brunner von Wattenwyl, 1891

Type locality.— GREECE: Sporades: island of Kos (leg. von Oertzen).

Depository.— Holotype male, NMW.

P. deplanatus: Brunner von Wattenwyl 1891: 27 description; Jacobson 1905: 330, 356: key, description; Kirby 1906: 376 taxonomic list; Ramme 1933: 507, 509 (arrangement), 510 (checklist), 538 (description); Werner 1936: 11 faunistics; Harz 1969: 144f description; Willemse 1982: 188 faunistics; Willemse 1984: 41 faunistic list; Willemse 1985a: 43 key; Otte 1997: 122 taxonomic list; Heller

Table 3. Frequency characteristics of male and female song (single measurements or means).

	Males			Females		
Species	Peak [kHz]	Bandwidth 10 dB below peak [kHz]	n	Peak [kHz]	Bandwidth 10 dB below peak [kHz]	n
hamatus	32.3	22.7-37.7	3	33	30-45	1
paros	26.5	22.0-35.0	4			
klausgerhardi	25	20-29	1			
deplanatus	33	29-40	1			
ikariensis	28	25-37	1			
unispinosus	33.6	27.6-41.4	7	36.0	30.3-45.0	3

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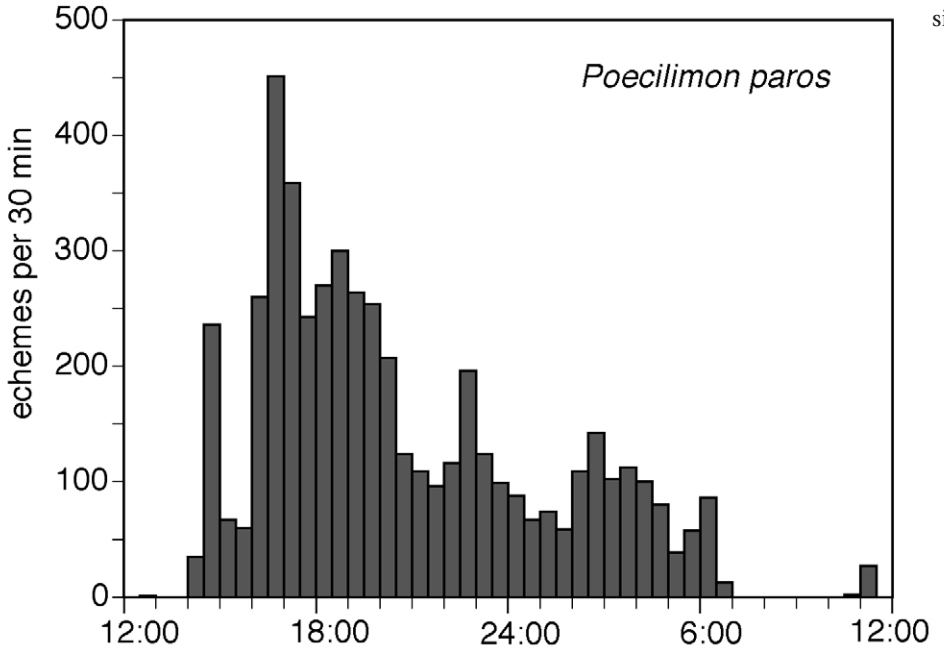


Fig. 8. Circadian activity pattern of *P. paros*' singing.

et al. 1998: 28 faunistic list; Naskrecki & Otte 1999: CD-ROM taxonomic list; Warchalowska-Sliwa *et al.* 2000: chromosomes (locality erroneously exchanged with *P. ikariensis*); Sfenthourakis & Legakis 2001: 1414 biodiversity; Willemse & Willemse 2008: 4, 20 faunistic list; McCartney *et al.* 2009: spermatophore size; Ullrich *et al.* 2010: phylogeny, DNA data.

Material examined.— GREECE: Southern Sporadhes: N. Dodekanissa: island of Kos: holotype (NMW); island of Kasos: 1 M, 1 F, coll. v. Oertzen (ZMB); island of Karpathos: 3 FF 1-30 iv 1983, coll. H. Pieper; 6 MM, 6 FF, Lefkos (35°35′N, 27°4′E), 15-20 v 2005, coll. K.-G. Heller, M. Heller, M. Volleth (SR); 1 M, 3 km west of Spoa (35°38′N, 27°7′E), 15 v 2005, coll. M. Heller, M. Volleth (SR);1 F, Agnontia (35°39′N, 27°10′E), 5 m, 17 v 2005, coll. K.-G. Heller; 4 MM, 3 FF, Mt. Lastos, 100 m below summit (35°34′N, 27°9′E), 900 m, 19 v 2005, coll. K.-G. & M. Heller, M. Volleth, E. Wolter (SR); 1 M, Bachtal südwestl. Diafani (35°46′N, 27°12′E), 19 v 1998, coll. H. Klugkist (SR).

Published localities.—GREECE: Southern Sporadhes: N. Dodekanissa, island of Kos (Brunner von Wattenwyl 1891, Ramme 1933), island of Karpathos (Ramme 1933, Werner 1936), island of Kasos (Ramme 1933). Distribution Fig. 11.

The distribution of this species is a little bit puzzling. The type locality, the island of Kos, is relatively far from all other records (see Fig. 11) and situated in a region where *P. hamatus* has to be expected. Besides the male holotype (NMW) and two females (ZMB, in ethanol) from Kos, there exists also a male and a female of this species (ZMB) from Kasos, an island close to Karpathos. All five animals were captured by the coleopterologist and famous collector of reptiles, insects and other animals, Eberhard von Oertzen, on a single excursion in 1887. The females from Kos and the specimens from Kasos are not mentioned in the description of the species by Brunner von Wattenwyl (1891), although the females from Kos bear labels "*Co*-Type" and hand-written labels "*Poecilemon deplanatus*, Brunner determ." (obviously written after Kirby's catalogue (1906) with the wrongly spelt genus name). Since Kos is far from Karpathos (and Kasos), where the species is quite common, a confirmation from that island would be highly welcome. At present an error in labelling of the animals of Kos (erroneously Kos instead of Kasos or Karpathos) cannot be excluded. Unfortunately the itinerary of von Oertzen (1888) does not help much. He must have collected the specimens in Kasos on 10-11th May 1887, stayed on Karpathos between 12th and 17th May and reached Kos not before 12th of June. However, although relatively late in season for *Poecilimon*, he collected *P. hamatus* (see above and *P. sanctipauli*, Heller & Sevgili 2005) on Nisyros only 2 days before his arrival in Kos.

Song.— The male calling song (Figs 4, 9) contains two different types of echemes. The short echemes had 2-6 syllables, which followed each other quite rapidly (22 to 24 Hz respectively (Table 1, calculated for 25°C, range 16-22 Hz at 20-30°C), within the echeme often slightly decreasing, *e.g.*, 27 Hz, 19.6 Hz, 15.5 Hz at 23°C), while in the long echemes the number of syllables was higher (5-11) and the syllable repetition rate much slower (range 6-8 Hz at 20-30°C). Both echeme types were observed in regular alternation as well as in nearly pure sequences. In the short echemes the stridulatory movement was simple (Fig. 4) and the syllables contained few (1-4) impulses. The slow rhythm in the long echemes was effected by short periods without wing movement between the syllables. The syllables also had a more complicated structure similar to that observed in the fast rhythm of *P. ikariensis*. After the end of the first impulse train one or several isolated impulses (or impulse groups) were produced, resulting in a total impulse number of up to 11. From the registration of the tegmen movement it is obvious that these elements were mostly produced during the final closing movement and are part of the syllable.

The female response (2 females recorded) typically occurred shortly after the syllables of a short echeme, mostly about 20-30 ms after the third (or rarely after the first or second) syllable of the male echeme. Often a second impulse was produced by the female about 50 ms later (Fig. 7). Sometimes also the first fast impulse seems to be missing. If a female was reacting to the second syllable, her response occurred in such a situation nearly synchronous with the third male syllable (see Figs 7 and 9). In addition to the two loud impulses, series of soft impulses were also observed, probably

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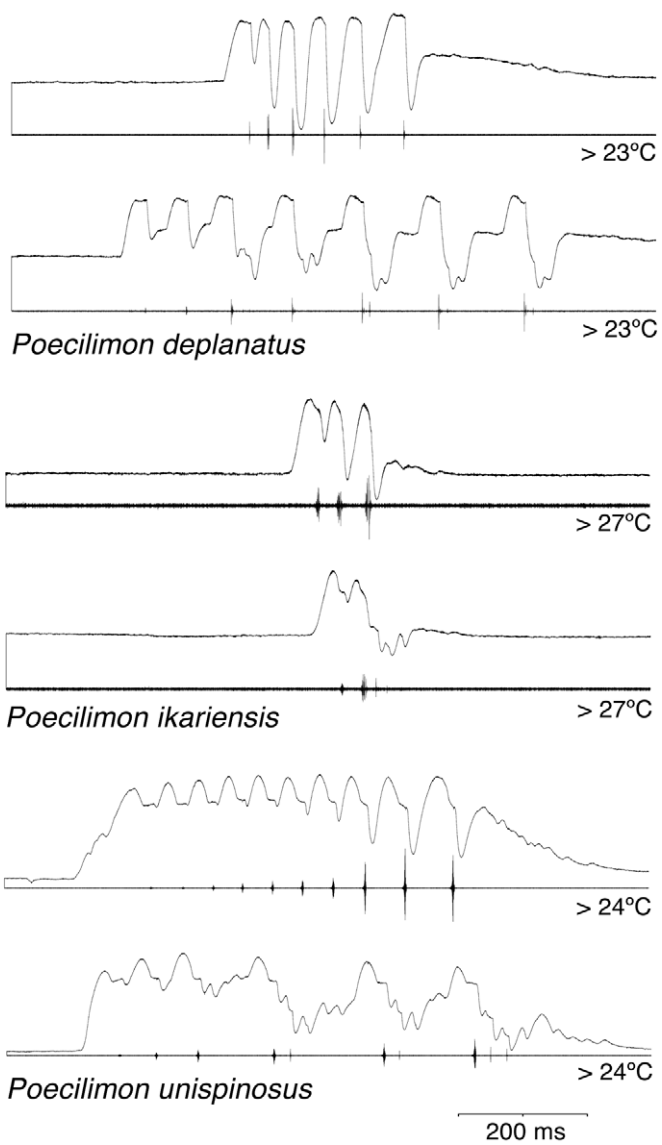


Fig. 9. Expanded oscillograms of stridulatory movements and song [synchronous registration of left tegmen movement (upward deflection represents opening, downward closing) and sound]. All three species show two different types of echemes.

similarly produced as in *P. hamatus* (Fig. 7). The male usually did not add more syllables to an echeme after having heard a female response.

For details of the stridulatory file see Fig. 3 and Table 1.

Poecilimon ikariensis Willemse, 1982

Type locality.—GREECE, Ikaria, pass between Aghios Kirykos and Karavostamon, 20 vi 1997, coll. M. C. & G. Kruseman.

Depository.— Holotype male, ITZ

P. ikariensis: Werner1934: 323f faunistics (as *P. hamatus*); Willemse 1982: 171f description; Willemse 1984: 38 faunistic list; Willemse 1985a: 43 key; Willemse 1985b: 19 faunistics; Otte 1997: 123 taxonomic list; Heller *et al.* 1998: 29 faunistic list; Naskrecki & Otte 1999: CD-ROM taxonomic list; Warchalowska-Sliwa *et al.* 2000: chromosomes (locality erroneously exchanged with *P. deplanatus*); Sfenthourakis & Legakis 2001: 1414 biodiversity; Willemse & Willemse 2008: 4, 21 faunistic list; Kenyeres et al. 2009: 192 biodiversity; McCartney *et al.* 2009: spermatophore size; Ullrich *et al.* 2010: phylogeny, DNA data.

Material examined.— GREECE: Southern Sporadhes: N. Samos: Island of Ikaria: 10 MM, 3 FF, 3 km nordwestl. Ag. Kyrikos (37°37′N, 26°16′E), 22 v 1998, coll. Heller & Volleth (SR); 2 MM, 1 F, 2 km nordnordwestl. Perdiki (37°40′N, 26°17′E), 23 v 1998, coll. Heller & Volleth (SR); 1 M, Perdiki (37°39′N, 26°17′E), 23 v 1998, coll. Heller & Volleth.

Other published localities.— GREECE, island of Ikaria: type locality (Willemse 1982) Khrisostomos (Willemse 1985b). Distribution Fig. 11.

Song.— The song consists of short echemes, which are presented alternating in slow and fast rhythm. In both phases an echeme contained mostly two main syllables. In the slow rhythm (intervals between echemes a few seconds) both (rarely three) syllables were similar in structure (simple syllables: duration 9.8 ms, 20.5 impulses; n=1/6; 27°C) and the syllable repetition rate slightly, but significantly, higher than in the other species (Table 1). In the fast rhythm (intervals between echemes one second or less; duration of phase with fast rhythm often 15-25 s, up to 46 s recorded) the structure was more complicated. The first syllable was softer than the second and sometimes missing completely, but it was always visible in the recordings of the stridulatory movements. In structure it was often similar to the louder second syllable. Here, after the end of the main impulse train, one or more (up to four) isolated impulses (or impulse groups) were produced. These groups were quite loud in some animals — in one specimen the main impulse trains were nearly completely missing and only these impulse groups were produced. They followed the main impulse train (Fig. 7) and also each other in periods of around 30 ms (as in *P. unispinosus*; Figs 7, 9), comparable to the expected female response time. From the registration of the tegmen movement it can be recognized that some of these elements were produced during the final closing movement, some by small separate movements.

For details of carrier frequency and stridulatory file see Fig. 3 and Table 1.

Poecilimon unispinosus Brunner von Wattenwyl, 1878

Type locality.— TURKEY: Magnesia (Manisa) near Smyrna (Izmir) (formerly another syntype from Bozdagh).

Depository.— Lectotype, male (Ünal 2010).

P. unispinosus: Brunner von Wattenwyl 1878: 42 description; Jacobson 1905: 330, 356: key, description; Kirby 1906: 376 taxonomic list; Ramme 1933: 507, 509 (arrangement), 510 (checklist), 537-8 (description); Werner 1934: 323f faunistics; (as *hamatus*); Bey-Bienko 1954: 136 description; Karabag 1958: 86 faunistic list; Ciplak 1993: 19 faunistic list; Otte 1997: 127 taxonomic list; Naskrecki & Otte 1999: CD-ROM taxonomic list; Heller *et al.* 1998: 30 faunistic list; Ciplak *et al.* 1999: 753 faunistic list; Warchalowska-Sliwa *et al.* 2000: chromosomes; Ciplak *et al.* 2002: 686 faunistic list; Willemse & Willemse 2008: 4, 23 faunistics; McCartney *et al.* 2009: spermatophore size; Ullrich *et al.* 2010: phylogeny, DNA data; Ünal 2010: 140 lectotype designation.

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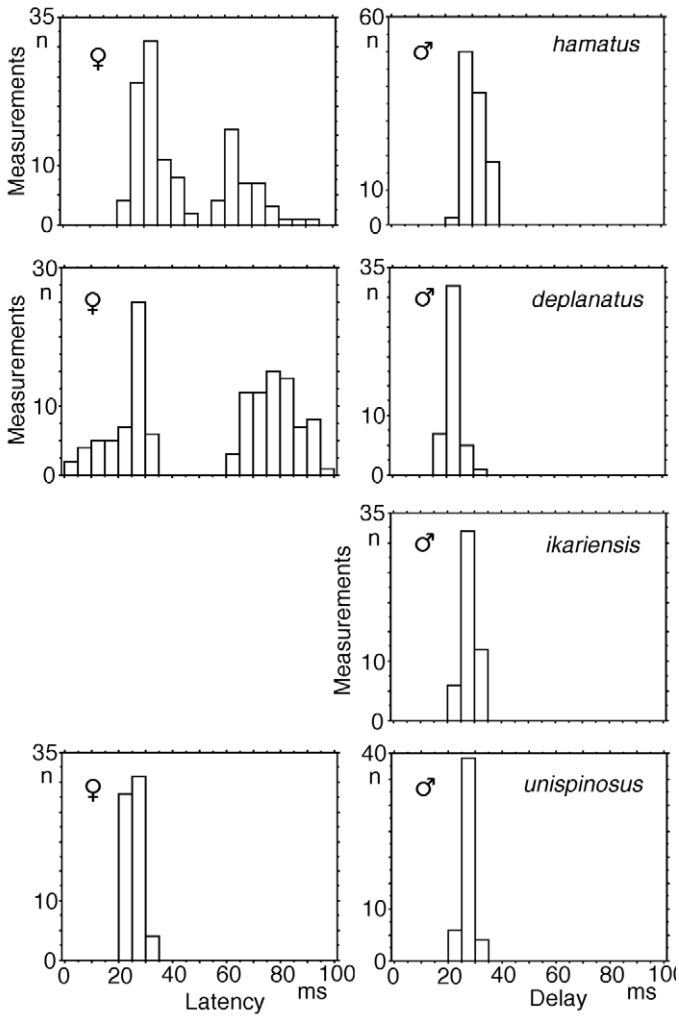


Fig. 10. Female imitation in male song. Comparison of the latency of female response (histograms on the left, measured from beginning of male trigger syllable to beginning of response) and time period to first isolated impulse in complex syllable of male song (histograms on the right, measured from beginning of male syllable to beginning of impulse).

Material examined.—GREECE: Northeastern Aegaean Islands: N. Hios: Island of Chios: 3 MM, 2 FF, 2 km westlich Kourounia (38°34′N, 25°53′E), 21 v 1995, coll. K.-G. Heller (SR); 8 MM, 5 FF, Sidirounta südlich Volissos (38°26′N, 25°58′E), 20 v 1995, coll. K.-G. Heller (SR); 2 FF, 2 km westlich Mesta (38°16′N, 25°54′E), 24 v 1995, coll. K.-G. Heller; 1 F, Vavili sw Chios-Stadt: Panagia Krina (38°18′N, 26°5′E), 23 v 1995, coll. K.-G. Heller (SR); 1 M, 6 FF, Potamia (Archaia) n Volissos (38°31′N, 25°55′E), 21 v 1995, coll. K.-G. Heller (SR); (specimens from Chios partly collected as subadult nymphs, moult in captivity).
TURKEY: **Manisa:** 1 F, Sipil Dagh Milli Parki (ca 3 km südl. Manisa) (38°34′N, 27°26′E), 600 m, 13 vi 2000, coll. K.-.G. Heller; **Izmir:** 2 FF, Zeytinlik, 38 km southeast of Turgutlu (38°16′59″N, 28°0′44″E), 3 vi 2005, coll. Klaus Reinhold.

Other published localities.—GREECE: N. Lesbos, island of Lesbos: Mytilini, Lebetymnos Mts (1 female; Werner 1934 as *hamatus*; determination *fide* Ünal 2010); TURKEY: **Izmir:** Boz-dagh Brunner von Wattenwyl 1878, Sevdiköy (=Seydiköy) Ramme 1933; Manisa: Magnesia (=Manisa) Brunner von Wattenwyl 1878; Distribution Fig. 11.

Morphology.— Judging from its distribution, the species may occur together with *P. hamatus*. Females can be identified by the shape of the upper basal lobe of the ovipositor, which is inflated and has no notch as in *P. hamatus* (Fig. 5).

Song.—The male calling song contains two different types of echemes (Figs 4, 8). One type has only simple syllables, which follow each other quite rapidly (21 to 22 Hz respectively (Table 1; calculated for 25°C), range 19-24 Hz at 22-25°C). The two last syllables were produced at a lower rate, the second-last at about 11-16 Hz, the last at 7-12 Hz. The number of syllables was relatively high, typically between 7 and 9 (range 6-11). The syllables were comprised of16.6 impulses (range 10-26; n=39) and had a duration of 10.3 ms (range 6-18; n=54). In the other echeme type the syllable rate at the beginning was similar, but dropped rapidly as the syllable type changed from simple to complex. The complex syllables were typically bi- or even tripartite, the main impulse train followed by one or two impulses (or short-impulse groups). As in *P. deplanatus*, here the syllables were separated by silent intervals. From the registration of the tegmen movement it can be recognized that some impulses were produced during the final closing movement, some by small separate movements. Such small movements occurred also between the syllables, but were mostly soundless (Fig. 9).

The females typically responded with a single impulse, produced by a rapid closing movement of the tegmina (delay to beginning of previous male syllable about 30 ms, Figs 7, 9). Their answer occurred after some syllables of an echeme consisting of simple syllables and the males stopped after having produced one more syllable.

For details of carrier frequency and stridulatory file see Fig. 3 and Tables 1 and 3.

Discussion

Phylogeny and biogeography.—At first glance the occurrence of a basal group of the widespread genus *Poecilimon* on some small islands in the Aegean Sea does not seem very plausible. However, another large bush-cricket genus with a supposed similar history, the genus *Eupholidoptera*, shows some striking resemblances.

Both genera have their origins probably on the Aegeid plate, as can be concluded from the present distribution of their species (see Figs 8, 9 in Ciplak 2004). *Eupholidoptera* seems to have evolved in the southern part of this plate in or near an area which now forms the island of Crete (Ciplak *et al.* 2010). The most basal species and species groups of *Eupholidoptera* are found in Crete. *Poecilimon* may have evolved in an area a little bit more northern than that of *Eupholidoptera* and did not reach Crete before it became an island for the first time, 10 million years before the present (Ciplak *et al.* 2010).

During the appearance of the Aegean Sea by the formation of the Mid-Aegean Trench (which started 12 Mya and was completed 9 Mya, see Allegrucci *et al.* 2009) some islands (and/or the Eastern border of the trench) in this postulated area of origin may have remained. Here an ancestral line of *Poecilimon* survived and could colonize the areas becoming available during the Messinian salinity crisis when the sea level dropped (about 5 Mya). Today only the Kiklades, Karpathos and the East Aegean islands are still available and inhabited by *Hamatopoecilimon*. Surprisingly, the ancestor of the group did not reach Crete nor the Greek mainland at the time of low sea level as it has been postulated for cave crickets of the genus *Dolichopoda* (Allegrucci *et al.* 2009), which may have had a similar distribution. In this respect the Aegean/Anatolian *Eupholidoptera prasina* group (and partly *E. smyrnensis)* and some other groups

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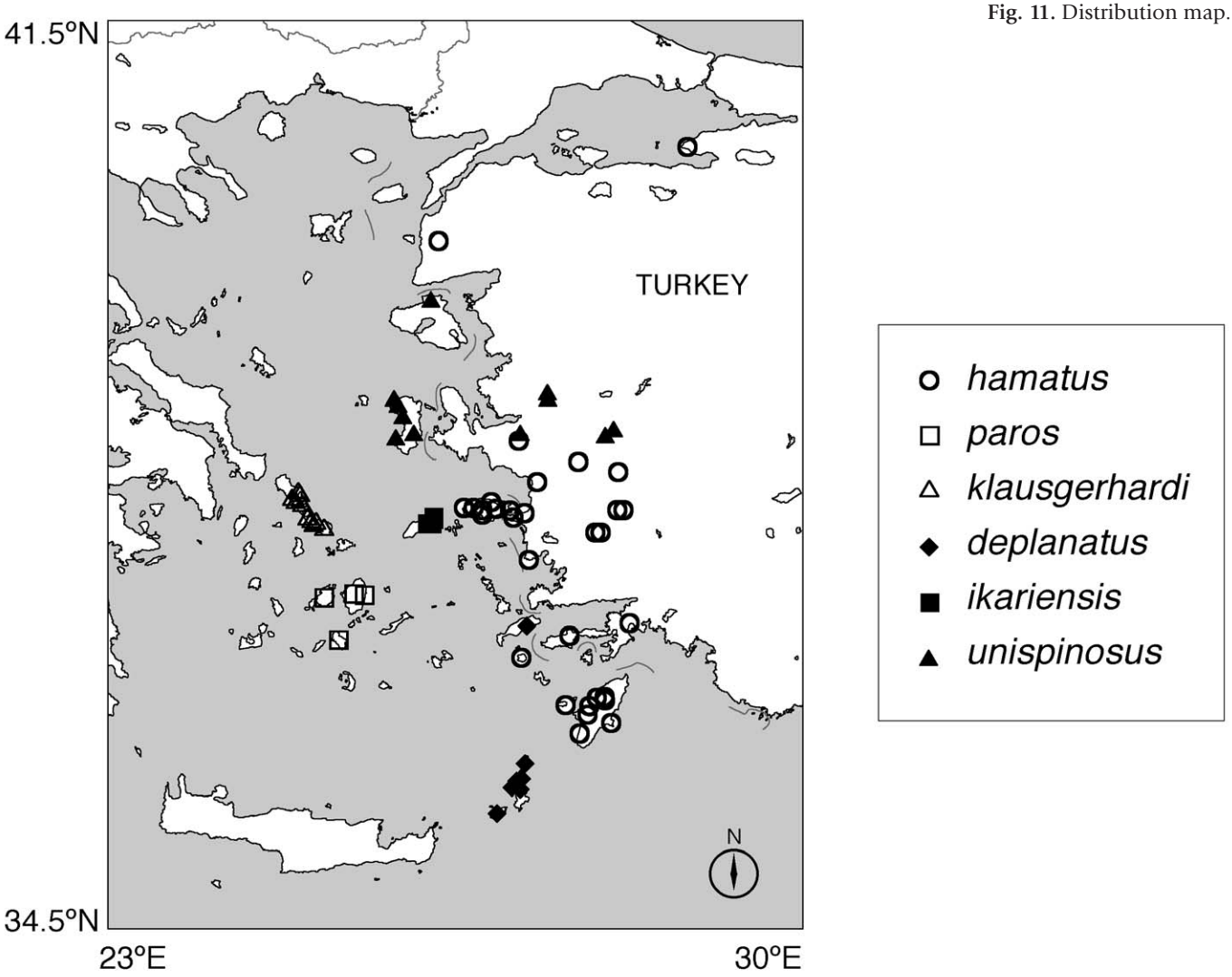


Fig. 11. Distribution map.

of animals and plants show the same pattern as *Hamatopoecilimon* (see Ciplak *et al.* 2010). The single *Poecilimon* species in Crete (*P. cretensis*) may have reached the island from the East, from Southern Anatolia (see data in Heller 2004, Ulrich *et al.* 2010) possibly during the same period (Messinian salinity crisis).

At present the distribution of the ancestral population of *Hamatopoecilimon* cannot be located more exactly. The relationship between all of its members is not fully resolved. There is a well-supported southern group containing *P. hamatus*, *P. paros* and *P. klausgerhardi*, which share the strongly bifid cerci. *P. hamatus* and *P. paros* are also sister species in the mt-DNA tree (Ullrich *et al.* 2010; *P. klausgerhardi* not studied), while *P. paros* and *P. klausgerhardi* are the only species which do not differ in song. The islands, where the latter two occur, became disconnected only 20,000 years ago (Perissoratis & Conispoliatis 2003). Future molecular studies may give hints, if both species separated just at that time. *P. deplanatus* may also belong to the southern group (Ullrich *et al.* 2010), while the two northern species *P. ikariensis* and *P. unispinosus* — closely related to each other according to both nuclear and mitochondrial DNA data — have split off earlier. *P. hamatus* and *P. unispinosus* are the only species which are found on islands as well as on the Anatolian mainland. The distribution of *P. hamatus* has similarities to that of *P. sanctipauli* (Heller & Sevgili 2005) and *Eupholidoptera smyrnensis* (Ciplak *et al.* 2009). All three occur on the island of Rhodes and the Anatolian mainland and have also been found (by v. Oertzen on 10-11 June 1887) on the volcanic island of Nisyros.

However, despite the similarities it is difficult to draw any firm conclusions. Nisyros has probably never been connected with the mainland, while Rhodes, which is separated from the mainland by relatively deep water, has had terrestrial connections, but not during the last glaciation (see Perissoratis & Conispoliatis 2003). *P. sanctipauli* has a distribution similar to *P. hamatus*, but it extends in the North only up to the region of Izmir, while *E. smyrnensis* is spread up to Makedonia on the European mainland. Like *P. hamatus*, *E. smyrnensis* has not been found on the island of Chios, where *P. unispinosus* occurs together with *Eupholidoptera prasina* (Ciplak *et al.* 2009). *P. deplanatus* lives on Karpathos, together with a third *Eupholidoptera* species, *E. uvarovi*, which is not closely related to either of the other two according to morphology (Ciplak *et al.* 2010).

Song evolution and sexual selection.—Many of the *Poecilimon* species which use the typical phaneropterid communication system (the male calls, the female responds acoustically) produce a calling song consisting of isolated syllables (*e.g.*, Heller 1984). Often these syllables are modulated in their amplitude by variation of the impulse rate or by different intensity of the impulses (*e.g.*, Chobanov & Heller 2010). There are, however, also *Poecilimon* species which produce quite short isolated syllables, which are in duration comparable to

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Hamatopoecilimon. Some of these species also use simple, as well as complex, syllables as described above. Representatives with this song type are mainly found in the *P. inflatus* group and in species near *P. jonicus* (Heller 2004). According to Ullrich *et al.* (2010) they all belong to one group, not closely related to *Hamatopoecilimon*, but with some species occurring in Southwest Anatolia nearly touching the range of *P. hamatus*. In addition there is one species, *P. bilgeri*, which is even more similar in song to *Hamatopoecilimon* than the above-mentioned forms. From the song it was considered to be related to *P. inflatus* (Heller 2004). Its DNA sequence data are ambiguous (Ullrich *et al.* 2010), but in any case neither near *P. hamatus* nor *P. jonicus*. This species is also found in Southwest Anatolia.

Under the assumption that the DNA tree is correct, the occurrence of such a song pattern or at least of short syllables in three different groups could be an indication that it might be ancestral for the whole genus.

All species of *Hamatopoecilimon* produce echemes. They can be very short containing two syllables only, as in *P. hamatus* or *P. ikariensis*, or consist of longer syllable groups (up to 14 elements). Both extremes are found in the northern and the southern groups, so that independent reductions or amplifications in syllable number must be assumed. Reasons for such song changes may be found either on an inter- or an intraspecific level. Species recognition by song seems to make no sense in allopatric insular species, but it cannot be completely excluded. In Anatolia the ranges of *P. unispinosus* and *P. hamatus* overlap and both species differ strongly in syllable number per echeme. The other species with short echemes, *P. ikariensis*, is at present restricted to the island of Ikaria, but theoretically may have been in contact with *P. unispinosus* only 20,000 years ago (see Perissoratis & Conispoliatis 2003). Even *P. deplanatus* may have had contact with *P. hamatus* if it occurs on Kos (but see species account).

On the other side, sexual selection seems to have strong influence on song structure in any case. The temporal structure of a complex syllable exactly mimics a male-female duet (see Fig. 10). These presumed duet imitations are known from many phaneropterid species (*e.g.*, Zhantiev & Korsunovskaya 1986, Heller 1990, Stumpner & Meyer 2001, Bailey *et al.* 2006), but they mostly or preferentially occur during male-female interactions. In *Hamatopoecilimon* they are produced seemingly indiscriminately by isolated males as well as in duets. There are several possibilities to explain such behaviour (see *e.g.*, Stumpner & Meyer 2001, Bailey *et al.* 2006), but for confirmation they all require specifically designed experiments. In any case, the males of the two species with two types of polysyllabic echemes produce long series of such imitations, whereas the female typically responds only once and the male stops its syllable series after having heard a response. During a long interaction, a female of *P. unispinosus* responded to the male song regularly but stopped as soon as the male produced complex syllables, and responded again to simple syllables. The complex signals may be directed to females, *e.g.*, with the meaning to attract a female more quickly by imitating another responding female competing for the nutritious spermatophore (McCarthey *et al.* 2009). They may be also or additionally directed against other males, *e.g.*, by making the localization of a responding female more difficult for eavesdropping males. At present we cannot decide between these hypotheses concerning the evolutionary context of the complicated sound signals, as their function remains unexplored.

Sexual selection may not only shape the song pattern, but also morphological structures which can give information about the quality of the mating partners. In tettigoniids, the most important morphological character in this respect, the cerci, typically evolve even faster than songs (Heller 2006, Ciplak *et al.* 2009). However, *P. paros* and *P. hamatus* were cited (*loc. cit.*) as one of the few examples with an opposite tendency. Looking on all species of the subgenus it becomes obvious that here both structures evolved quite fast. *P. paros* and *P. klausgerhardi* differ only in morphology, possibly as the result of a very fast change (see above). The remaining three species differ in song as well as in genital morphology. Thus the subgenus represents a group of species quite suitable for a comparison of the speed in ethological and morphological evolution and the build-up of reproductive isolation.

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