A review of *Chorthippus* species with angled pronotal lateral keels from Greece with special reference to transitional populations between some Peloponnesean taxa (Orthoptera, Acrididae)

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This paper presents a summary of the current knowledge on the systematics of the Greek taxa of *Chorthippus*, morphologically characterised by angled lateral pronotal keels (usually grouped as *Glyptobothrus*). Prior to this paper, based on traditional morphology, ten taxa of *Chorthippus* with angled lateral pronotal keels were recognized from Greece. Based on morphology as well as (and more importantly so) bioacoustics thirteen Greek taxa are now recognised. With addition of a few additional related taxa that occur only outside Greece, all are treated in this paper: *Chorthippus apricarius apricarius* (Linnaeus, 1758), *C. vagans vagans* (Eversmann, 1848) (not in Greece), *C. v. cypriotus* (Uvarov, 1936) stat. nov. [Cyprus], *C. v. africanus* Nadig, 1981 [N. Africa], *C. v. dissimilis* subspec. nov., *C. willemsei* Harz, 1971, *C. biroi* (Kuthy, 1907), *C. sangiorgii* (Finot, 1902), *C. bornhalmi* Harz, 1971, *C. biguttulus euhedickei* von Helversen, 1989, *C. biguttulus parnassicus* subspec. nov., *C. moreanus* spec. nov., *C. mollis mollis* (Charpentier, 1825), *C. mollis pechevi* Karaman, 1975 [Bulgaria], *C. mollis lesinensis* (Krauss, 1888) stat. nov. [Dalmatia], *C. crassiceps* (Ramme, 1927), *C. parnon* spec. nov. and *C. pulloides* (Ramme, 1927). A key to the Greek taxa is presented and for each taxon data on morphology, bioacoustics, ecology, differential diagnosis and distribution are provided.

Using bioacoustics and morphology most populations in Greece can be easily and reliably identified. However in the Peloponnese, populations occurring in the contact zones of the disjunct distribution areas of *C. pulloides*, *C. crassiceps*, *C. parnon* and *C. moreanus* show intermediate morphological and bioacoustical characteristics. Identification of these transitional populations is cumbersome, arbitrary and commonly impossible. In recent research such populations have been treated as hybrid populations occurring in hybrid zones between naturally hybridizing species. The situation in the Peloponnese requires further research (*e.g.* behavioural and molecular analysis), to disentangle the degree of speciation, to assess species delimitations, their taxonomic status, palaeobiogeography, evolution and the phylogeny within this group.

Introduction

Up to date more than 250 species and subspecies are recognized within the genus *Chorthippus* (s.l.) Fieber, 1852 (Otte *et al.*, 2005) (figs 1-2). With a few exceptions of nearctic distribution, all species are palaearctic, ranging from widely spread to strictly local. Due to overall morphological similarity, the taxonomy of *Chorthippus* is difficult and a source of instability of nomenclature.

Fig. 1. *Chorthippus bornhalmi*, male. Thessaloniki, 2008. Photo Roy Kleukers.

The group of species treated in this study is usually designated as *Glyptobothrus* Chopard, 1951 (type-species *C. binotatus* (Charpentier, 1825)**,** described as a subgenus of *Chorthippus* and roughly defined by angled pronotal lateral keels, particularly strongly divergent in the metazona.

Recently Storozhenko (2002) re-organised *Chorthippus* and raised *Glyptobothrus* to generic rank. One of his key characters is the tympanal aperture, wide and oval-shaped in *Chorthippus*, (s. str.) as to narrow and slit-like in *Glyptobothrus*. However, this character is not always reliable.

For instance while *brunneus* and *jacobsi*, both arranged under *Glyptobothrus* may hybridise (Saldamando *et al.*, 2004; 2005), *brunneus* may also hybridise with *bornhalmi* (Kleukers *et al.*, 2004) that is assigned to *Chorthippus*. Another example refers to the nominate subspecies of *vagans* that typically has a wide-open oval tympanal aperture, characteristic to *Chorthippus*. However, in *v. cypriotus* comb. nov. and especially in *v. dissimilis* subspec. nov. this aperture is much narrower and fits into *Glyptobothrus*. A third example is *crassiceps* with a comparatively wide tympanal aperture as in *Chorthippus* but which is quite close to nominate *mollis* that belongs to *Glyptobothrus*.

Also the name "*biguttulus*-group" as used in recent literature is not well defined. This group includes *biguttulus, mollis, brunneus* and its allies, a number of similar species roughly characterized by slit-like tympanal apertures, angled pronotal lateral keels, fully developed wings (with divergent cubital veins) and lack of any striking feature of coloration (*e.g.* Ragge *et al.*, 1990). However the wings may be short in members apparently belonging to this group (*e.g. pulloides*) and slit-like tympanal apertures may occur in species considered not belonging to the "*biguttulus*-group" (*e.g. vagans dissimilis*).

Fig. 2. *Chorthippus biroi*, male. Palaikastro (Crete), 2008, leg. Jos Tilmans. Photo Roy Kleukers.

Apparently the taxonomic delimitations of *Glyptobothrus* as well as the "*biguttulus*-group" are not clear. Therefore we refrain from using the name *Glyptobothrus* and instead refer to a group of species of the genus *Chorthippus*, characterized by angled pronotal lateral keels, restricting the term "*biguttulus*-group" strictly to *biguttulus* and its closest relatives.

Some twenty years ago it was assumed that in Greece this group of species was represented by the fully winged species *brunneus brunneus, biguttulus hedickei, mollis mollis, lesinensis, crassiceps, apricarius* and the short winged *pulloides, sangiorgii, willemsei* and *biroi* (Willemse, 1984). At the same time it was noted that much uncertainty existed on the status of a number of these taxa and on the occurrence in Greece of *Chorthippus vagans* (Willemse, 1984; 1985; 1986).

Chorthippus belongs to the Gomphocerinae, a subfamily with a well known bioacoustic behaviour. As we presently know, songs and other bioacoustic characters play a very important role in their mate recognition system and provide a reliable means of identification. In the mid 1970s techniques were developed for simultaneous recording of leg movement and sound (Elsner, 1974) under laboratory conditions which have been improved since then. Since the 1980s equipment for field recordings became easier to obtain and have been used since to record songs of Greek Orthoptera. The introduction of these new techniques and studies based on them have improved our understanding considerably as shown by the following examples.

Bioacoustic studies by Ingrisch & Pavicevic (1985) confirmed the earlier suggestion (Willemse, 1985) that all previous *brunneus* records of Greece actually refer to *bornhalmi*. In the same paper, again based on characteristics of the song Ingrisch & Pavicevic (1985) proved *lagrecai* to be synonymous with *bornhalmi*. They also presented the first reliable record of Greek *vagans*. The identification of the latter was merely based on characteristics of the song because morphological characters agreed with *mollis* rather than *vagans*. Again based upon bioacoustic characters Von Helversen (1989) described *biguttulus euhedickei* for populations ranging from southern Jugoslavian Macedonia and northern Greece to western Anatolia.

Ragge *et al.* (1990) introduced the song of another not yet described species from the Peloponnese (now *moreanus* spec. nov.), pointing out that this species is not identical with *crassiceps* as suggested in Willemse (1984) and also that the name *crassiceps* should be limited to *mollis* "sing-alikes" from its type-locality, the island of Poros (Willemse, 1985). Fieldwork in Greece after 1990 showed that the number of taxa is even larger than previously assumed. The preliminary findings of fieldwork carried out over the last 15 years also indicate that the situation in Greece, as far as species delimitations within *Chorthippus* is concerned is complicated, particularly in the Peloponnese, presenting open and most interesting questions.

The songs represented in the diagrams (figs 223-259) are included on the cd which is added to this paper.

This paper is an interim report, giving an updated survey of the available data on these members of *Chorthippus* throughout Greece. It may be helpful to recognize most populations without arbitrating their ranking and leaving open questions and problems. We are convinced that these groups of populations in this particular area of Europe present a most welcome opportunity for further studies on speciation and evolution, phylogeny and palaeobiogeography.

Methods

Morphology

Due to the overall similarity of the species in this group, the use of morphological and colour characters is of limited value. Most distinctive morphological characters are found in the male but some are more evident in the female (*e.g.* width of head and fastigium verticis, tympanal aperture, pronotal disc and location of its principal transverse sulcus).

In a few taxa the head is conspicuously large and wide. This inflation of the head capsule was measured as the longest distance between the genae (seen from above) compared to the length of the pronotum. Sometimes the fastigium verticis is unusual wide. In these cases the interocular distance was

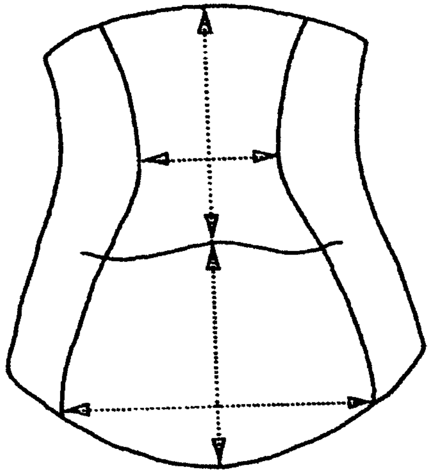
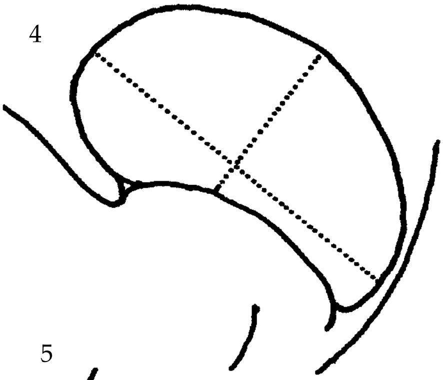


Fig. 3. Diagram of the pronotum, showing the methods of measuring the minimum and maximum width of the pronotal dorsum and the length of pro- and metazona.



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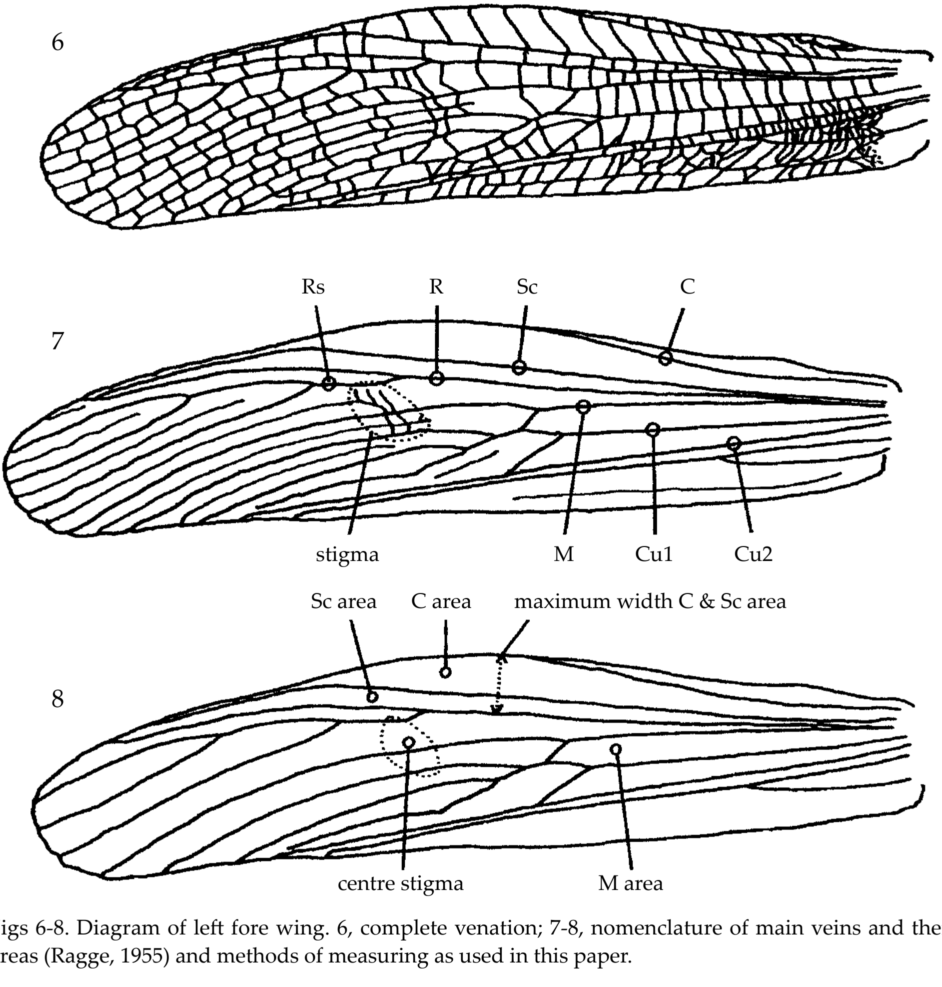
Figs 4-5. Diagram of the left tympanum, showing the methods of measuring the shortest and largest distance between its external margins.

measured as the shortest distance between the upper medial margins of both eyes as compared to the largest diameter of the eye. The length of the pronotal prozona and metazona were measured along the mid-line, the smallest and greatest width of the disc as the narrowest distance between the lateral keels at the point of angulation in the prozona and the largest one between the lateral keels in the metazona respectively (fig. 3). The width of the tympanal aperture was defined by measuring the shortest and largest distance between its external margins (figs 4-5).

Nomenclature of the main veins of the fore wing and their areas as in Ragge (1955) (figs 6-8). Measurements of the male fore wing were taken as pointed out in Ragge *et al.* (1988): length of the fore wing, also in relation to that of the hind femur; width of Sc area along the same line of the greatest width of the C area. Regarding the latter it is noteworthy that the width of the Sc area quite commonly is not greatest along the same line of the greatest width of the C area. Therefore, exceptionally, the greatest width of Sc area, often located at the bifurcation of Rs, was also measured. The length of the hind

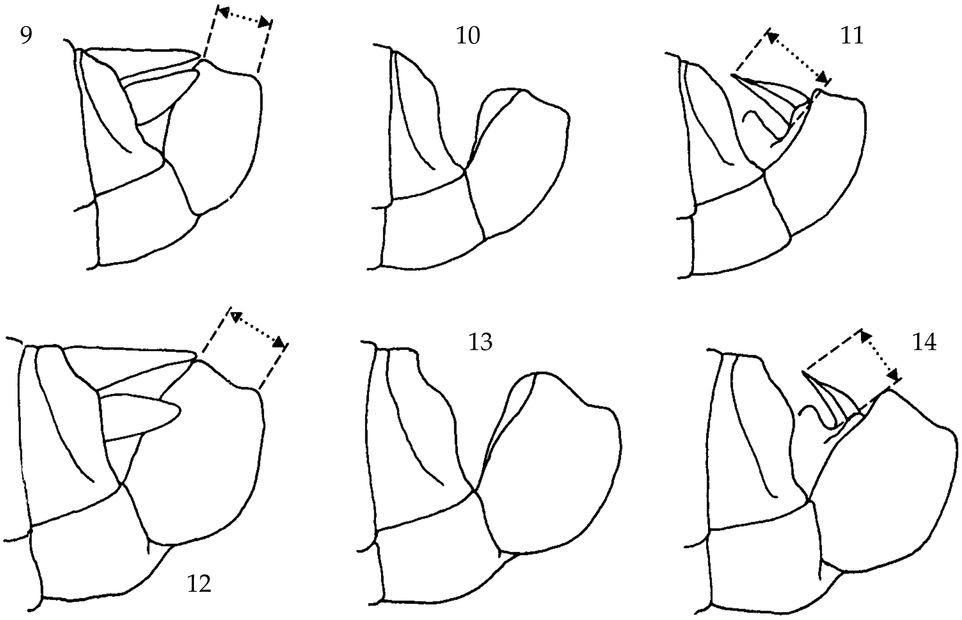


Figs 6-8. Diagram of left fore wing. 6, complete venation; 7-8, nomenclature of main veins and their areas (Ragge, 1955) and methods of measuring as used in this paper.

femur was measured from the anterior margin of the upper basal lobe to the hind margin of the upper knee-lobe. The length of the stridulatory file was measured as in Ragge *et al.* (1988). The distance between file and hind knee was taken from the terminal distal peg or bristle to the tip of the hind knee. The spacing of the stridulatory pegs is not uniform along the whole length of the file, the proximal pegs and particularly the distal ones are commonly more widely spaced. Although a detailed measuring of the spacing of the stridulatory pegs would have given more useful data, we obtained at least some information on the number of stridulatory pegs per millimeter by taking the ratio between the total length of the file and the total number of pegs. In a few cases the length of the tip of the male subgenital plate was measured and taken from the distal point of the plate to the distal point of insertion of the pallium (figs 9-14).

Coloration of the discussed taxa is commonly similar, with as major exception in some cases the colour of the hind tibia. Particulars of male (including the phallic complex) and female abdominal terminalia have been used only by exception, as well as the hairiness of the ventral thorax. Details of a number of other characters (*e.g.* frontal ridge, foveolae, meso- and metasterna of the thorax, aspect of pronotal lateral keels, length of hind wing) have not been used, mainly because of poor reliability or correlation with already used and more reliable parameters.

Wild M5 and Leitz Wetzlar microscopes with graduated eyepieces have been used for morphological measurements. Biometric data are summarised in tables and given at the end of this paper.



Figs 9-14. Diagram of male abdominal terminalia (9 & 12 in situ, 10 & 13 with subgenital plate slightly pulled down, pallium intact, 11 & 14 same with pallium pulled down) showing difference in length of the tip of the subgenital plate and freely exposed part of the apex of phallus. 9-11, *Chorthippus vagans dissimilis* (9) from Akhaia, Potamia, (10) from Akhaia, Kato Lousoi, (11) from Attika, Varnavas; 12-14, *C. mollis mollis* (12) from Voiotia, Mt. Parnassos, (13) from Kilkis, Evzoni, (14) from Arta, Vourgareli.

The pictures of habitus, fore wing, pronotum and tympanal apertures all are given on the same scale so as to be comparable to each other. Habitus pictures are present for both sexes. Pictures of the fore wing are usually only given for the male, pictures of pronotum and tympanal aperture are only given for the female.

Bioacoustics

For the recordings of songs in the field or of males kept in a cage, the following equipment has been used: Uher 4200 Monitor tape recorder, AKG D202 E1 microphone with low frequencies cut-off (after modification); tape speed 19 cm/s. More recently a TASCAM DA-P1 recorder with Sennheiser microphone (module K6 with head ME 40) has been used.

Oscillographic analysis of these recordings has been performed on samples (16 bits, 44,1 kHz sample rate) by means of computer programs (Praat, Soundedit and Bias Peak).

Key specimens were transferred to the Zoological Institute, Friedrich Alexander University of Erlangen (Germany). Here, simultaneous recording of the songs and registration of the movements of the hind legs was performed. For this purpose a small piece of a special reflective sheet (3M-company) was fixed to the ends of both hind femora and two optoelectronic cameras recorded the movement of the legs synchronously with the song (Von Helversen & Elsner, 1977). For the recording of the song a 1/2″ Bruel & Kjaer microphone (frequency range up to 40 kHz) was used. Because the optoelectronic cameras work completely silent, synchronous recordings of leg movement and song were possible. Data were stored on a Racal tape recorder and digitized or more recently stored directly in digital form, on the disk of a computer with help of a DSP-card (sample rate 50 kHz). Analysis was done with Turbolab software.

Some recordings have been made from males moving both legs, but with one of the fore wings removed. This resulted in a sound recording of the movements of the other leg only. These "unilateral" songs give a good insight in the sound production of one leg that may be obscured in a two-legged recording (see also under terminology).

Sound recordings on which this paper has been based are deposited in the collections of the three authors. The original registrations of the leg movement are kept, for the time being, at the Friedrich-Alexander-Universität, Erlangen, Germany. Voucher specimens of whom sound recordings are available, carry labels with a cross-reference to the recording. As a rule cross-references to sound recordings are not included in the lists of material studied. However, for material listed under the heading "Atypical and transitional populations" cross-references to sound recordings (if available) are included.

Terminology of bioacoustics

Terminology of bioacoustics in Orthoptera is not consistent, neither world wide nor among European countries. In this publication we follow the broadly accepted terminology used by D. Ragge (*e.g.* Ragge & Reynolds, 1998). This terminology describes sound elements, as produced by single or compound movements in the stridulatory organs. As already pointed out by these authors (l.c. pp. 28-29), sometimes the stridulatory movements are so complicated that difficulties may arise in applying some terms.

Problems include the presence of incomplete or interrupted to-and-fro movements and (near) silent movements.

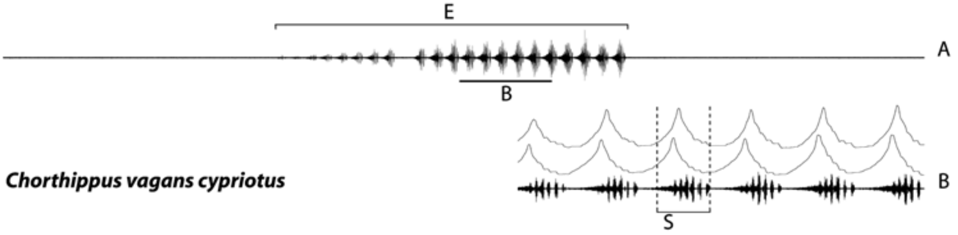
A special problem applies to gomphocerine grasshoppers, which use both the left and right hind legs, two stridulatory organs producing a single song. The leg movements of a number of European gomphocerine grasshoppers have been studied extensively (*e.g.* Elsner, 1974) and usually show a different movement for each leg. The two legs may show a different velocity, phase lag or amplitude. They may even move in an opposite direction (antidrome). The movement of a single leg usually produces a clear pattern of sounds, commonly well recognisable with the terminology of D. Ragge. However, the sound produced by a second leg, as a result of differences in movement, overlaps more or less the sound of the other leg in a majority of the cases (compare figs 243 and 244) and may obscure the exact limitation of sound units. The exact limits of sound units are also difficult to assess when leg movements produce very little sound. Sometimes pauses between sound units are more or less noisy. Such noisy pauses may play a significant role in bioacoustic communication (Von Helversen *et al.*, 2004).

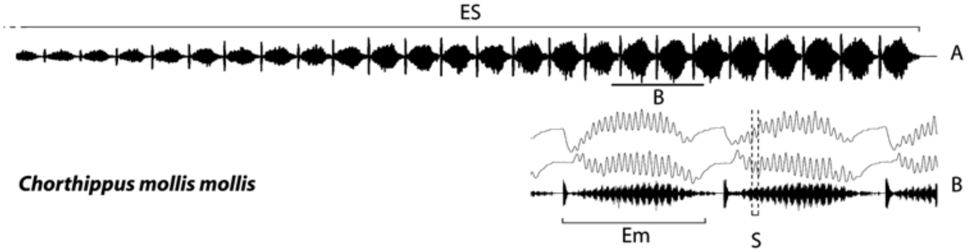
Comparing the bilateral movements of the hind legs in our studied material, it is apparent that particularly the terms syllable and echeme sometimes are difficult to assign. The new technology of movement registration (Von Helversen & Elsner, 1977) makes a re-evaluation of the terminology of sound units inevitable, particularly of the

Figs 15-16. Oscillograms of male calling songs, illustrating the terminology used in this paper and showing examples of **molloid** and **biguttuloid** patterns of syllables and echemes:
Chorthippus species, A: overview oscillogram of 10 s; B: detailed oscillogram of 1 s, with synchronous registration of the movements of the left and right hind leg in both upper tracks; abbreviations: ES: echeme sequence; E: echeme (Em: echeme suggesting molloid pattern, Eb: echeme suggesting biguttuloid pattern); S: syllable (S1: starting loud syllable of biguttuloid pattern; S2: following (often) weak syllable of biguttuloid pattern).

▶

Fig. 15. *Chorthippus vagans cypriotus* (legends see fig. 226); the sound units are syllables (S), produced by an almost synchronous to-and-fro movement of both hind legs, showing gaps and pulses during the downward movement; the syllables are well separated from each other by a less noisy inter-syllabic interval during the start of the upstroke; the complete song is defined as an echeme;
C. mollis mollis (legends see fig. 239); the syllables (S) consist of quite uniform, fast, uninterrupted, vibrating to-and-fro movement of both legs, producing a series of sounds that are grouped in echemes (Em), each of the latter well separated from each other by an inter-echemic less noisy interval. In the case of typical *m. mollis* these echemes often preceded by a strong and commonly unilateral downstroke hemisyllable, producing the "tick". In this publication we address the assemblage of vibrating syllable movements followed by an interval as a **molloid** pattern and molloid echeme (Em) respectively; the complete song of *mollis* is considered an echeme-sequence;
C. crassiceps (legends see fig. 243, note that this registration refers to a male with one fore wing removed); in essence identical to the *mollis* song above, with a clear molloid pattern;
C. pulloides (legends see fig. 248); in essence identical to the *mollis* song above, with a clear molloid pattern;
C. pulloides, atypical (bioacoustically) (Greece, Akhaia, Erimanthos, below Kriovrisi, 13.vi.1992, O. von Helversen; registration 3); at least part of the syllables (S1, S2) may be grouped as in *C. moreanus* (or *biguttulus*, see fig. 16), showing a biguttuloid pattern (Eb), but quite remarkably these biguttuloid echemes again are grouped in echemes (E) that are well separated by inter-echemic intervals like in *C. pulloides* (or *C. mollis*); like in *C. mollis* the song consists of an echeme-sequence;


Chorthippus vagans cypriotus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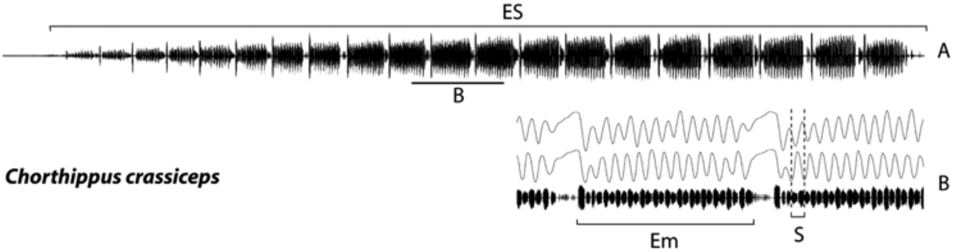
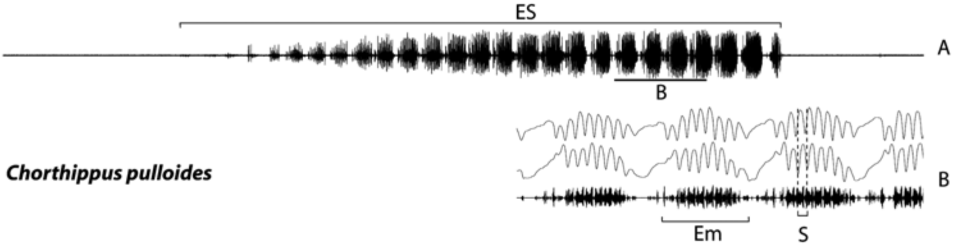
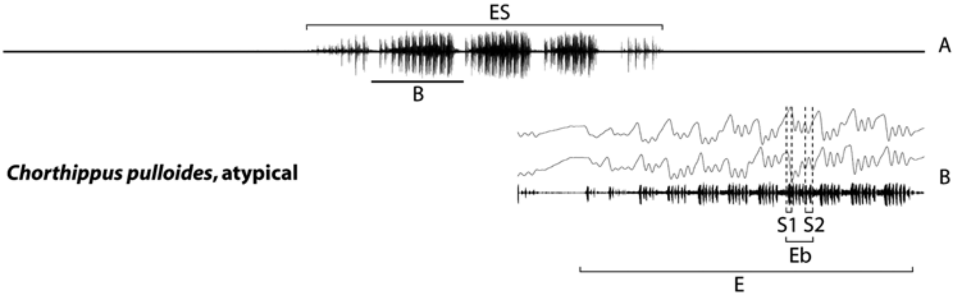
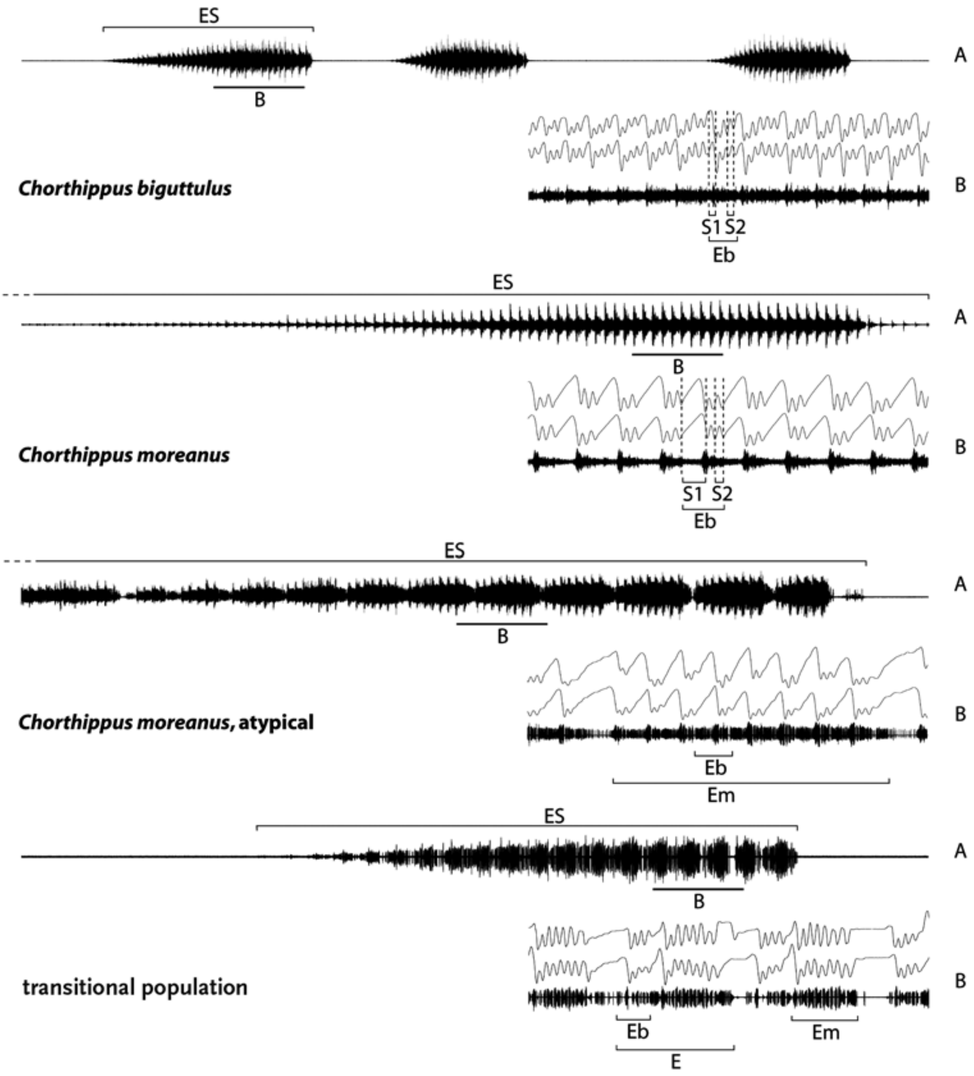

Chorthippus crassiceps


Chorthippus pulloides


Chorthippus pulloides, atypical



term syllable and echeme. In fact, these terms should integrate the differences in movement between the left and right hind leg (see for instance pattern I & II in Elsner, 1974). It is not the scope of the present study to propose a redefinition of the terminology used in bioacoustics. Instead an explanation is given below of these terms as applied in this paper, in order to assure a consistent and comprehensible use in this publication. The most important terms are illustrated in figs 15 and 16.

Calling song: the song produced by an isolated male.
Courtship song: the song produced by a male when close to a female.
Rivalry song: the song produced by two or more males reacting to one another.
Aftersong: in several species of gomphocerine grasshoppers the main part of the song

◀ Fig. 16. *Chorthippus biguttulus biguttulus* (legends see fig. 233); the sounds clearly show small groups, starting with a sound with large amplitude produced by a syllable with a strong down stroke (the main syllable, S1), immediately followed by associated 2-3 (sometimes slightly more) smaller to-and-fro movements producing sounds of lower amplitude (S2). The upward movement of the first syllable (S1) is relatively silent. This is especially recognisable in an unilaterally produced song but largely effaced in two legged registrations.

We assign a **biguttuloid** pattern to this group of leg movements and sounds. Together they produce a biguttuloid echeme (Eb); these follow each other continuously until completing the echeme-sequence; in this interpretation the song of *C. biguttulus* consists of usually a series of 2-4 echeme-sequences.

Note: It has been argued that the first strong down stroke marks start and end of one complete up- and downward movement of the leg that includes additional leg movements, the whole assembly being interpreted as a syllable (D. & O. von Helversen 1975). The complete song of *C. biguttulus* then is described as a series of 2-4 echemes. Yet, we prefer to follow Ragge & Reynolds (1998) and consequently use common sense when dealing with these complicated patterns;

C. moreanus (legends see fig. 238); the movement pattern and resulting sounds are very much like in *C. biguttulus*, with a clear biguttuloid pattern; echemes consisting of a strong syllable (S1) with 2 (-5) associated syllables with a clearly lower amplitude (S2). As in *C. biguttulus* the upward movement of the strong syllable is quieter than the rest of the echeme and marks the delimitation of adjacent echemes; the song is an echeme sequence;

C. moreanus, atypical (bioacoustically) (legends see fig. 256); this song shows a biguttuloid syllabic pattern (Eb) but in the course of the song more or less regularly grouped in longer echemes (E) with longer intervals suggesting affinity with the echeme-sequence of *C. pulloides* (or *C. mollis*);

Calling song of a transitional, non-identifiable population, bridging *C. moreanus* and *C. pulloides* (legends see fig. 258); this song also shows a combination of biguttuloid (Eb) and molloid (Em) elements; however inconsistently arranged, not showing a clearly recognisable pattern of either of the two.

is loud and may be followed by a very quiet part. This quiet part, often at the end of the courtship song, is called aftersong.

Syllable: the sound unit produced by one upward and downward movement of the hind legs, as far as these movements produce sound, excluding very soft or soundless parts of these movements. Regardless of the presence of leg movements, the silent parts between syllables are regarded as intervals.

If the sound is produced by one unidirectional movement of the hind legs (upward or downward) it is named **hemisyllable**; if two successive hemisyllables, up- and downwards and both movements produce a separate sound it may be named **diplosyllable**.

These movements may be fast, complete to-and-fro and (almost) not interrupted (*e.g.* during the vibrating part of the echeme of *mollis*) but also slower, hesitant and showing momentary breaks in movement and creating gaps in sound production (*e.g.* during a syllable of *vagans*) (figs 15-16).

Gap: momentary break (between 1-20 ms) in the sound production during upstroke or downstroke hemisyllables due to a short pause in leg movement.

Interval: clear break in sound production (silent or near silent) between the syllables (inter-syllabic), echemes (inter-echemic) or echeme-sequences, regardless of the leg movements. In most species during intervals the legs move slower and more hesitant. Intervals are often seen when the legs are moved upwards or in combination with a true short break of moving of one or both legs before the start of the next syllable or echeme. Exceptionally the legs may continue their to-and-fro movements (*e.g. sangiorgii*) during intervals.

Pulse: the sound produced by a partial movement of the legs within a syllable. Pulses are separated by gaps (intra-syllabic breaks).

Tooth-stroke: sound produced by one peg of the stridulatory file hitting the wing; in gomphocerine grasshoppers these sounds usually overlap and are not discernible in an oscillogram.

Echeme: the sound produced by a first-order assemblage of syllables. Echemes include inter-syllabic intervals but exclude the inter-echemic interval (figs 15-16). In some species echemes are clearly separated by an interval but in other species this interval may be less distinct. For instance in *biguttulus* a strong syllable is followed by a few commonly quieter syllables. Such a group of syllables in our concept is also called echeme, irrespective of the presence of a clear inter-echemic interval. Using this concept in the case of *biguttulus* values the presence of noisy intervals that prove to be important in the acoustic behaviour of the species (Von Helversen *et al.*, 2004). Our concept is illustrated and explained below (figs 15-16), introducing the terms **molloid** and **biguttuloid** to define certain syllabic and echemic structures in gomphocerine grasshoppers.

Echeme-sequence: the sound produced by a first-order assemblage of echemes. Echeme-sequences include inter-echemic intervals but exclude the interval between echeme-sequences (figs 15-16).

Abbreviations and depositories

Abbreviations throughout the text, tables, diagrams etc. referring to the (male) fore wing, are as follows (compare also figs 6-8): C: costal vein; C area: costal area; Cu1: first cubital vein; Cu2: second cubital vein; R: radial vein; Rs: radial sector; Sc: subcostal vein; Sc area: subcostal area.

Depositories of material are abbreviated as follows:

BMNH/L:	British Museum of Natural History, London
CH-MHN/G:	collection K. Harz, Muséum d'Histoire Naturelle, Geneva
CKo:	collection P. Kočárek, Ostrava, Czech Republic
CvH:	collection O. von Helversen, Friedrich-Alexander-Universität, Erlangen, Germany
CI:	collection S. Ingrisch, Bad Karlshafen, Germany
CK:	collection M. Karaman, now with Ivo Karaman, Novi Sad, Yugoslavia
CKr:	collection H. Kriegbaum, Zoologische Staatssammlung, München
CM:	collection F. Mayer, Museum für Naturkunde der Humboldt-Universität, Berlin
CN-MHN/G:	collection A. Nadig, Muséum d'Histoire Naturelle, Geneva
CO:	collection B. Odé, Amsterdam
CP:	collection K. Papapavlou, Athens
CS:	collection J. Szijj, Essen, Germany
CT:	collection J. Tilmans, Gouda, The Netherlands
CW:	collection Willemse (will be a public collection in the future), Eygelshoven, The Netherlands
HNHM/B:	Hungarian Natural History Museum, Budapest

LS/L:	Linnean Society, London
MNHN/P:	Musée Nationale de l'Histoire Naturelle, Paris
MNHU/B:	Museum für Naturkunde der Humboldt-Universität, Berlin
MHN/G:	Muséum d'Histoire Naturelle, Geneva
NM/P:	Narodni Muzeum, Praha
NMNH/S:	National Museum of Natural History, Sofia
NM/W:	Naturhistorisches Museum, Vienna
SMN/S:	Staatliches Museum für Naturkunde, Stuttgart
ZI/L:	Zoologiska Institution, Lunds Universitet, Lund
ZI/P:	Zoological Institute, Russian Academy of Science, St. Petersburg
ZI/U:	Zoologiska institution, Uppsala Universitet, Uppsala
ZMMSU/M:	Zoological Museum of Moscow State University, Moscow

References

In addition to those used throughout the text, references listed under the taxa refer to original descriptions, changes in nomenclature and papers dealing with original Greek material as far as not already referred to in Willemse (1984).

Systematic part

Grouping

The taxa treated in this paper are arranged in groups, characterised by typical species. At the end some bioacoustically poorly or non-identifiable atypical populations are treated. Taxa provided with an asterisk do not occur in Greece.

***apricarius* group**

typical species: *Gryllus (Locusta) apricarius* Linnaeus, 1758: 433 (type see below)
Chorthippus apricarius apricarius (Linnaeus, 1758)

***vagans* group**

typical species: *Oedipoda vagans* Eversmann, 1848: 12 (types, Orenburg area, ZI/P?)
vagans complex:
Chorthippus vagans vagans (Eversmann, 1848) *
Chorthippus vagans africanus Nadig, 1981 *
Chorthippus vagans dissimilis subspec. nov.
Chorthippus vagans cypriotus Uvarov, 1936 comb. nov. *
Chorthippus willemsei Harz, 1971
Chorthippus biroi (Kuthy, 1907)

***brunneus* group**

typical species: *Gryllus brunneus* Thunberg, 1815: 256 (holotype female; Sweden; ZIU/L)
brunneus complex:
Chorthippus brunneus brunneus (Thunberg, 1815) *
Chorthippus bornhalmi Harz, 1971

***biguttulus* group**

typical species: *Gryllus (Locusta) biguttulus* Linnaeus, 1758: 433 (lectotype male; locality unknown; LS/L)

biguttulus complex:
Chorthippus biguttulus biguttulus (Linnaeus, 1758) *
Chorthippus biguttulus hedickei (Ramme, 1942) *
Chorthippus biguttulus euhedickei von Helversen, 1989
Chorthippus biguttulus parnassicus subspec. nov.
Chorthippus moreanus spec. nov.

***mollis* group**

typical species: *Gryllus mollis* Charpentier, 1825 (lectotype male; Silesia; ZIL/L)

mollis complex:
Chorthippus mollis mollis (Charpentier, 1825)
Chorthippus mollis lesinensis (Krauss, 1888) *
Chorthippus mollis ignifer (Ramme, 1923) *
Chorthippus mollis pechevi Karaman, 1975 *
pulloides-crassiceps complex:
Chorthippus crassiceps (Ramme, 1927)
Chorthippus parnon spec. nov.
Chorthippus pulloides (Ramme, 1927)
Chorthippus sangiorgii (Finot, 1902)

atypical and transitional populations (the Peloponnese)
atypical *Chorthippus moreanus* spec. nov.
atypical *Chorthippus pulloides* (Ramme, 1926)
non-identifiable populations

Identification

Due to the overall morphological similarity, the usefulness of morphological characters is limited. The male calling song offers a more reliable way of identification. For instance typical *crassiceps* and *parnon*, which are morphologically very similar, are easily distinguishable by their calling song. On the other hand morphologically distinct populations may belong to the same species as proven by the similarities in their calling songs. To reach a reliable identification it is strongly recommended to record or describe the song of individual specimens.

Morphological key

The key given here is based on morphological characters of males and not of both sexes, unless otherwise stated. Some species are recognisable at a glance. However, due to individual and particularly geographic variation and occurrence of atypical, transitional populations, characters of taxa may show overlap (below "Atypical and transitional populations" behind *pulloides*). As a result some taxa are keyed out twice while other taxa can not be keyed out beyond a group of distinct species which are morphologically very similar.

Biometric data refer to relatively small numbers of specimens and certainly do not cover the whole range of naturally occurring variability. This holds both for data given in this key as well as data given in the species descriptions, comparisons, tables and diagrams. The reliability of biometric data is limited. Biometrics of any individual specimen may slightly be out of the ranges given in this publication. It is strongly recommended to compare the diagnosis with other details given under the treated taxa, particularly those of the song.

1. Fore wing of male extending just beyond tip of abdomen (fig. 23), in female just reaching tip of abdomen or shorter (fig. 24), Cu1 and Cu2 veins fused except near the base, M area in the male unusually widened and showing a series of parallel cross-veins (fig. 72); widely spread in the palaearctic region and in Greece occurring in mountains of the northern and central mainland (fig. 260) .... *apricarius apricarius*

\- Fore wing of variable length, from extending far beyond tip of the abdomen to much shorter than the abdomen but Cu1 and Cu2 always divergent, M area not remarkably wide (figs 73-138) **2**

2. Tip of flexed fore wing reaching beyond tip of abdomen, fore wing with apical part beyond the stigma well developed, male fore wing at least 1.1 times as long as hind femur; due to variability, compare also couplets 9-11 (figs 27, 36, 38, 40, 42, 44, 50, 52, 78-80, 88, 93-103, 110-113) **3**

\- Fore wing shorter, reaching tip of abdomen or shorter, apical part beyond stigma (if visible) reduced, length of male fore wing at most 1.1 times length of hind femur (figs 31, 33-34, 54, 56, 58, 60, 62, 64, 66, 68, 70, 82-87, 104-107, 114-138) **9**

3. Stridulatory file (in both sexes) mostly with fewer than 90 pegs (55-89); habitus, pronotum, fore wing as in *bornhalmi* (see below), the fore wing always extending well beyond tip of hind knee and with long apical part (beyond the stigma); widely spread north of Greece but very probably absent from Greece .... *brunneus brunneus*

\- Stridulatory file commonly with more than 90 pegs, fore wing from extending well beyond to just reaching tip of hind knee **4**

4. Fore margin of male fore wing rather bowed by expanded C & Sc areas (figs 93-97), width of combined C & Sc areas commonly more than 1.0 mm (0.95-1.4 mm) (fig. 208); male stridulatory file long (4.2-5.8 mm), unusually far extending towards the base of the hind knee (also in female), in the male from 1.2-2.2 times as long as the distance from the terminal distal peg to the tip of the hind knee (fig. 208); in Greece known from the mainland but only north of the Peloponnese (fig. 264) .... *biguttulus euhedickei*

\- Fore margin of male fore wing less conspicuously bowed (figs 78-79, 88, 98-104, 110-113), combined C & Sc areas commonly less than 1.0 mm wide (0.65-1.05 mm) (fig. 208); male stridulatory file shorter (2.6-4.7 mm), extending less far distad, from 0.6-1.2 times as long as distance from distal terminal peg to tip of hind knee (fig. 208) **5**

5. Fore wing relatively slender, long, extending well beyond tip of hind knee in both sexes (figs 36, 37, 88), in male from 1.35-1.75, in female 1.35-1.58 times as long as length of the hind femur; distance from centre of stigma to tip of fore wing in male from 5.3-7.3, in female 7.4-8.8 mm; pronotum with lateral keels relatively strongly angled, metazona of pronotum relatively long and wide (particularly obvious in female, figs 157-159), greatest width of metazona of male 2.15-2.70, in female 3.0-3.9 mm (fig. 207); number of stridulatory pegs in male 105-153; ventral surface of thorax commonly strongly hairy; ranging from western and southern Balkans into Anatolia, common throughout all of Greece, both mainland and the Peloponnese and known from many islands (fig. 263) .... *bornhalmi*

- Fore wing relatively less slender, shorter, in male 1.00-1.49, in female 1.01-1.44 times the length of the hind femur (figs 27, 42, 44, 50, 52, 78-79, 98-104, 110-113); distance stigma to tip of fore wing shorter, in male 2.7-6.3, in female 4.0-7.2 mm; pronotum (figs 150-151, 162-163, 165-167) with lateral keels relatively less angled, greatest width of metazona in male 1.7-2.7, in female 2.4-3.3 mm; number of stridulatory pegs in male 94-189 (135-189 *vagans dissimilis*, 95-122 *biguttulus parnassicus*, 100-136 *moreanus*, 94-134 *mollis mollis*); ventral side of thorax commonly with sparse hairs **6**

6. Stridulatory file longer, in male commonly 3.7-4.7 mm with commonly between 135-189 stridulatory pegs (figs 205-206); known from a number of sites in the Peloponnese, the Greek mainland, the island of Samothraki, some eastern Aegean islands and western Anatolia (fig. 261) .... *vagans dissimilis*

- Stridulatory file shorter, in male commonly 2.6-3.8 mm with commonly between 94-134 stridulatory pegs (figs 205-206) **7**

7. Stridulatory file relatively longer, in male commonly 0.85-1.1 times as long as distance from terminal peg to tip of hind knee (fig. 211); male fore wing with R commonly distinctly bend near the branching of Rs (figs 98-102), Sc area measured at the point of the maximum width of C area relatively narrow, ratio width C/Sc area commonly from 2.2-3.3 (fig. 211); known from the summit of Mt. Parnassos (above 1600 m) (specimens with a more or less similar morphology also occur on a few other mountains in Central Greece and Ipiros) (fig. 265) .... *biguttulus parnassicus*

- Stridulatory file relatively shorter, in male commonly 0.60 to 0.85 times as long as distance from terminal peg to tip of hind knee (fig. 211); male fore wing with R commonly less distinctly bend near bifurcation of Rs or almost straight distad (figs 103-104, 110-113); Sc area, measured at the point of the maximum width of C area, relatively wide, ratio width C/Sc area commonly from 1.5-2.2 (fig. 211) **8**

8. Habitus slender (figs 50-53); Greek mainland and a few offshore islands, all north of the Peloponnese (fig. 266) .... *mollis mollis*

- Habitus less slender (figs 44-45) ....
........some specimens of typical populations of *moreanus*

9. Fore wing of male about of similar length as hind femur, ratio length of fore wing against length of hind femur 0.95-1.14 (figs 44, 54, 58, 103-107, 114-116, 118-120) (only the Peloponnese) **10**

- Fore wing of male commonly considerably shorter than length of hind femur, ratio length of fore wing against length of hind femur 0.6-1.0 (figs 31, 33-34, 56, 60, 62, 64, 66, 68, 70, 82-87, 117, 121-138) (both the Peloponnese, Greek mainland and a number of islands **12**

10. Head normal in both sexes (figs 44-45), greatest width equal or less than pronotal length (ratio length of the pronotum against greatest width of the head 1.01-2) (figs 163, 212-213); tympanal aperture commonly narrower, ratio greatest diameter against smallest one 3.5-7.1 in male, 5-11 in female (fig. 192, table 10); confined to the southern part of the central Peloponnese (fig. 268) .... typical populations of *moreanus*

\- Head remarkably inflated in both sexes, particularly obvious in the female (figs 54-55, 58-59) greatest width of the head commonly slightly exceeding pronotal length (ratio length of the pronotum against greatest width of the head 0.83-1.04) (figs 168-169, 212-213); tympanal aperture commonly wider, ratio greatest diameter against smallest one 2.8-4.2 in male, 3.5-5 in female (figs 197-198, table 10); confined to the northeastern and southeastern part of the Peloponnese **11**

11. Occuring only in the island of Poros and adjacent part of the extreme northeastern part of the Peloponnese (fig. 268) (compare also table 16 and fig. 218) .... typical populations of *crassiceps*

\- Range confined to the southeastern Peloponnese, including the island of Kithira (fig. 268) (compare also table 16 and fig. 218) .... *parnon*

12. Tympanal aperture relatively wide, smallest diameter at least 1/3 of the largest diameter but commonly slightly more (figs 183-187) **13**

\- Tympanal aperture narrower, smallest diameter commonly distinctly less than 1/3 of the largest diameter (figs 199-203) **14**

13. Habitus slender (figs 33-35); fastigium verticis narrower, interocular distance in male 0.6-0.7, in female 0.8-1.0 mm; hind knee and hind tibia always of general colour, lower side sometimes black; fore wing with membrane (figs 85-87, 143) glassy transparent as usual, C area with well developed series of transverse veinlets, Sc area of fore wing remarkably narrow, 1/3-1/4 as wide as C area; only known from Crete and several islands of the Kiklades (fig. 262) .... *biroi*

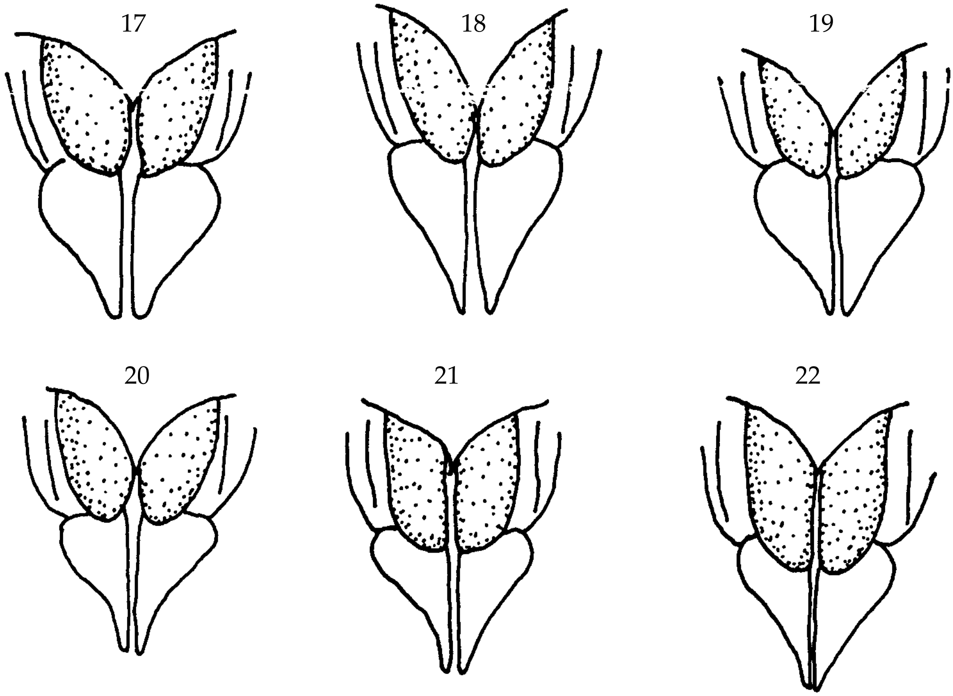
Habitus more thickset (figs 31-32); fastigium of vertex wider, interocular distance in male 0.8-1.0, in female 1.1-1.3 mm; hind knee dark brown or black, hind tibia all over red, exceptionally of general colour; fore wing with membrane (figs 82-84, 141) less transparent, C area with transverse veinlets less well developed, Sc area of male fore wing as usual, 1/2-1/3 as wide as C area; only known from uplands in the Peloponnese and western mainland of Greece (fig. 262) .... *willemsei*

14. Fore wing of male commonly lacking a stigma, without indication of an "apical part", tip convex, regularly and widely rounded (figs 121-132) **15**

\- Fore wing of male commonly not lacking a stigma, with a reduced "apical part", tip slightly tapering and more narrowly rounded (figs 117, 133-138); only occurring in the Peloponnese (fig. 268) .... morphologically atypical populations of the *pulloides-crassiceps* complex (and *parnon* ?), and transitional populations bridging this complex with typical *moreanus*

15. Habitus slender (figs 66-67); fastigium verticis narrower, distance between the eyes narrow, in male 0.5-0.7, in female 0.8-1.0 mm (fig. 170); tympanal aperture relatively wider (figs 202-203); known from the Ionian islands of Kefallonia, Ithaki and Levkas (and others?) (fig. 267) .... *sangiorgii*

\- Habitus robust (fig. 60-65); fastigium verticis wider, distance between eyes larger, in male 0.8-0.9, in female 1.1-1.4 mm (figs 171-173); tympanal aperture narrow (figs 199-201); known from the uplands of western mainland of Greece and the Peloponnese (figs 267-268) .... *pulloides*



Figs 17-22. Diagram of ventral view of lower ovipositor valves showing the ventral basivalvular sclerites in *Chorthippus.* 17, *C. bornhalmi* from Pieria, Mt. Olimbos; 18-19, *C. mollis mollis* (18) from Arta, Vourgareli, & (19) from Voiotia, Mt. Parnassos; 20, *C. vagans vagans* from Austria, Marchfeld, Oberweiden; 21-22, *C. vagans dissimilis* (21) from Akhaia, Potamia & (22) from Attika, Varnavas.

Figs 23-71. *Chorthippus*, **habitus** of male and female, lateral view (unless otherwise stated, from Greece, collected by the Willemse's and in CW).

Figs 23-24. *Chorthippus apricarius apricarius*. 23, male, Trikala, Mt. Neraidha, west of Pertouli, 1650 m, 1.viii.2003; 24, female, Pieria, Mt. Pieria above Katafigion, 1600 m, 27.vii.1974.

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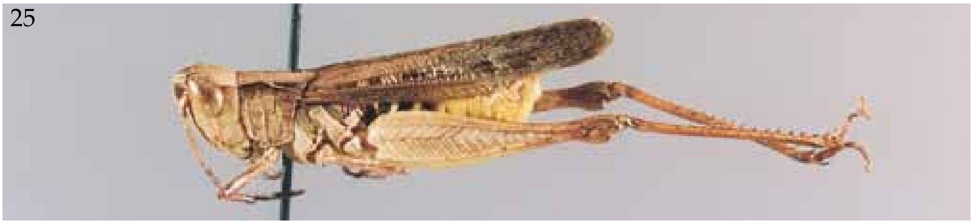

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Figs 25-26. *Chorthippus vagans africanus*. 25-26, male & female paratype. Algérie, Grande Kabylie, Col Talmetz, 1000 m, 18.vii.1979, A. Nadig (CN-MHN / G).

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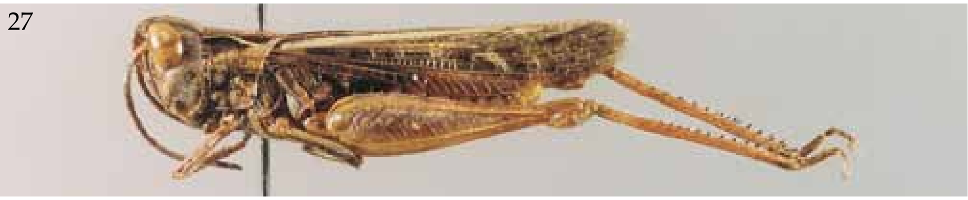

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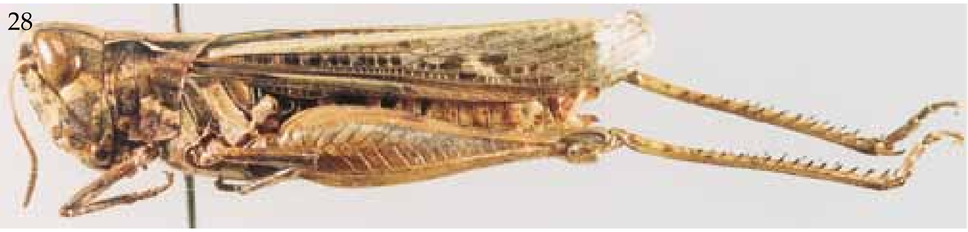

Figs 27-28. *Chorthippus vagans dissimilis*. 27-28, male holo- & female allotype, Akhaia, south of Kalavrita, Kastelli, 980 m, 10.ix.1989.

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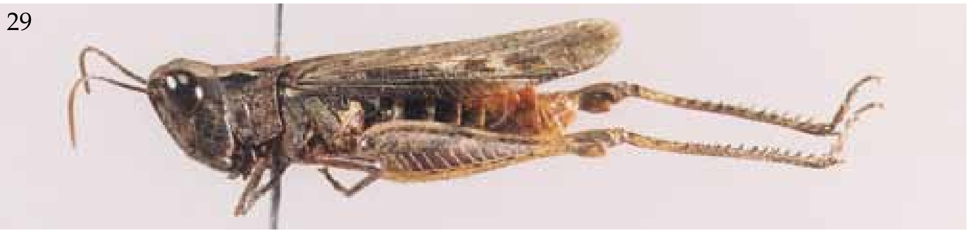

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Figs 29-30. *Chorthippus vagans cypriotus*. 29-30, male & female, Cyprus, Lefkosia district, Machairas forest, 10 km SE Lazanias, 1100 m, 2.x.2005, J.M. Tilmans & J.F.R. Tilmans-Smid (CT).

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Figs 31-32. *Chorthippus willemsei*. 31-32, male & female paratype, Akhaia, Mt. Chelmos above Kato Lousoi, 1700-2000 m, 1.viii.1970.

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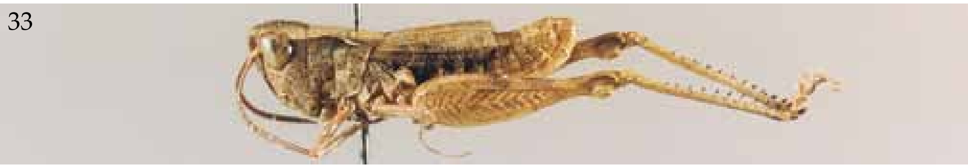

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Figs 33-35. *Chorthippus biroi*. 33, male, Kriti, Ag. Galini (NW of Timbaki), 0-40 m, 3.vii.1973; 34, male, Kikladhes, Tinos Isl., Mt. Tsiknias, SW side, 250-450 m, 1.viii.2004; 35, female, Kriti, Lakki-Omalos, 30 km S of Chania, 750 m, 4.viii.1973.

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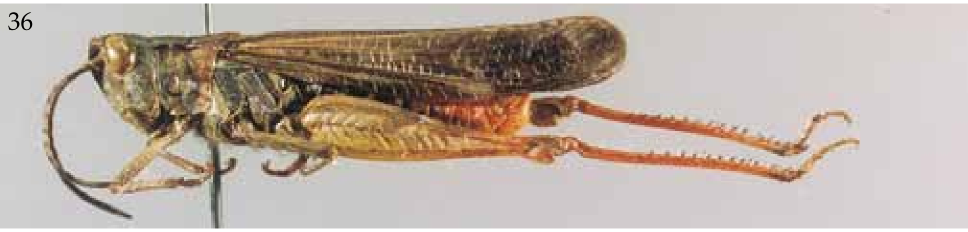

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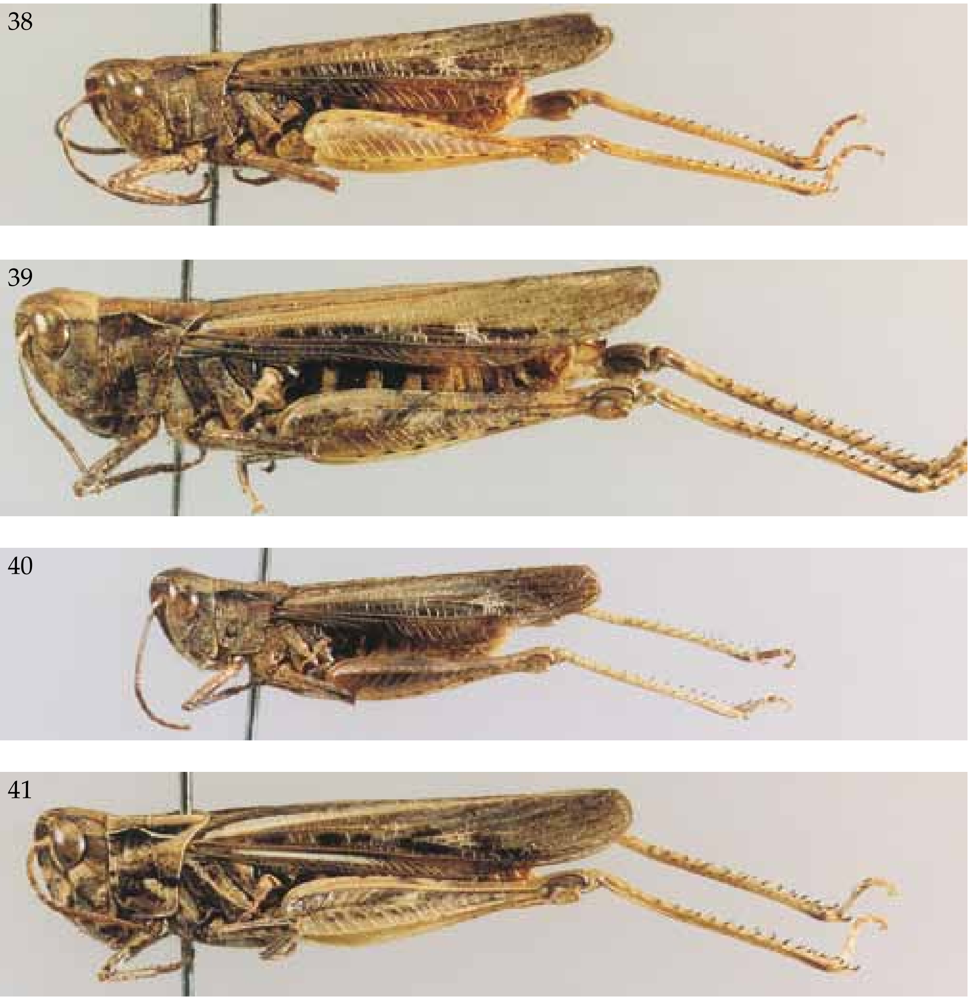
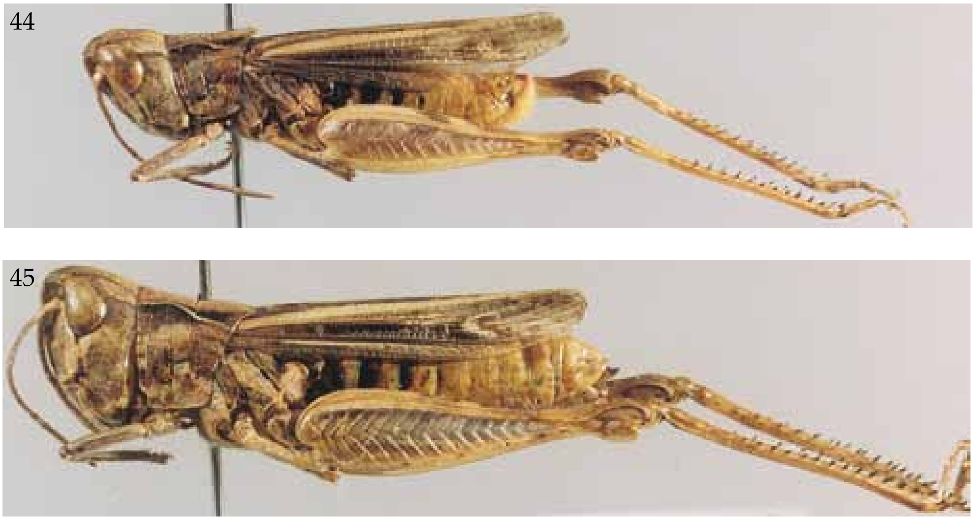
Figs 36-37. *Chorthippus bornhalmi*. 36, male, Pieria, Leptokaria-Karia, 500-1000 m, 16.vii.1976; 37, female, Akhaia, Sella-Pititsa, 450-600 m, 8.vii.1991.



Figs 38-41. *Chorthippus biguttulus euhedickei.* 38, male topotype, Kavalla, Mt. Pangaion above Akrovouni, 1250-1900 m, 15.viii.1979; 39, female, Pieria, Leptokaria-Karia, 500-1000 m, 24.vii.1973; 40-41, male & female, Voiotia, Mt. Parnassos near Gerondhovrachos, 1500 m, 23.vii.2000.

Figs 42-43. *Chorthippus biguttulus parnassicus*: 42-43, male holo- & female allotype, Fthiotis, Mt. Parnassos above ski centre Kelaria, 2000 m, 2.ix.1989.



Figs 44-45. *Chorthippus moreanus*. 44-45, male holo- & female allotype, Ilia, ruins of Bassae near Andritsena, 1100 m, 7.ix.1989.

Figs 46-47. *Chorthippus mollis lesinensis.* 46-47, male & female topotype, Kroatia, Hvar Isl., 500 m south of Pitve, 300 m, 13.viii.1996, R. Kleukers.

Figs 48-49. *Chorthippus mollis pechevi*. 48-49, male lecto- & female paralectotype, Bulgaria-Varna, Kranevo 12.viii.1967, leg. M. Karaman (CK).

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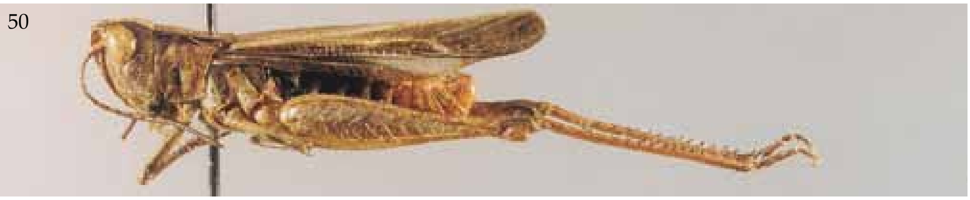

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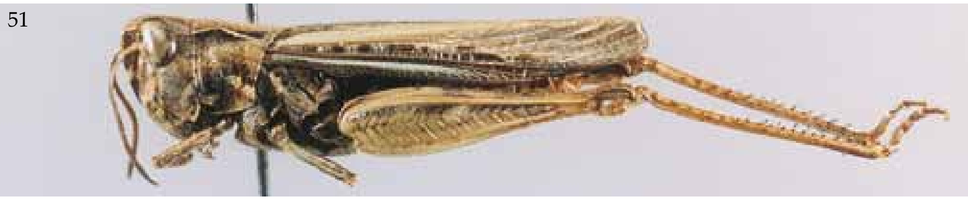

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Figs 50-53. *Chorthippus mollis mollis*. 50-51, male & female, Serrai, Mt. Vrondhous above Serrai, 1000-1150 m, 30-31.viii.1979; 52-53, male & female, Arta, Mt. Gavrogo below summit Yerabi, above Megalochari, 1500-1750 m, 3-4.viii.2003.

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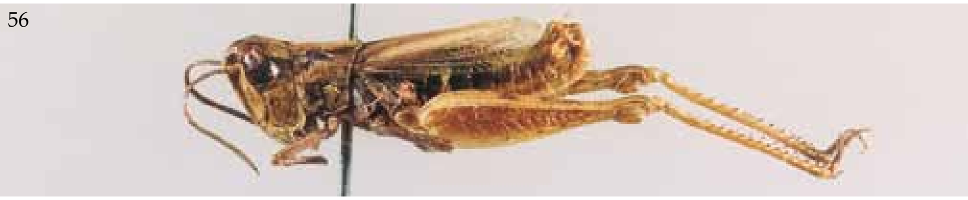

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Figs 54-57. *Chorthippus crassiceps*. 54-55, male & female topotype, Argolis, Poros Isl., circuit along island, 50-200 m, 4-5.viii.1988 (male) & 13.ix.1989 (female); 56-57, male & female, Argolis, Arachnaio Mts, Limnes-Ayionori, 600 m, 2.viii.1991.

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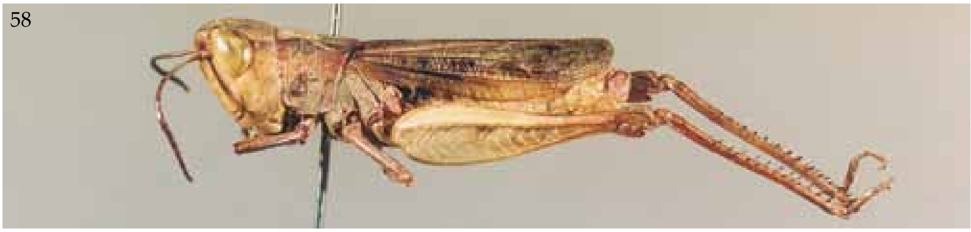

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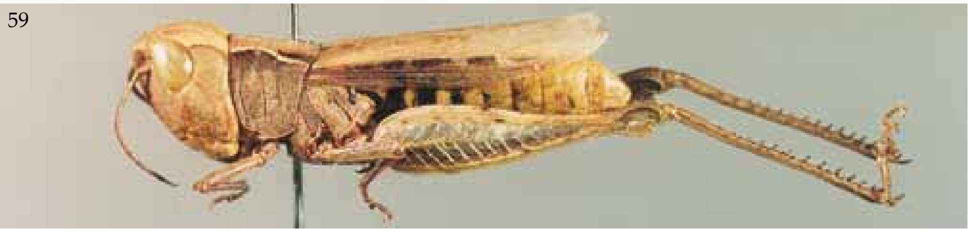

Figs 58-59. *Chorthippus parnon*. 58-59, male holo- & female allotype, Lakonia, 500 m south of Monemvasia, 8.x.1992, R. Kleukers.

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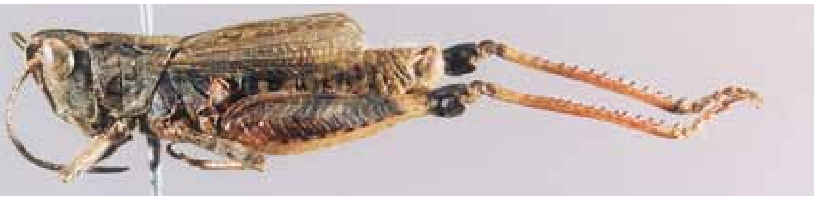

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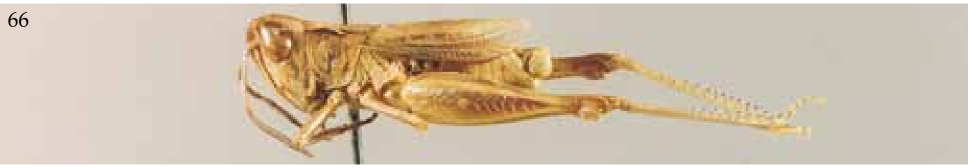

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Figs 66-67. *Chorthippus sangiorgii*. 66-67, male & female, Kefallinia Isl., Mt. Ainos, 1000-1300 m, 2-3. vii.1986.

◀ Figs 60-65. *Chorthippus pulloides*. 60-61, male & female topotype, Akhaia, Mt. Chelmos (= Aroania), 1500-1700 m, 27.vii.1991 (male) & 1700-2000 m, 1.viii.1970 (female); 62-63, male & female, Ioannina, Mt. Kakardhitsa above Pramandha, 1800-1850 m, 27.vii.2003; 64-65, male & female, Aitolia-Akarnania, Mt. Akarnanika above Thirion, 1000-1400 m 9-10.vii.1986 (male) & 800-1400 m, 18.vii.2000 (female).

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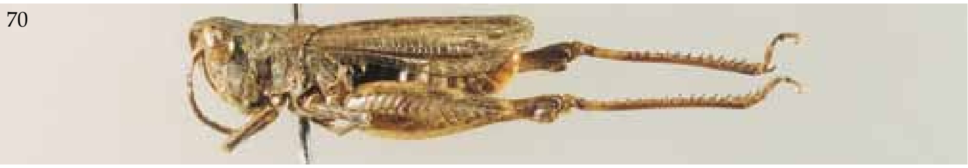

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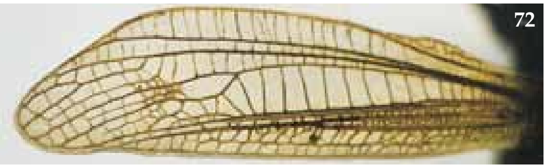
Figs 68-71. Non-identifiable transitional populations bridging *Chorthippus moreanus* and *C. pulloides - crassiceps* complex. 68-69, male & female, Arkadhia, N & S of Valtesiniko, near Vitina, 1300 m, 10.ix.1989; 70-71, male & female, Arkadhia, south of Vitina, 4 km south of Elatis, 1200 m, 11.ix.1989.

Figs 72-143. *Chorthippus*, **left fore wing**. 72-138, male, dorsal view; 139-143, female, dorso-lateral view (unless otherwise stated from Greece, collected by the Willemse's and in CW).

Fig. 72. *Chorthippus apricarius apricarius*, Trikala, Mt. Avgo above Pefki, 1550-2000 m, 30.vii.2003.

Figs 73-75. *Chorthippus vagans vagans*. 73, The Netherlands, Hatertse & Overasseltse vennen, 30.viii.1985; 74, Russia, Poltava region, Mirgorod district, 23.vii.1996, V. Sorochintzi & V. Vedenina; 75, Italy, Apulia, Gravina / Altamura, 30-31. viii.1989, O. von Helversen.

Figs 76-77. *Chorthippus vagans africanus*. 76, Algérie, Grande Kabylie, Forêt Akfadou, 1100-1300 m, 18.vii.1979, A. Nadig (paratype); 77, Grande Kabylie, Col Talmetz, 1000 m, 18.vii.1979, A. Nadig (topoparatype).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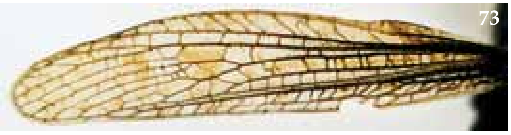
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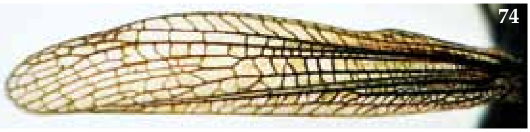
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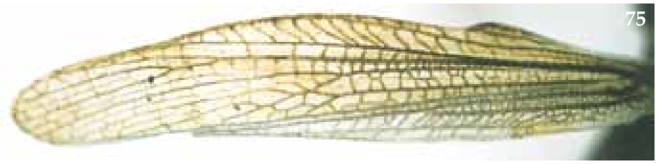
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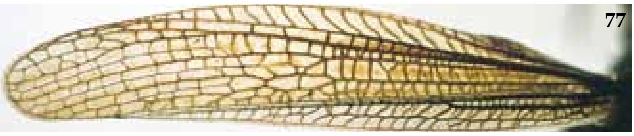
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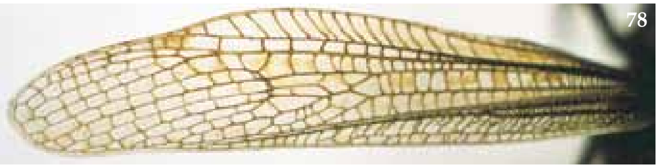

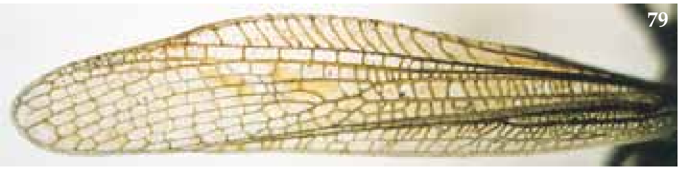

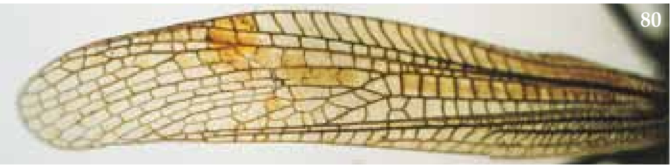

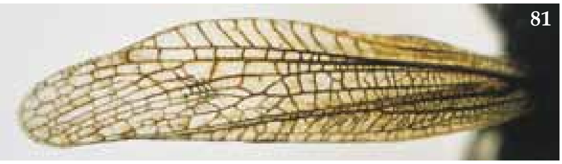

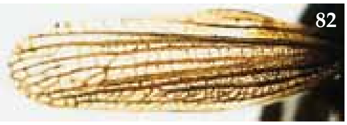

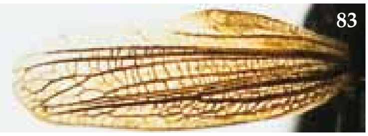

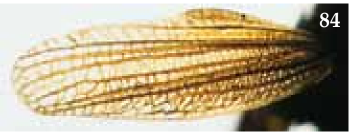

Figs 78-80. *Chorthippus vagans dissimilis.* 78-79, Akhaia, south of Kalavrita, Kastelli, 980 m, 10.ix.1989 (topoparatypes); 80, Turkey, Antalya prov., Akseki pass, 29.ix-12.x.1989, O. von Helversen.

Fig. 81. *Chorthippus vagans cypriotus,* Cyprus, Troodos, Mt. Olympos 36S VD87836413, 1930 m, 24.vii.2001, B. Odé (topotype) (CO).

Figs 82-84. *Chorthippus willemsei.* 82, Akhaia, Kalavrita, Mt. Chelmos above Kato Lousoi, 1700-2000 m, 1.viii.1970 (topoparatype); 83, Evritania, Karpenision, Mt. Timfristos, 1800-2100 m, 29.vii.1971 (paratype); 84, Lakonia, pass between Sparti & Kalamata, 1200 m, 24.vii.1970 (paratype).

Figs 85-87. *Chorthippus biroi*. 85, Kriti, Kedros Ori, Chordakion, 450 m, 1.viii.1973; 86, Kriti, Lefka Ori, Linoseli above Xiloskalo, 1600-1800 m, 5.viii.1973; 87, Kikladhes, Tinos Isl., E of Koumaros, 360 m, 31.vii.2004.

Fig. 88. *Chorthippus bornhalmi*, Fthiotis, Mt. Oiti between Pavliani & Kastania, 1300-1700 m, 19.ix.1989.

Figs 89-92. *Chorthippus biguttulus biguttulus.* 89, Germany, Berlin, Grunewald, W. Ramme; 90-91, The Netherlands, Zeeland, Vrouwenpolder, 1-2.viii.1964; 92, The Netherlands, Limburg, Eygelshoven, industrieterrein Julia, 9.viii.1997.


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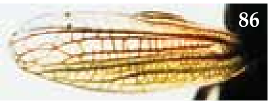
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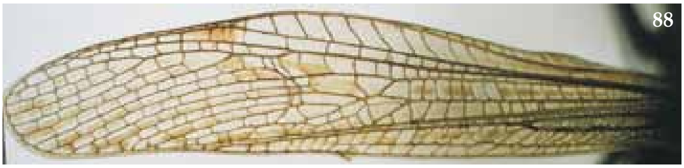
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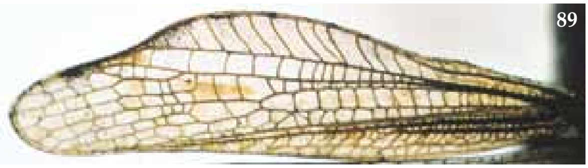
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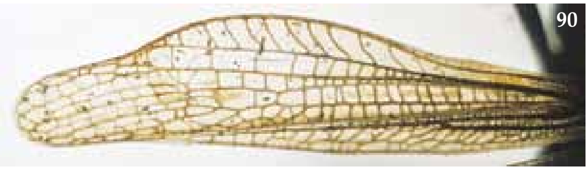
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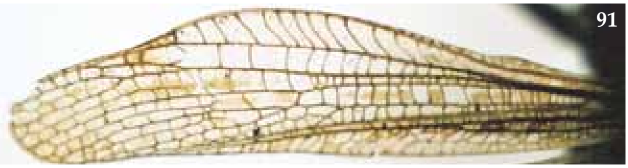
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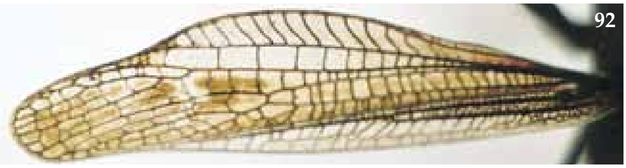
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Figs 93-96. *Chorthippus biguttulus euhedickei.* 93-94, Pieria, M. Olimbos above Sparmos, refuge B, 1800-1900 m, 14.viii.1966; 95, Voiotia, Mt. Parnassos, 1460 m, main road to ski centres, 22.vii.2000; 96, idem, 1500 m, near Gerondovrachos, 23.vii.2000.


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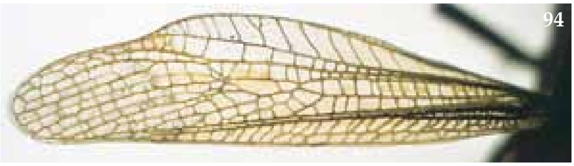
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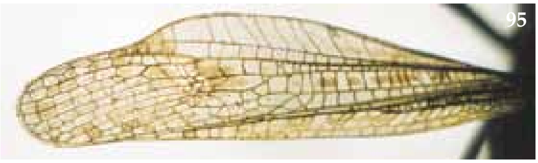
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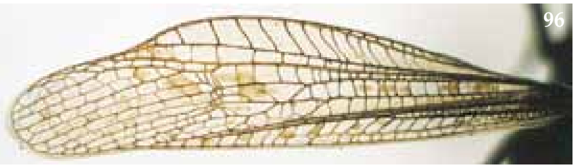
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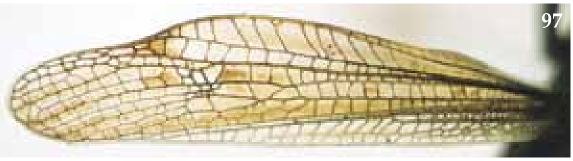
Figs 97-98. *Chorthippus biguttulus euhedickei* / *biguttulus parnassicus* contact zone: Voiotia, Mt. Parnassos, 1600 m, road to ski centres, 2 km after exit to Gerondhovrachos, 23.vii.2000, road verge with *Stipa* grasses, pine forest; 97, conform *b. euhedickei*; 98, conform *b. parnassicus.*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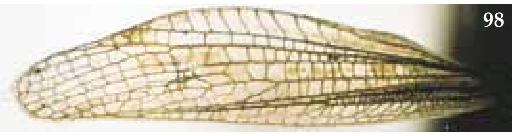
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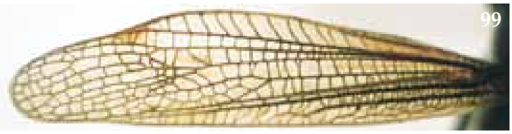
Figs 99-102. *Chorthippus biguttulus parnassicus*, Fthiotis, Mt. Parnassos; 99, 1680 m, between ski centres Kelaria & Fterolakis, 2.ix.1989; 100-101, 1900 m, above ski centre Fterolakas, 3.ix.1989; 102, 2000 m, above ski centre Kelaria, 2.ix.1989 (all topoparatypes).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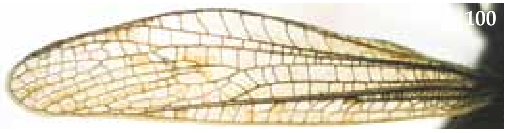
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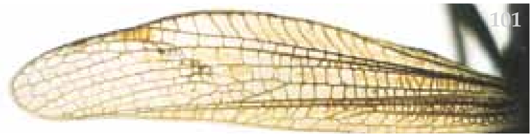
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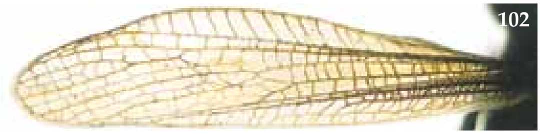
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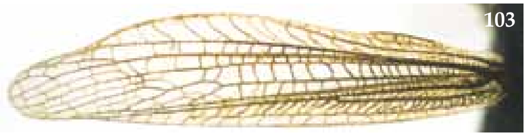
Figs 103-107. *Chorthippus moreanus*. 103, Ilia, ruins of Bassae near Andritsena, 1100 m, 7.ix.1989 (paratype); 104, Messinia, Petra-Kakaletri, 600 m, 8.ix.1989; 105-106, Lakonia, Mt.Taiyetos above Anoyeia, 1250-1550 m, 1.viii.1991; 107, Arkadhia, north of Elliniko, near Dhimitsana, 1100 m, 9.ix.1989.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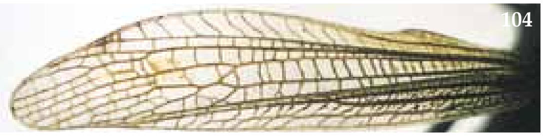
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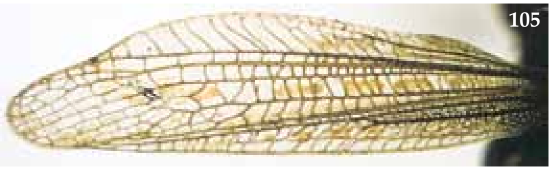
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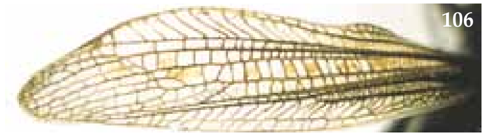
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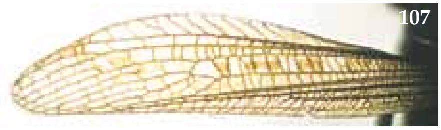
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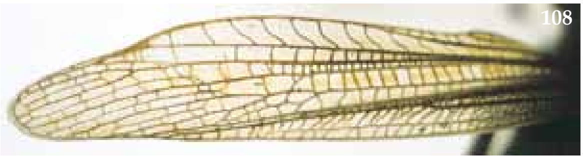
Fig. 108. *Chorthippus mollis lesinensis*, Kroatia, Hvar Isl., 500 m south of Pitve, 300 m, 13. viii.1996, R. Kleukers (topotype).

Fig. 109. *Chorthippus mollis pechevi*, Bulgaria-Varna, Kranevo 12.viii.1967, M. Karaman (paralectotype) (CK).

Figs 110-113. *Chorthippus mollis mollis*. 110, Kilkis, Evzoni, along highway, 150 m, 20.ix.1989; 111, Ioannina, Mt. Tomaros above Varyadhes, 1200-1600 m, 2. viii.1978; 112-113, Voiotia, Mt. Parnassos, between Arachova and ski centres, 1300 m, 2. ix.1989.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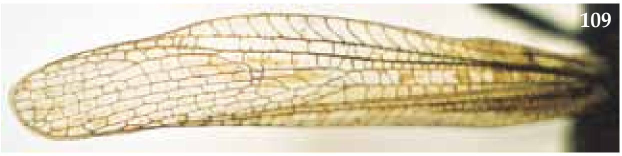
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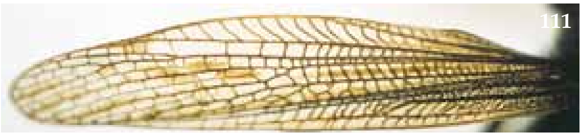
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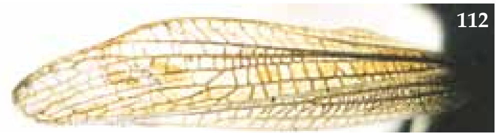
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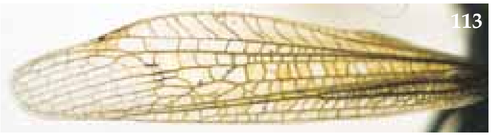
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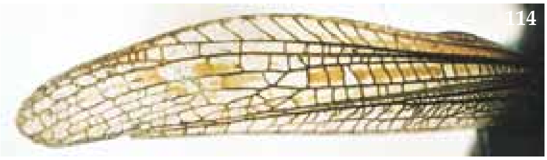
Figs 114-117. *Chorthippus crassiceps*. 114-115, Argolis, Poros Isl., circuit along island, 50-200 m, 4-5.viii.1988 (topotypes); 116, Argolis, Mt. Dhidhimo near summit, 1050 m, 14.ix.1989; 117, Argolis, Arachnaio Mts, Limnes-Ayionori, 600 m, 2.viii.1991.

Figs 118-120. *Chorthippus parnon*. 118, Lakonia, 3 km south of Monemvasia, 5.x.1992, R. Kleukers (paratype); 119-120, Lakonia, Kithira Isl., 4.5-5.5 km south of Pelagia, 320 m, 25-27.vii.2001.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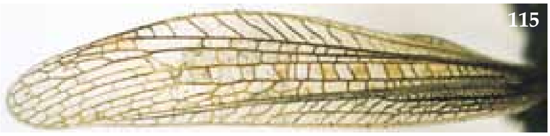
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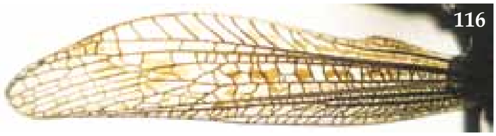
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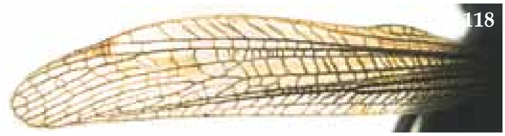
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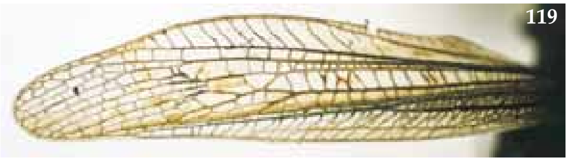
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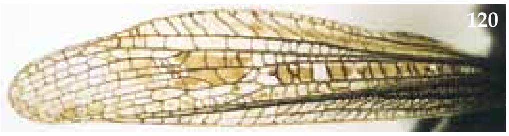
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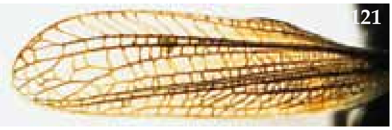
Figs 121-130. *Chorthippus pulloides*. 121-122, Akhaia, Kalavrita, Mt. Chelmos (= Aroania) above Kato Lousoi, 1700-2000 m, 1.viii.1970 (topotypes); 123-124, Arkadhia, Mt. Mainalon above Kardhara, 1550-1981 m, 27.vii.1975 & 2.viii.1988; 125, Aitolia-Akarnania, Mt. Akarnanika above Thirion, 800-1400 m, 18.vii.2000; 126-127, Ioannina, Mt. Kakardhitsa above Pramandha, 1800-1850 m, 27.vii.2003; 128, Akhaia, Mt. Panakhaikon, pass southeast above Mirali, 1100 m, 8.viii.2003; 129-130, Lakonia, Mt. Taiyetos above Anoyeia, 1600-1700 m, 1.viii.1991.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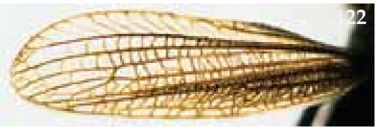
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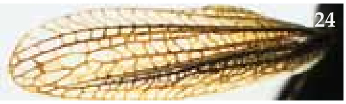
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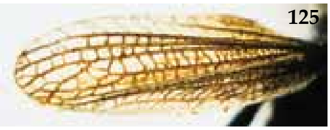
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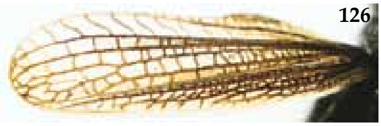
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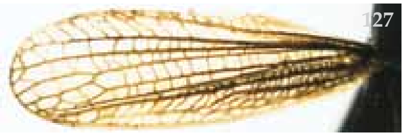
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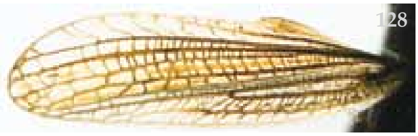
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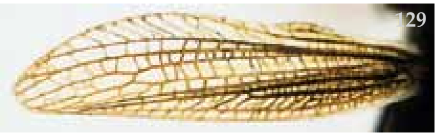
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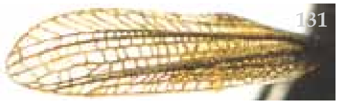
Figs 131-132. *Chorthippus sangiorgii,* Kefallinia Isl., Mt. Ainos, 1000-1300 m, 2-3.vii.1986.

Figs 133-138. Non-identifiable, transitional populations between *C. moreanus* and *C. pulloides/crassiceps*. 133, Lakonia, Polidrosos, northeast of Sparti, near bridge, 1000 m, 31.vii.1991; 134, Lakonia, northeast of Sparti, 5 km west of Polidrosos, 950 m, 31.vii.1991; 135-136, Arkadhia, north & south of Valtesiniko, 1300 m, 10.ix.1989; 137-138, Arkadhia, south of Vitina, 5 km south of Elatis, 1200 m, 11.ix.1989.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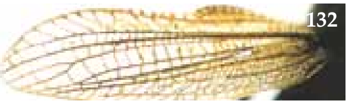
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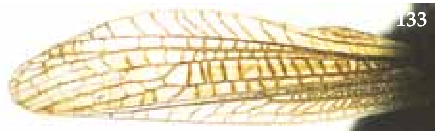
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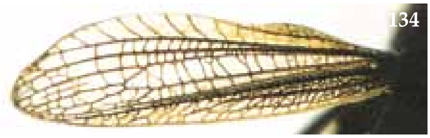
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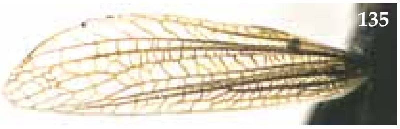
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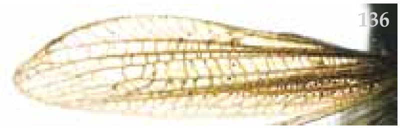
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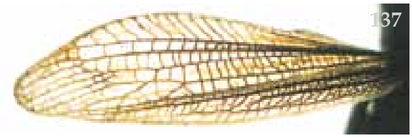
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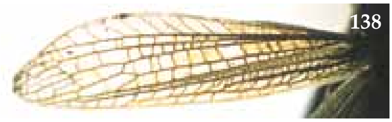
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Figs 139-140. *Chorthippus pulloides*. 139, Akhaia, Mt. Chelmos, 1700-200 m, 1.viii.1970 (topotype); 140, Aitolia-Akarnania, Mt. Akarnanika, above Thirion, 800-1400 m, 18.vii.2000.

Fig. 141. *Chorthippus willemsei*, Mt.Chelmos, 1700-200 m, 1.viii.1970 (topotype).

Fig. 142. *Chorthippus sangiorgii*, Kefallinia Isl., Mt. Ainos, 1000-1300 m, 2-3.vii.1986.

Fig. 143. *Chorthippus biroi*, Kriti, Lefka Ori, Linoseli above Xiloskalo, 1600-1800 m, 5.viii.1973.


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Figs 144-173. *Chorthippus*, pronotum of female, dorsal view (unless otherwise stated from Greece, collected by the Willemse's and in CW)

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Fig. 144. *Chorthippus apricarius apricarius*, Greece, Trikala, Mt. Avgo above Nea Pefki (NE of Mesochora), 1550-2000 m, 30. vii.2003.

Figs 145-147. *Chorthippus vagans vagans*. 144, Russia, Poltava region, Mirgorod district, 23. vii.1996, V. Sorochintzi & V. Vedenina; 145, Germany, Bellinchen bei Berlin, 18.viii.1938; 146, Italy, Potenza, Bosco Cupolicchio, 900 m, 4.ix.1956, M. La Greca.

Fig. 148. *Chorthippus vagans africanus*, Algerie, Grande Kabyl, Forêt Akfadou, 1100-1300 m, 18.vii.1979, Nadig (paratype).

Fig. 149. *Chorthippus vagans cypriotus*, Cyprus, Lefkosia district, Machairas forest, 10 km SE Lazanias, 1100 m, 2.x.2005, J.M. Tilmans & J.F.R. Tilmans-Smid (CT).

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Figs 150-151. *Chorthippus vagans dissimilis*. 150, Peloponnisos, Akhaia, Kastelli (south of Kalavrita), 980 m, 10.ix.1989 (topoparatype); 151, Attika, Varnavas (near Marathon), 450 m, 16. ix.1989 (paratype).

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Figs 152-153. *Chorthippus willemsei*. 152, Peloponnisos, Akhaia, Mt. Chelmos, 1700-2000 m, 1. viii.1970 (topoparatype); 153, Fthiotis, Mt. Oiti, summit Koriphin, 1900-2158 m, 7.viii.1972.

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Figs 154-156. *Chorthippus biroi*. 154, Kriti, Mt. Lefka, Omalos plateau, 1000 m, 4.viii.1973 (topotype); 155, Kriti, Mt. Lefka, Linoseli above Xiloskalo, 1600-1800 m, 6.viii.1973; 156, Kikladhes, Tinos Isl., pass E of Koumaros, 360 m, 31.vii.2004.

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Figs 157-159. *Chorthippus bornhalmi*. 159, Kikladhes, Mykonos, NW of Kalafati, 50 m, 21.v.2004; 160, Evros, 870 m, 19 km E of Nea Sandha, 1.vii.2000; 161, Peloponnisos, Arkadhia, Mt. Mainalon above Kardharas, 1600 m, 10-11.vii.1974.

Figs 160-161. *Chorthippus biguttulus euhedickei*. 157, Pieria, Mt. Olimbos near refuge B, 1800-1900 m, 11.viii.1966; 158, Voiotia, Mt. Parnassos, main road to ski centre, 1400 m, 23.vii.2000.

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Fig. 162. *Chorthippus biguttulus parnassicus*, Fthiotis, Mt. Parnassos above ski centre Fterolakas, 1750 m, 10.viii.1988 (topoparatype).

Fig. 163. *Chorthippus moreanus*, Peloponnisos, Ilia, ruins of Bassae, 1100 m, 7.ix.1989 (topoparatype).

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Fig. 164. *Chorthippus mollis lesinensis*, Croatia, Hvar, 500 m S of Pitve, 300 m, 13.viii.1996, R. Kleukers (topotype).

Figs 165-167. *Chorthippus mollis mollis.* 165, Thesprotia, Mt. Chionistra (1644 m), above Elataria (N of Paramythia), 1400-1600 m, 25.vii.2003; 166, Arta, Mt. Gavrogo above Megalochari, below summit Yerabi, 1500-1750 m, 3-4.viii.2003; 167, Voiotia, Mt. Parnassos, Arachova to ski centres, 1300 m, 2.ix.1989.

Fig. 168. *Chorthippus crassiceps,* Argolis, Poros Isl., along circuit of island, 50-200 m, 3.ix.1989 (topoptype).

Fig. 169. *Chorthippus parnon,* Peloponnisos, Lakonia, 3 km S of Monemvasia, 8.x.1992, R. Kleukers (paratype).

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Fig. 170. *Chorthippus sangiorgii*, Ionian Is, Kefallinia, Mt. Ainos, 1000-1300 m, 2-3.vii.1986.

Figs 171-173. *Chorthippus pulloides*. 171, Peloponnisos, Akhaia, Mt. Chelmos above Kato Lousoi, 1700-2000 m, 1.viii.1970 (topotype); 172, Peloponnisos, Arkadhia, Mt. Mainalon above Kardhara, 1500 m, 2.viii.1988; 173, Aitolia-Akarnania, Mt. Akarnanika above Thirion, 800-1400 m, 18.vii.2000.

Figs 174-203. *Chorthippus*, left tympanum of female (unless otherwise stated, from Greece, collected by the Willemse's and in CW).


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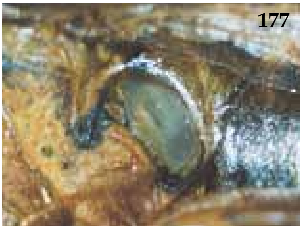
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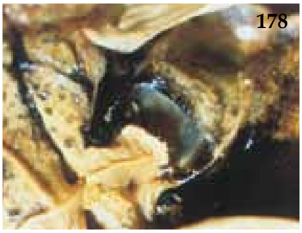
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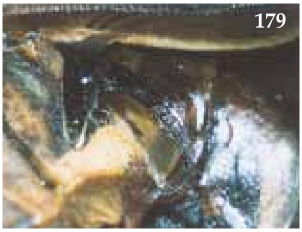
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Figs 174. *Chorthippus apricarius apricarius*, Trikala, Mt. Avgo above Nea Pefki (NE of Mesochora), 1550-2000 m, 30.vii.2003.

Figs 175-177. *Chorthippus vagans vagans*. 175, Russia, Poltava region, Mirgorod district, 23. vii.1996, V. Sorochintzi & V. Vedenina; 176, Lower Austria, Anniger, 13.ix.1904, R. Ebner; 177, France, Gorges du Tarn, Montignac, 18.vii.1976, F. Weverling.

Fig. 178. *Chorthippus vagans africanus,* Algerie, Djurdura, Tala Guilef, 1100 m, 21.vii.1979, A. Nadig.

Fig. 179. *Chorthippus vagans cypriotus,* Cyprus, Lefkosia district, Machairas forest, 10 km SE Lazanias, 1100 m, 2.x.2005, J.M. Tilmans & J.F.R. Tilmans-Smid (CT).

Figs 180-182. *Chorthippus vagans dissimilis*. 180, Akhaia, Potamia, SE of Paos, 600 m, 29.vii.1988, shade of large oaks along Lhadon river; 181, Fokis, Lilaia (Mt. Parnassos), 750 m, *Quercus* forest, 2.ix.1989; 182, Insel Samothraki, Küstenstreife 3 km vor Ortschaft Therma, 25.viii.1982, Dr. Zilch (all paratypes).

Figs 183-184. *Chorthippus willemsei*. 183, Evritania, Proussos, Kastania to Aghiro Pighadhi, below summit Mt. Triandhafillia, 1380-1460 m, 9.viii.2004; 184, Peloponnisos, Mt. Erimanthos ab. Kalentzi, 1700-2000 m, 4.viii.1970.

Figs 185-187. *Chorthippus biroi*. 185, Kriti, Kedros Ori, Ano Meros, 500-700 m, 1.viii.1973; 186, Kikladhes, Tinos Isl., E of Koumaros, 360 m, 31.vii.2004; 187, Kriti, Gavdos Isl., between Kastri and Ambelos, 300 m, 24.vi.2000, J.M. Tilmans & J.F.R. Tilmans-Smid (CT).

Fig. 188. *Chorthippus bornhalmi*. Ipiros, Konitsa, 10-12 km S of Samarina (Mt. Smolikas), 12-1400 m, 21.vii.2001.

Figs 189-190. *Chorthippus biguttulus euhedickei*. 189, Mt. Olimbos, refuge B, 1800-1900 m, 14.viii.1966; 190, Voiotia, Mt. Parnassos, main road to ski centre, 1460 m, 22.vii.2000.

Fig. 191. *Chorthippus biguttulus parnassicus*. Fthiotis, Mt. Parnassos, 1750 m, near ski centre Fterolakis, 10.viii.1988 (topoparatype).

Fig. 192. *Chorthippus moreanus*. Ilia, ruins of Bassae near Andritsena, 1100 m, 7.ix.1989 (topoparatype).

Fig. 193. *Chorthippus mollis lesinensis*. Kroatia, Hvar Isl., 500 m south of Pitve, 300 m, 13. viii.1996, R. Kleukers (topotype).

Figs 194-196. *Chorthippus mollis mollis*. 194, Yugoslav Makedonia, Titov Veles, lake Mladost, 250 m, 31.viii.1989; 195, Ioannina, Mt. Mitsikeli above Lingiadhes, 1100 m, 23.vii.2003; 196, Voiotia, Mt. Parnassos, main road to ski centre, 20 & 24. vii.2000, 1320 m, road verge in pine forest.

Fig. 197. *Chorthippus crassiceps*. Argolis, Poros Isl., circuit along island, 50-200 m, 4-5.viii.1988 (topotype).

Fig. 198. *Chorthippus parnon.* Peloponnisos, Lakonia, Monemvasia, 500 m east of Elliniko, 6.x.1992, R. Kleukers (paratype).

Figs 199-201. *Chorthippus pulloides*. 199, Peloponnisos, Akhaia, Mt. Chelmos, Kato Lousoi, 1000 m, 31.vii.1970 (topotype); 200, Aitolia-Akarnania, Mt. Akarnanika above Thirion, 800-1400 m, 18.vii.2000; 201, Ioannina, Mt. Kakardhitsa above Pramandha, 1800-1850 m, 27. vii.2003.

Figs 202-203. *Chorthippus sangiorgii*. 202, Kefallinia Isl., Mt. Ainos, 1000-1300 m, 2-3.vii.1986; 203, Kefallinia Isl., Dhilinata, 2-3.vii.1986 (topotype).

Specific part

APRICARIUS GROUP

typical species: *Gryllus (Locusta) apricarius* Linnaeus, 1758: 433 (type probably lost)

Chorthippus apricarius apricarius (Linnaeus, 1758)

(figs 23-24, 72, 144, 174, 260, cd 38)

Gryllus (Locusta) apricarius Linnaeus, 1758: 433 (type probably lost, see below).

Chorthippus (Glyptobothrus) apricarius apricarius; Willemse, 1984: 147, map 202 (full Greek references & localities); 1986: 76, figs 1008-1011 (identification).

Chorthippus (Chorthippus) apricarius apricarius: Storozhenko, 2002: 11 (taxonomic status).

Material studied.— MAKEDHONIA: Drama, Rodhopi Mts. Area, Elatia Centre, 1450 m, 10.viii.1985 & 3 km N of Elatia Centre, 1450 m, 15.viii.1985 & 9 km NE of Elatia Centre, 1450 m, 13.viii.1985 & Kriovrisi (5 km NW of Elatia Centre) 1400 m, 11.viii.1985 & Vathiremma 1400 m (N of Elatia Centre), 15.viii.1985 & Partheno Dasos (= Zagradenia), 1400-1700 m, 12.viii.1985 & Megali Panayia (20 km NW of Elatia Centre), 1350 m, 11.viii.1985. Katerini, Pieria Mts, Fteri (10 km NW), 1500 m, 25.vii.1974 & above Katafigion, 1600 m, 24.vii.1974. Florina, Mt. Vernon, Mt. Bela Voda (= Pisodherion), 1700-1971 m, 27.vii.1972 & 3 km S of pass, 1500-1600 m, 13.viii.1988. THESSALIA: Kardhitsa, eastern slopes of Mt. Voutsikaki (W of techn. lake Tavropou or Plastira & SW of Filakti), 1720 m, 29.vii.2000 & Kazarma Range (1977 m = Zigourolivadho), below summit Moutsiara (2133 m) (2133 m) (joined with Voutsikaki), 1640-1900 m, 15.vii.2002, saddle above timberline, low vegetation, grazed, WGS84 N39°18′13.8″ E21°37′23.5″. Trikala, W of Pertouli, Mt. Neraidha above Neraidhochori, below summit Boudhoura (2010 m), 1650 m, 1.viii.2003, open pine forest, WGS84 N39°33′08.3″ E21°26′32.0″ (series of which 1 ♂, 1 ♀ in BMMH/L; 1 ♂, 1 ♀ in ZI/P); Mt. Avgo above Nea Pefki (NE of Mesochora), 1550-2000 m, 30.vii.2003, from grassy meadows to stony slopes, WGS84 N39°28′39.1″ E21°22′45.0″ - N39°29′19.2″ E21°22′40.5″. IPIROS: Ioannina, Mt. Grammos, W of Aetomilitsa, along road E of Plikati, 700-2000 m, 10.viii.2006; Mt. Lakmos above Mikro-Peristeri-Rahoula, 1850 m, 13.vii.2002, stony slopes at N side of summit Gianaki (2198 m) close to Peristeri (= Tsoukarela, 2295 m), WGS84 N39°42′18.5″ E21°07′52.1″; Mt. Kakardhitsa (Mt. Athamanika, connecting Mt. Lakmos & Mt. Tzoumerka) above Matsouki (N of Pramandha), slopes below summit Katarachias (2280 m), 1800-1850 m, 27.vii.2003, WGS84 N39°35′13.0″ E21°10′37.5″ - N39°32′42.4″ E21°11′13.2″; (together 49 ♂ and 84 ♀, all collected by the Willemse's & unless otherwise stated in CW).

Recognition and bioacoustics (cd 38).— Descriptions can be found elsewhere and for the acoustics, the reader is referred to *e.g.* Ragge & Reynolds (1998). Greek *apricarius* agrees fully with the nominate subspecies which is well known, well defined and easily recognisable. Figures are given here of the male and female habitus (figs 23-24), male fore wing (fig. 72), female pronotum (fig. 144) and its tympanum (fig. 179).

Differential diagnosis.— The fused cubital veins and the enlarged M area with the regularly arranged transverse veins in the male are most characteristic (fig. 72).

Discussion.— The type of *apricarius* is absent in the Linnaean collection of the Linnean Society of London (Marshall, 1983). The type-locality is considered to be "Sweden, Öland" (Åsberg & Stearn, 1973). Harz (1975) designated both a male and a female as "neotype" (MHN/G) but for several reasons, these are to be considered invalid (Marshall, 1983).

Distribution.— This species has a very wide range, from West Europe far into temperate Asia. In Greece confined to high mountain pastures or forest clearings in northern continental Greece, extending from eastern to western Makedhonia and southward along the Pindhos Range. Apart from the six localities recorded in Willemse (1984, map 202), the species became known from another nine sites (fig. 260).

VAGANS GROUP

typical species: *Oedipoda vagans* Eversmann, 1848: 12 (types Orenburg area, ZI/P: ?).

Chorthippus vagans (Eversmann, 1848)

The range of typical *vagans (vagans vagans)* is known to reach from the British islands into southeastern Russia and from Denmark to the Iberian Peninsula and Italy (*e.g.* Harz, 1975; Ragge & Reynolds, 1998). Its occurrence in the southern Balkans was badly known and old records from some Aegean islands and Anatolia needed confirmation (Harz, 1975; Willemse, 1984).

Recently Nadig (1981) described *vagans africanus* from Algeria. His diagnosis was based on the tympanal aperture being slightly narrower than in the nominate form, a relatively longer pronotal metazona and a relatively narrower Sc area of the male fore wing. Its song was unknown but has now been recorded for the first time (see below) and proved to be very closely related to that of *vagans vagans*.

As for Greece, some old records have been considered doubtful because based on the morphology no specimens could be identified as *vagans* among the rich material at hand (Willemse, 1984). Ingrisch & Pavicevic (1985), however, reported *vagans* from northern Greece. Their identification was based on the calling song of a single male. Unexpectedly the general appearance and morphological features of this specimen agreed with *mollis* rather than *vagans*. This record showed that the "sing-alikes" of *vagans* in Greece, including those from Aegean Islands and West Anatolia invariably lack some of the morphological key characters of typical *vagans* (Ragge *et al.*, 1990). This may well explain why old records of *vagans* from these areas have been considered doubtful, because the morphology of the specimens did not agree with typical *vagans*.

Another not yet published discovery is that *Chorthippus cypriotus*, described from Cyprus by Uvarov (1936), also produces a *vagans*-like song. Like in Greek and Anatolian populations of *vagans*, the morphology of *cypriotus* disagrees with typical *vagans vagans* if not more so. Despite the difference in morphology, the similarity of the songs of *cypriotus* and *vagans* seems a valid argument to consider *cypriotus* a subspecies of *vagans*.

Chorthippus reissingeri, known from Southeast Spain (Harz, 1972) and originally described as subspecies of *mollis*, also produces a *vagans*-like song (Ragge & Reynolds, 1998). The morphology of this species, however, differs strikingly from that of *vagans* (s.l.). Apart from the characters mentioned in Ragge & Reynolds (1998), the head is much wider than the length of the pronotum and in the male the number of stridulatory pegs is below 100 and the pegs are more widely spaced, about 20 per mm. Whether the last characters are consistent is uncertain by lack of sufficient material. The exact status of *C. reissingeri* within the *C. vagans* group is not further discussed here as it falls outside the scope of this study.

Summarizing the following intraspecific taxa among *vagans* (s.l.) are recognised: *C. vagans vagans*, *C. vagans africanus*, *C. vagans dissimilis* and *C. vagans cypriotus.*

Key to the intraspecific taxa of *Chorthippus vagans* (table 1; fig. 204)

1. Tympanal aperture wide open, maximum distance between edges in male 1.7-2.4 (mean 2.0), female 1.7-2.7 (mean 2.2) times their minimum distance (figs 175-177); pronotal sulcus in or just beyond middle of pronotal length, ratio length prozona to length metazona in male 0.92-1.12 (mean 1.02), female 0.94-1.05 (mean 0.98) (figs 145-147); Europe except southeastern Balkans .... *vagans vagans*

\- Tympanal aperture narrower, maximum distance between edges in male 2.38-4.25, in female 2.1-5.5 times their minimum distance (figs 178-182); pronotal sulcus in or before middle of pronotal length, ratio length prozona to length metazona in male 0.73-0.93, female 0.68-0.90 (figs 148-149,150-151); elsewhere **2**

2. Tympanal aperture relatively less narrow, maximum distance between edges in male 2.38-2.65 (mean 2.5), in female 2.17-3.55 (mean 2.6) its minimum distance (fig. 178); male fore wing relatively narrow, fore edge with costal areas less bulging, ratio length of fore wing to width of the combined C & Sc areas (measured along same line) in the male 15-19 (mean 17) (figs 76-77); Morocco, Algeria, Tunis .... *vagans africanus*

\- Tympanal aperture relatively narrower, maximum distance between edges in male 2.67-4.25, female 2.85-5.45 its minimum distance (figs 179-182); male fore wing relatively wider, fore edge with costal areas well bulging, ratio length of fore wing to width of combined C & Sc areas (measured along same line) in the male 12-17 (figs 78-81); elsewhere **3**

3. Stridulatory file short, in male 2.9-3.5 (mean 3.13), female about 4.1-4.4 mm; number of pegs lower, male about 115-119, female about 107-117; Cyprus .... *vagans cypriotus*

\- Stridulatory file longer, in male 3.7-4.7 (mean 4.1), female 4.5-5.0 (mean 4.8) mm; number of pegs larger, in male 135-189 (mean 163), female 122-176 (mean 148); southern Balkans, western Anatolia .... *vagans dissimilis*

Chorthippus vagans vagans (Eversmann, 1848)

(figs 20, 73-75, 145-147, 175-177, 204, tables 1, 20-21)

Oedipoda vagans Eversmann, 1848: 12 (types Orenburg area, S. Russia; ZI/P ?, not studied).
Chorthippus (Glyptobothrus) vagans: Willemse, 1984: 146 ("previous records from Greece need confirmation").
Chorthippus (Chorthippus) vagans vagans: Storozhenko, 2002: 12 (taxonomic status).

Material studied.— Topotypes: Russia, W of Orenburg, Rostov region, 25 km NE of Oblirskaya, 17. vii.1991, M. Bukhvalova (3 ♂, 3 ♀, in ZMMSU/M).
Additional material from The Netherlands, Belgium, France, Iberian Peninsula, Germany, Italy, Slovakia, Austria and Russia (96 ♂, 177 ♀, in CW).

Recognition.— This species superficially resembles *brunneus, biguttulus, mollis* and morphologically similar taxa. It belongs to the group characterized by angled pronotal lateral keels, fully developed wings with recognisable precostal area and divergent cubital veins (figs 73-75) and lack of any striking colour pattern. The wide-open oval tympanal aperture (figs 175-177) in combination with almost equal length of pro- and metazona of the pronotum (figs 145-147) are considered key characters for this species. Biometric data for the male and female are given in table 20-21.

Table 1. More or less distinct morphological data between *Chorthippus vagans vagans*, *C. v. africanus*, *C. v. dissimilis* and *C. v. cypriotus* (fig. 204).

	vagans vagans	*vagans africanus*	*vagans dissimilis*	*vagans cypriotus*
ratio maximum / minimum diameter of tympanum	♂ 2.07 (1.74-2.39) ♀ 2.22 (1.76-2.70)	♂ 2.50 (2.38-2.65) ♀ 2.63 (2.17-3.55)	♂ 3.51 (2.67-4.25) ♀ 4.18 (2.85-5.45)	♂ 3.83 (3.05-4.23) ♀ 3.36-4.25
idem, Nadig, 1981		♂ 2.4-3.1 ♀ 2.4-2.8		
ratio length of prozona / length of metazona	♂ 1.02 (0.92-1.12) ♀ 0.98 (0.94-1.05)	♂ 0.85 (0.79-0.93) ♀ 0.86 (0.82-0.90)	♂ 0.83 (0.73-0.91) ♀ 0.79 (0.68-0.88)	♂ 0.89 (0.86-0.93) ♀ 0.75-0.90
ratio length of fore wing / width of comb. C & Sc area	♂ 14.9 (12.9-16.9)	♂ 17.1 (15.1-19.0)	♂ 15.5 (13.5-17.0)	♂ 13.2 (11.9-14.2)
ratio length of fore wing / maximum width of Sc area	♂ 37 (30-51)	♂ 52 (46-57)	♂ 44 (37-52)	♂ 38.4-42.9
idem, Nadig, 1981	♂ 45 (36-55) ♀ 66 (54-75)	♂ 63 (56-86) ♀ 81 (76-93)		
length of stridulatory file	♂ 3.6 (2.8-4.25) ♀ 4.9 (4.5-5.2)	♂ 3.87 (3.65-4.0) ♀ 4.87 (4.5-5.1)	♂ 4.13 (3.7-4.7) ♀ 4.82 (4.5-5.0)	♂ 3.13 (2.9-3.5) ♀ 4.1-4.4
number of stridulatory pegs	♂ 141 (115-169) ♀ 139 (121-157)	♂ 149 (129-165) ♀ 141 (131-154)	♂ 163 (135-189) ♀ 148 (122-176)	♂ 117 (115-119) ♀ 107-117
ventral basivalvular sclerite of lower ovipositor valve	touching each other medially over shorter distance (fig. 20)	touching each other medially over shorter distance	touching each other medially over longer distance (figs 21-22)	touching each other medially over shorter distance

More details on morphology, taxonomy, nomenclature as well as on bioacoustics and ecology are found in many publications: *e.g.* Brunner von Wattenwyl, 1882; Chopard, 1951; Bey-Bienko & Mishchenko, 1951; Faber, 1953; Jacobs, 1953; Richards & Waloff, 1954; Harz, 1957, 1960, 1975; Ragge, 1965; Marshall & Haes, 1988; Bellmann, 1993; Bellmann & Luquet, 1995; Kleukers *et al.*, 1997; Treiber in Detzel, 1998; Ingrisch & Koehler, 1998; Ragge & Reynolds, 1998; Nielsen, 2000; Storozhenko, 2002; Schlumprecht & Waeber, 2003.

Bioacoustics.— An overview of its bioacoustics is given in Ragge & Reynolds (1998).

Differential diagnosis.— The distinction between the nominate and other forms of this species is given above in the key and discussed under *v. dissimilis* (fig. 204, table 1).

Discussion.— To compare the other subspecies with the nominate form, it was necessary to be certain that *vagans* from western and central Europe indeed represents the nominate one. The type-locality of *vagans* is the area of Orenburg, Southeast Russia (Eversmann, 1848: “Habitat rarius in provincia Orenburgensi.”). We got opportunity to study some material west of Orenburg (Rostov region, 25 km NE of Oblirskaya, 17. vii.1991, M. Bukhvalova, ZMMSU/M), including oscillograms of their song. Their morphology, song and individual variation fully agreed with material at hand from large parts of central and West Europe.

Distribution and ecology.— The range of nominate *vagans* extends from Denmark

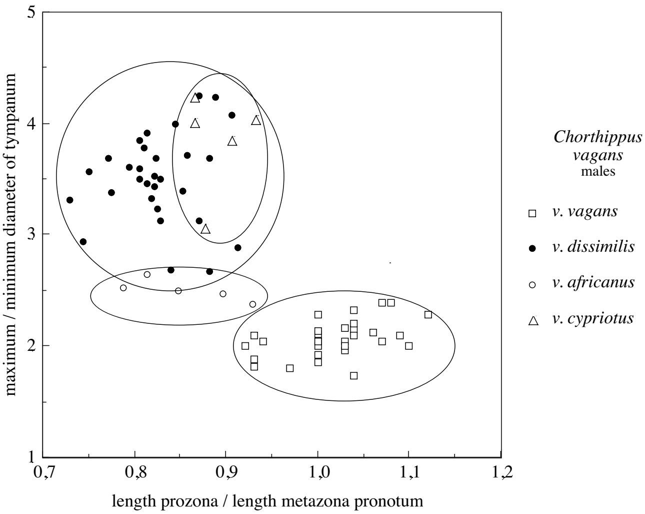


Fig. 204. Scatter diagram showing a plot of the ratio of the length of the prozona to the length of the metazona of the pronotum against the ratio of the maximum to minimum diameter of the tympanum in males of *Chorthippus vagans vagans*, *C. v. dissimilis*, *C. v. africanus* and *C. v. cypriotus*.

southwards into the Iberian Peninsula and Italy and from the British Isles eastwards to southern Russia and Kazakhstan (Childebaev & Storozhenko, 2001). Its distribution in the Balkans is badly known and discussed under *v. dissimilis*.

Ecological data can be found in the more recent publications listed above.

Chorthippus vagans africanus Nadig, 1981

(figs 25-26, 76-77, 148, 178, 204, 223, tables 1, 20-21, cd 1)

Chorthippus (Glyptobothrus) vagans africanus Nadig, 1981: 188, figs 1, 3, 5, 7 (♂ holotype, ♀ allotype, Algérie, Grande Kabylie, Col Talmetz, 1000 m, 18.vii.1979, leg. Nadig in CN-MHN/G; additional material from Algeria & Morocco).

Chorthippus (Chorthippus) vagans africanus: Storozhenko, 2002: 12 (taxonomic status).

Material studied.— ALGERIA: Algérie Grande Kabylie: Col Talmetz, 1000 m, 18.vii.1979 leg. Nadig (3 ♂, 2♀); Algérie Grande Kabylie Foret Akfadou 110-1300 m, 18.vii.1979 leg. Nadig (1 ♂, 1♀); Algérie Tala Guilef 1100 m, 21.vii.1979 leg. Nadig (1 ♂, 1♀) (all paratypes, partly in CN-MHN/G & CW).
TUNESIA: Ain Draham 17.x.1993 leg. S. Calvo (1 ♀) (CW) & Teboursouk, ix.1997, leg. Dagmar Dachlauer (1 ♂) (CvH).

Recognition.— Compare the original description and characters given here in the key. Habitus of male and female as in figs 25-26, male fore wing as in figs 76-77, pronotum and tympanum of female as in figs 148 & 178, Biometric data are given in the original description and in table 20 and 21.

Bioacoustics (fig. 223, cd 1).— The song of this species was unknown. Based upon the only available recording, the calling song very much resembles the calling song of the nominate form. The available recording shows an echeme of about 10 s, with about 70 syllables, repeated at the rate of about 7/s. The echeme begins quietly and reaches maximum intensity near the end of the echeme. Syllables show the distinct pattern of movement for the nominate form (see figs 15, 223 and paragraph about terminology). Syllables consist of a weak upstroke hemisyllable and a strong downstroke hemisyllable with

3-4 clear gaps that coincide with short pauses in the downward movement of the legs.

Differential diagnosis (table 1).— The distinction with nominate *vagans* is discussed in the original description. The tympanal aperture (fig. 178) is slightly narrower than in *v. vagans* but wider than in *v. dissimilis* and *v. cypriotus*. The location of the pronotal sulcus (Nadig, 1981, figs 1-2) (fig. 148), just in front of the middle of the pronotal length, differs from *v. vagans* and is shared both with *v. dissimilis* and *v. cypriotus*. The subspecies *africanus* differs from all other forms of *vagans* in the more elongate shape of the fore wings with a less bowed fore edge and a relatively narrow Sc area (Nadig, 1981, figs 5-8) (figs 25-26, 76-77).

Discussion.— Although morphological differences with the other subspecies are clear, no distinction was found in song characters. However, we have only been able to study one song of a single male. Recording and analysis of additional songs and specimens is needed to confirm the lack of distinct song characters.

Distribution and ecology.— The subspecies *v. africanus* was known from Morocco and Algeria (Nadig, 1981) but its range reaches also Tunisia as already suspected (Nadig, 1981). Data on habitat and life cycle are not yet reported except for Nadig's remark that the species occurs above 1000 m altitude.

***Chorthippus vagans dissimilis* subspec. nov.**

(figs 9-11, 21-22, 27-28, 78-80, 150-151, 180-182, 204-208, 224-225, 261, tables 1-4, 20-21, cd 2, 3)

Chorthippus (Glyptobothrus) mollis mollis [nec Charpentier]: Willemse, 1984: 145 (partim, to wit all material from the Peloponnese); Ingrisch & Pavicevic, 1985: 69 (partim: Nea Sanda & ? Tsopan & ? Nea Karvali & ? Skepaston).

Stenobothrus vagans: Brunner von Wattenwyl, 1882: 118 (Mt. Taiyetos). (?)

Stenobothrus bolivari [nec Brunner von Wattenwyl]: Giglio Tos, 1914: 2 (Rodhos). (?)

Stauroderus bolivari ? [nec Brunner von Wattenwyl]: Werner, 1936: 12 (Kos). (?)

Chorthippus (Stauroderus) vagans: Jannone, 1936: 165, 225, figs 1-7 (partim *bornhalmi*?) (Kos, Kalimnos, Telendhos, Patmos, Rodhos, Karpathos).

Stauroderus vagans: Salfi, 1937: 4 (Rodhos). (?)

Chorthippus aff. *lesinensis* ?: Willemse, 1984: 146 (Jannone's records from Karpathos & Dhodekanisos).

Chorthippus (Glyptobothrus) vagans: Ingrisch & Pavicevic, 1985: 69 (single male from Mt. Pangaion, N. Greece): Schmidt, 1990: 251 (oscillogram, a single male from Mt. Oiti, C. Greece, specimen could "not be traced").

Chorthippus vagans: Ragge *et al.*, 1990: 244 (atypical form occurring in Greece).

Chorthippus (Glyptobothrus) brunneus [nec Thunberg]: Popov *et al.*, 2001: 125 (Bulgaria, partim).

Chorthippus mollis [nec Charpentier] & *bornhalmi* [nec Harz]: Popov & Chobanov, 2004: 283-284 (partim?).

Material studied.— ♂ holotype, ♀ allotype, 19 ♂, 14 ♀ paratypes, labelled: "Hellas, Peloponnisos, Akhaia, Kastelli (south of Kalavrita), 980 m, 10.ix.1989, F. Willemse, stony slope above village, grasses, grazed, *Quercus* shrubs" (all in CW, except 1 ♂, 1 ♀ paratype in BMNH/L & 1 ♂, 1 ♀ paratype in ZI/P).
Additional paratypes:
PELOPONNISOS: Akhaia, Stena (S of Klitoria) 400 m, 2.viii.1988, shade of trees (1 ♂); Akhaia, Potamia (SE of Paos), 600 m, 29.vii.1988, shade of large oak trees (3 ♂, 5 ♀); Akhaia, Agridhi (30 km S of Kalavrita), 750 m, 29.vii.1988, grasses under chestnut trees (6 ♂, 5 ♀); Akhaia, A. Vlasias (N of Klitoria) 500 m, 2.viii.1988, orchard of nut trees, bare ground, dry grasses (4 ♂); Akhaia, 800 m, S of Egio, Mt. Klokos, 3 km N of Fteri, 28.vii.2002, open *Abies* & *Quercus* forest, poor undergrowth, WGS84 N38°10'17.1" E022°04'44.8" (6 ♂); Akhaia, Kato Lousoi (4 km S), 900 m, 2.viii.1988, cultivated land, shade of isolated

Crataegus tree (7 ♂, 1 ♀; Akhaia, Kato Lousoi (1 km N), 1000 m, 31.vii.1970 (1 ♂, 1 ♀) & 30.vii.1988, bare ground without vegetation in shade of oak tree next to church (1 ♂, 1 ♀); Akhaia, Kalavrita, ca. 13-15 km W, Waeldern/Weiden, 23.vii.1980, S. Ingrisch (1 ♂, labelled *m. mollis*) (CI) & Kalavrita, 16.viii.1998, F. Mayer (2 ♀) (CM); Akhaia, Mega Spilea, viii.1986, O. von Helversen (1 ♂) (CvH); Akhaia, Livartzi-Lekhouri (Psofidhia), 700-900 m, 15.vii.1991, valley of Aroania river, cultivated area, mixed vegetation (2 ♂, 3 ♀); Akhaia, Aroania village (W of Klitoria), 1000 m, 2.viii.1970 (6 ♂, 1 ♀); Arkadhia, Panayitsa 500 m, 28.vii.1975 (2 ♂, 1 ♀); Arkadhia, N of Vlakherna, 600 m, 2.viii.1988, bare ground, shade of trees (1 ♂); Korinthos, Mt. Oliyrtos above Kandhela, 900-1200 m, 26.vii.1975 (1 ♂) & above Lavka, 18.vii.1991 (4 ♂, 1 ♀); Korinthos, E side of Mt. Aroania, above Feneos village, 17.vii.1991, before (1100 m, *Quercus*) and at pass height (1400 m, open spot with herbs, shrubs, grasses) (2 ♂, 2 ♀); Korinthos, Feneos pass, 1000-1200 m, 17.vii.1991, forest clearing with mixed vegetation (3 ♂, 2 ♀); Korinthos, Mt. Killini above Trikala, 1200-1700 m, 6.viii.1970 (2 ♂, 4 ♀) & between Kaliani-Mouzion, 20.vii.1981, S. Ingrisch (1 ♂, labelled *m. mollis*) (CI); Stymphalia, Wiese/Ufer, 17.vii.1981, S. Ingrisch (1 ♂, labelled *m. mollis*) (CI); Soulion, 3 km NO, Kieferwald, 17.vii.1981, S. Ingrisch (1 ♀, labelled *m. mollis*) (CI); Kastania, Berge SW (= Mt. Oliyirtos), ueber 1000 m, Tannenwald, 17.vii.1981, S. Ingrisch (1 ♂, labelled *m. mollis*) (CI); CENTRAL GREECE: Attika, Kalivia Paralias-Anavissos, 40 m, 31.vii.2005, WGS84 N37°47′33.7″ E023°54′03.3″ (1 ♂); Attika, Mt. Kithironas, Lestoni near Panaghia, 640 m, 2.viii.2005, WGS84 N38°10′43.3″ E023°19′52.6″ (1 ♂); Attika, 510-1100 m, Mt. Yerania, road to OTE station, 23.vii.2001, open forest with *Pinus* and above 1000 m *Abies*, undergrowth *Erica*, stony ground (7♂, 2♀, of which 1 ♂ in BMNH/L & 1 ♂ in ZI/P); Attika, Anoxi (S of Marathon lake) 150 m, 7.viii.1988 (11 ♂, 1 ♀); Attika, Varnavas (near Marathon), 450 m, 16.ix.1989, pine forest, dry ground with grasses (15 ♂, 9 ♀ of which 1 ♂, 1 ♀ BMNH/L); Keratea, 4.x.1984, H. Schmalfuss (1 ♂, 1 ♀) (CW); Fokis (Mt. Parnassos), 2 km above Lilaia, 750 m, 2.ix.1989, shrubs, *Quercus* forest (3 ♂, 1 ♀); Aetolia-Akarnania, Mt. Tsakalakis near Elefteriani, 900 m, 6.viii.2004, WGS84 N38°32′31.8″ E021°51′03.3″, pine forest clearing (1 ♂); IPIROS: Ioannina, Konitsa, 10-12 km S of Samarina, 1200-1400 m, near crossing of small river betw. Dhistrato-Samarina, 12.vii.2001, forests, burned in 2000, verge of road, WGS84 N40°04′27.0″ E020°59′42.0″ (1 ♀); MAKEDHONIA: Kavalla, Mt. Pangaion, 1800-1900 m, 19.vii.1982, alpine Matten, Gipfelregion, S. Ingrisch (1 ♂) (in CI); THRAKI: Rodhopi, Chara Koma, ca. 8 km von Nea Sandha, ca. 800-900 m, lichter, beweideter Eichenniederwald, 7.vii.1981, S. Ingrisch (1 ♂ in CI, labelled *m. mollis*); Evros, 400 m, S of Kirki to Alexandroupolis, 14.vii.2001, dense *Quercus-Pinus* forest, verge of road, very dry (1 ♂); Evros, 0-5 m, Anthia, 3 km S, near coast, 15.vii.2001, lagoons, partly salty and covered with low vegetation, Juncus & Tamarisk, WGS84 N40°50′29.0″ E025°59′17.8″ (1 ♂); THRAKIAN IS: Samothraki, Küstenstreifen 3 km vor der Ortschaft Therma, 25. viii.1982, Dr. Zilch (2 ♂, 4 ♀) (in CvH); E. AEGEAN IS: Lesbos, Mitilini, 18.x.1973, A.C. & W.N. Ellis (3 ♂, 2 ♀) (CW); Anaxos Skoutarou, 0 m, 6.vii.1989 (1 ♂) & 6 km NW Andissa, 200 m, 4.vii.1989 (1 ♂, 1 ♀), J.M. Tilmans & J.F.R. Tilmans-Smid (CT); Chios, 1 km W Karies, 300 m, 2.vii.1989, J.M. Tilmans & J.F.R. Tilmans-Smid (1 ♂) (CT); Ikaria, 5 km SW Mileopo, 200 m, 23.vi.1989 (3 ♂, 1 ♀) & 3 km SE Kosikia, 500 m, 23.vi.1989 (1 ♀) & 6 km NE Langadha, 750 m, 24.vi.1989 (1♂, 1 ♀) & Profitis Ilias, 600 m, 24.vi.1989 (2 ♂) & Ayios Kiriaki, 50 m, 25.vi.1989 (1 ♀), all. J.M. Tilmans & J.F.R. Tilmans-Smid (CT); Samos, ix.1995, O. von Helversen (3 ♂, 3 ♀) (2 ♂, 2 ♀ CvH, 1 ♂, 1 ♀ CW); Pyrgos, 6.vi.1963 & Vathy, 15.v.1963, S. Daan & V. van Laar (2 ♀) (CW); 6 km NE Mitilinioi, 250 m, 29.vi.1989, J.M. Tilmans & J.F.R. Tilmans-Smid (CT) (1 ♂); Kos, 5 km SW Andimakhia, 150 m, 17.v.1997 (4 ♂, 4 ♀) & 5.v.1991 (2 ♂, 3 ♀) & 27.v.1991 (3♂) & 8 km SW Andimakhia, 175 m, vii.1991 (1 ♂, 2 ♀), all. J.M. Tilmans & J.F.R. Tilmans-Smid (CT); Kalimnos, 3 km S Vathis, 100 m, 14.v.1997 (5 ♂, 1 ♀), J.M. Tilmans & J.F.R. Tilmans-Smid (CT); Leros, *Quercus* macrolepis forest, 21.vii.1997, K. Papapavlou (1 ♂); 3 km SW Koulouki, 50 m, 13. (7 ♂) & 4 km SE Partheni, Mt. Klidhi, 250 m, 15. (1 ♂, 3 ♀) & 3 km E Partheni, Mt. Klidhi, 125 m, 15. (5 ♂, 4 ♀) & 1.5 km SW Xirokambos, Mt. Katavati, 100 m, 16. (4 ♂, 2 ♀) & Ayia Kioura, 2 km N Partheni, 0 m, 11. (2 ♂, 4 ♀) & Alinda, 0 m, 15., all v.1997, all. J.M. Tilmans & J.F.R. Tilmans-Smid (CT); Patmos, Kambos beach, 0 m, 7.v.1997 (2 ♂, 1 ♀) & 2 km W Groikos, 75 m, 9.v.1997 (2 ♂, 1 ♀), all. J.M. Tilmans & J.F.R. Tilmans-Smid (CT); Rodhos, 4 km N of Salakos & 4 km S of Kritinia & Lindhos, 19-28.v.1983, R. Danielson (3 ♂, 2 ♀) (CW); BULGARIA: Struma Valley, 2 km S of Kamenitsa vill. (Blagoevgrad distr., Strumyani), 250 m, Q. *coccifera* community, between bushes on the ground, 12-13.x.2006, D. Chobanov (2 ♂, 2 ♀); Struma Valley: Kresna gorge N of Kresna (Blagoevgrad distr.), 400-450 m, 27.ix.1997, D. Chobanov (1 ♂, 1 ♀); Struma Valley: Kozhuh hill near Rupite vill. (Blagoevgrad distr., Petrich), 100-200 m, 5.viii.1997, D.

Chobanov (1 ♂, 2 ♀); S Pirin Mts: SE slope of Sveti Iliya hill near Kalimantsi vill. (Blagoevgrad distr., Sandanski), Q. *coccifera* community, 450-510 m, 11.ix.-5.x.2003, M. Langourov (1 ♂, 1 ♀); S Black Sea coast: Meden Rid hill NW of Sozopol, W of Rosenmine settlement (Burgas distr.), sparse xerothermic oak (*Quercus* spp.) forest, 100-200 m, 21.viii.2004, D. Chobanov (1 ♂, 1 ♀) (Bulgarian material partly in NMNH/S & CW). TURKEY: Prov. Antalya, Akseki pass, 29.ix-12.x.1989, O. von Helversen (2 ♂, 1 ♀) (in CvH); Boz Dag, 1000 m, 15.viii.1986, O. von Helversen (1 ♂) (in CvH); Prov. Burdur, Celtikci Cecidi 1225 m, S Burdur, trockene Hugel, beweidete, eher xerotherme Grass- und Krautfluren, 1.vii.1986, H. Kriegbaum & O. von Helversen (1 ♂) (in CvH). (unless otherwise stated collected by the Willemse's and in CW).
Additional material tentatively arranged under *v. dissimilis*, all collected by S. Ingrisch (CI), labelled *m. mollis*, morphological cf *v. dissimilis* but confirmation of identity by song wanted: GREECE: THRAKI: Evros: Tsopan, 2 km suedlich Avra, leichter Nordhang, Lichtungen in beweideten Eichenniederwald, Quellbach, 6.vii.1981 (1 ♂). MAKEDHONIA: Drama: Falakron Oros, ueber Xiropotamos, ca. 100-800 m NN, 28.vii.1982, felsige suedexponierte, beweidete Haenge (1 ♀); Kavalla: Nea Karvali, felsige Trockenhaenge, 15-20.vii.1982 (2 ♂); Thessaloniki: Vertiskos, Khoumnikon-Skepaston, 13.vii.1982, (2 ♂); THESSALIA: Magnisia: Mt. Pilion, Xourinthi, Kastanienwald, 23.vii.1981 (1 ♂, 1 ♀) & NW Haria, Wald, 22.vii.1981, (1 ♂).

Recognition (table 1).— Male and female differ from nominate form as follows: size slightly larger (figs 27-28), pronotal prozona as long as in nominate form but metazona slightly longer, transverse sulcus not located in the middle of pronotal length as in nominate form but in front of the middle; greatest width of pronotal disc measured at its hind edge larger than in nominate form (figs 150-151); tympanal aperture narrower than in nominate form, minimum distance between its margins about 1/3 to 1/4 of the maximum distance, not 1/2 as in nominate form (figs 180-182); fore wing (figs 78-80) longer and with few exceptions extending from just to well beyond tip of hind knee in both sexes; hind femur and stridulatory file slightly longer than nominate form, number of stridulatory pegs slightly larger but spacing per mm as in nominate form; abdominal terminalia, including phallic complex as in nominate form but exposed part of ventral basivalvular sclerites of lower ovipositor valve slightly longer and touching each other medially over a longer distance than in nominate form (figs 21-22). Coloration as in the nominate form.

Measurements (length in mm): body ♂ 15-18, ♀ 21-23; pronotum ♂ 2.7-3.7, ♀ 3.5-4.6; elytron ♂ 12.2-16.5, ♀ 14.8-17.6; hind femur ♂ 8.9-11.7, ♀ 11.1-13.4. Biometric data for the male and female in table 20-21.

Bioacoustics (figs 224-225, cd 2-3).— Based upon the available recordings, the calling song very much resembles the calling song of the nominate form. The available recordings show an echeme of variable duration, from at least 4 seconds up to almost one minute. Syllables are repeated at the rate of about 4-8/s. The echeme begins quietly and reaches maximum intensity between about halfway the echeme and the end of the echeme. Syllables show the distinct pattern of movement of the nominate form (see fig. 15 and paragraph about terminology). Syllables consist of a weak upstroke hemisyllable and a strong downstroke hemisyllable with 6-8 clear gaps of about 10-15 ms that coincide with short pauses in the downward movement of the legs. The syllables are well separated from each other by an inter-syllabic interval, coinciding with the first part of the upstroke of the hind legs.

The courtship song is more prolonged, with the echeme starting very quietly with a gradual crescendo and lasting up to 5 minutes or longer.

Differential diagnosis.— *Chorthippus v. dissimilis* is easily distinguished from nominate *vagans* (table 1) by its narrower tympanal aperture, longer pronotal metazona and distally wider pronotum with its sulcus located in front of the middle of the pronotal length (fig. 204). The fore wings are longer, particularly obvious in the female where they commonly extend well beyond the tip of the hind knee, while the fore wings of the female in *v. vagans* commonly extend scarcely or not beyond the tip of the hind knees. The longer stridulatory file with a larger number of pegs in *v. dissimilis* may be associated with the greater length of the hind femur. While the male abdominal terminalia of all subspecies of *vagans* appear not clearly distinct from each other, the ventral basivalvular sclerites of the lower ovipositor valves (figs 21-22) of *v. dissimilis* are commonly longer than in other forms of *vagans* (fig. 20), but this difference is subtle. Distinction between *v. dissimilis* and *v. africanus* and *v. cypriotus* is given in the key above and in table 1.

In continental Greece, north of the Peloponnese, *v. dissimilis* may occur syntopically with *m. mollis*. Due to overlap of most biometric data, characters of pronotum, tympanal aperture and forewings are commonly not reliable to separate *v. dissimilis* from *mollis*, particularly not the relatively large and slender form of nominate *mollis* of the lowlands in northern Greece, adjacent former Jugoslavia and Bulgaria (fig. 110). More reliable features in both sexes are commonly found in the length of the stridulatory file and the number of pegs. The file in *m. mollis* is shorter than in *v. dissimilis* and the number of pegs lower than in the *vagans* subspecies (figs 205-206). Also the more inflated male subgenital plate and its longer tip (figs 12-14) in *mollis* are useful to separate both species (fig. 205). The length of the freely exposed part of the apex of phallus in *mollis* is shorter (0.55-0.65 mm) (fig. 14) than in *vagans* (s.l.) (0.65-0.85 mm) (fig. 11). The ventral basivalvular sclerites of the lower ovipositor valves touch each other medially commonly over a shorter distance in *mollis* (figs 18-19) than in *v. dissimilis* (figs 21-22). Distinctive characters are summarized in table 2. The song, however, is the most reliable character to recognise both species.

Another sympatric species of *v. dissimilis* is *bornhalmi*. The latter is very common and has a wide range of habitats, including those of *v. dissimilis*. Both species were often found syntopic. Morphological distinction between *v. dissimilis* and *bornhalmi*, though

Table 2. Morphological data which may be helpful separating *Chorthippus vagans dissimilis* from Greek *C. mollis mollis* (figs 205, 206).

	vagans dissimilis	*mollis mollis* (Greece)
length of stridulatory file (mm)	♂ 4.13 (3.7-4.7) ♀ 4.82 (4.5-5.0)	♂ 3.15 (2.6-3.65) ♀ 4.13 (3.8-4.6)
number of stridulatory pegs	♂ 163 (135-189) ♀ 148 (122-176)	♂ 113 (94-134) ♀ 109 (92-120)
length of tip of male subgenital plate (mm) (figs 9-14)	0.37 (0.20-0.50)	0.72 (0.60-0.85)
length of exposed part of apex of phallus (mm)	ca. 0.65-0.85 (fig. 11)	ca. 0.55-0.65 (fig. 14)
ventral basivalvular sclerite of lower ovipositor valve	touching each other medially over a longer distance (figs 21-22)	touching each other medially over a shorter distance (figs 18-19)

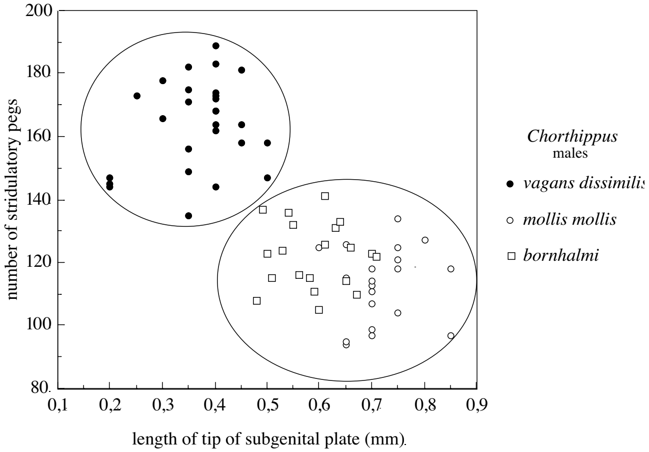


Fig. 205. Scatter diagram showing a plot of the length of the tip of the subgenital plate (mm) against the number of stridulatory pegs in males of *Chorthippus vagans dissimilis*, *C. mollis mollis* and *C. bornhalmi*.

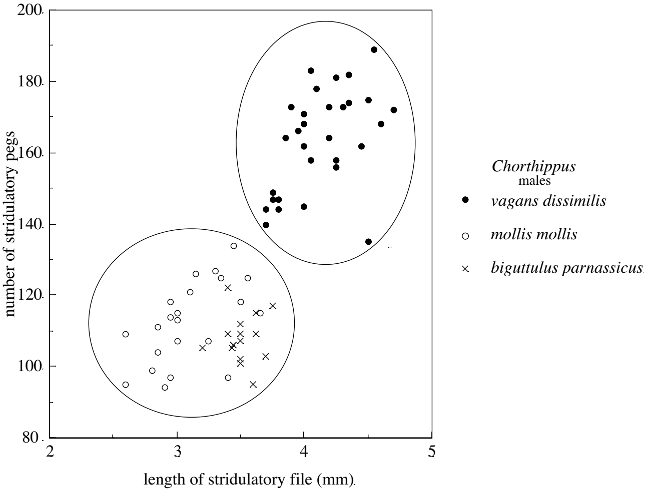


Fig. 206. Scatter diagram showing a plot of the length of the stridulatory file (mm,) against the number of stridulatory pegs in males of *Chorthippus vagans dissimilis*, *C. mollis mollis* and *C. biguttulus parnassicus*.

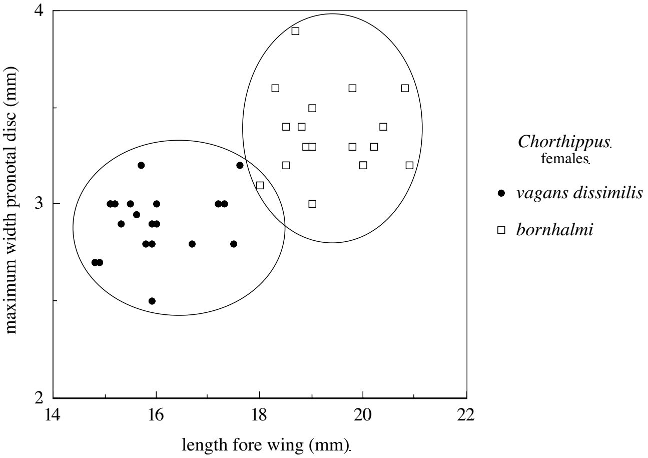


Fig. 207. Scatter diagram showing a plot of the length of the fore wing (mm) against the maximum width of the pronotal disc (mm) in females of *Chorthippus vagans dissimilis* and *C. bornhalmi*.

Table 3. Morphological data which may be helpful to discriminate between *Chorthippus vagans dissimilis* and *C. bornhalmi* (figs 205, 207).

	vagans dissimilis	*bornhalmi*
length of fore wing	♂ 13.8 (12.2-16.5) ♀ 15.9 (14.8-17.6)	♂ 15.3 (13.4-16.9) ♀ 19.4 (18.0-20.9)
distance from stigma to tip of fore wing	♂ 5.2 (4.6-6.3) ♀ 6.6 (5.6-7.2)	♂ 6.3 (5.4-7.3) ♀ 8.0 (7.4-8.8)
ratio distance from stigma to tip of fore wing / length of fore wing	♂ 0.37 (0.35-0.40) ♀ 0.39 (0.33-0.42)	♂ 0.41 (0.36-0.44) ♀ 0.42 (0.40-0.44)
ratio length prozona / length metazona	♂ 0.83 (0.73-0.91) ♀ 0.79 (0.68-0.88)	♂ 0.71 (0.58-0.82) ♀ 0.69 (0.66-0.74)
maximum width of pronotal disc (mm)	♂ 2.21 (1.9-2.7) ♀ 2.91 (2.5-3.3)	♂ 2.39 (2.15-2.7) ♀ 3.36 (3.0-3.9)
ratio maximum / minimum width of pronotal disc	♂ 2.33 (2.10-2.65) ♀ 2.49 (2.31-2.80)	♂ 2.62 (2.21-2.94) ♀ 2.78 (2.57-3.25)
ratio maximum / minimum diameter of tympanum	♂ 3.51 (2.67-4.25) ♀ 4.18 (2.85-5.45)	♂ 3.86 (2.77-5.38) ♀ 3.73 (2.80-5.03)
number of stridulatory pegs	♂ 163 (135-189) ♀ 148 (122-176)	♂ 124 (105-153) ♀ 103 (83-118)
number of stridulatory pegs per mm	♂ 40 (30-45) ♀ 31 (27-37)	♂ 31 (26-37) ♀ 20 (17-22)
length fore wing / length hind femur	♂ 1.37 (1.23-1.49) ♀ 1.31 (1.17-1.44)	♂ 1.55 (1.38-1.73) ♀ 1.45 (1.35-1.58)
length of tip of male subgenital plate (mm)	0.37 (0.20-0.50)	0.61 (0.50-0.70)
ventral basivalvular sclerite of lower ovipositor valve	touching each other medially commonly over a longer distance (figs 21-22)	touching each other medially commonly over a shorter distance (fig. 17)
integument (ventral thorax)	commonly with few hairs	commonly with dense hairs

commonly not difficult, may be arbitrary in some individuals due to overlapping of biometric data. No single character has been found to separate males of both taxa consistently (table 3). The habitus of *v. dissimilis* (figs 27-28) is commonly more robust than of *bornhalmi* (figs 36-37).The integument of *bornhalmi*, particularly of the ventral side of the thorax, is commonly strongly hairy while in *v. dissimilis* scarcely. The fore wings in *bornhalmi* (fig. 88) are more slender than in *v. dissimilis* (figs 78-80). In *bornhalmi* the apical part of the wing (distance between stigma and tip of wing) is longer and the tip of the flexed fore wing surpasses the tip of the hind knee slightly more in *bornhalmi* than in *v. dissimilis*. The tympanal aperture in *bornhalmi* is sometimes slightly narrower (fig. 188 against 180-182). The pronotum in *bornhalmi* (figs 157-159) has its lateral keels commonly more angled, often particularly shown in the female sex (figs 150-151 & 207) and the pronotal sulcus is often more in front of the middle of the pronotal length. The length of the stridulatory file is almost equal but the number of stridulatory pegs in *v. dissimilis* is commonly larger and the spacing of the pegs narrower than in *bornhalmi*. The length of the tip of the male subgenital plate in *bornhalmi* is commonly more than 0.5 mm, exceeding slightly that in *v. dissimilis* (fig. 9) but overlap seems well possible (fig. 205). The exposed part of the apex of the phallus in *v. dissimilis* (fig. 11) is slightly longer than in *bornhalmi* but also here the difference is not large. The ventral basivalvular sclerites of the lower ovipositor valve in *bornhalmi* (fig. 17) commonly touch each other medially over a shorter distance than in *v. dissimilis* (figs 21-22) but sometimes there is no difference at all.

Because many characters of *vagans dissimilis* and *bornhalmi* may overlap, in doubtful cases the song is most helpful for a reliable identification. The duration of the echeme in *bornhalmi* much shorter, 2-4 s against at least 4 s up to almost 1 minute or more in *vagans*; the syllable repetition rate in *bornhalmi* is faster, 7-10/s against 4-8/s in *vagans*; the intra-syllabic gaps and inter-syllabic intervals in *bornhalmi* are shorter and less sharply defined than in *vagans*. The number of intrasyllabic gaps usually is 1-3 in *bornhalmi* against 3-8 in *vagans* (compare figs 224-225 with fig. 232).

The distinction between *v. dissimilis* and *biguttulus euhedickei* is clear (width of combined C areas and length of stridulatory file; fig. 208, table 4). Distinction of *v. dissimilis* with *b. parnassicus* is possible by shorter fore wings (figs 27-28 & 78-80 against 42-43 & 99-102), narrower tympanal aperture (figs 180-182 against 191) and shorter stridulatory file with fewer pegs in the male of the latter (fig. 208, table 4).

Discussion.— Because the song and habitat (see below) of *v. dissimilis* and nominate *vagans* are similar, we consider both taxa conspecific. Morphological differences, however, are relatively large, at least among our available material. It may be expected that populations occurring geographically between the known ranges of both subspecies will show transitional characters. Such an area covers large parts of former Yugoslavia, extending between Slovenia and Yugoslav Makedhonia and parts of Bulgaria. Among rich material at hand from former Yugoslavia neither examples of the nominate form nor of *v. dissimilis* were found. Also references from this area as well as from Bulgaria are scarce: *e.g.* Adamovic, 1975; Buresh & Peshev, 1955; Cejchan, 1963; Ramme, 1951: 107; Peshev, 1970a, 1970b & 1974; Us, 1967, 1968. The question arises whether *vagans* indeed is rare, local or largely absent in this area. An explanation for this apparent distribution gap could be that typical *vagans* is replaced in this area by *v. dissimilis*

Table 4. Biometric data which may be useful to separate *Chorthippus vagans dissimilis* from *C. biguttulus parnassicus* and *C. biguttulus euhedickei* (figs 205, 208).

	vagans dissimilis	*biguttulus parnassicus*	*biguttulus euhedickei*
ratio maximum / minimum diameter tympanum	♂ 3.51 (2.67-4.25) ♀ 4.18 (2.85-5.45)	♂ 4.95 (3.38-6.36) ♀ 7.13 (6.0-7.7)	♂ 4.54 3.0-6.7) ♀ 5.07 (3.2-7.5)
length fore wing (mm)	♂ 13.8 (12.2-16.5) ♀ 15.9 (14.8-17.6)	♂ 11.3 (10.6-12.1) ♀ 14.4 (14.1-14.8)	♂ 13.3 (11.0-15.5) ♀ 16.4 (15.1-18.2)
width combined C & Sc area (mm)	♂ 0.89 (0.75-1.0)	♂ 0.84 (0.76-0.97)	♂ 1.15 (0.95-1.38)
ratio combined C & Sc area × 100 / length fore wing	♂ 6.45 (5.89-7.42)	♂ 7.49 (6.74-8.55)	♂ 8.69 (7.55-9.75)
length of stridulatory file (mm)	♂ 4.13 (3.7-4.7) ♀ 4.82 (4.5-5.0)	♂ 3.51 (3.2-3.75) ♀ 4.5 (4.3-4.7)	♂ 5.12 (4.2-5.77) ♀ 5.71 (5.2-6.3)
ratio length of stridulatory file / distance distal peg-tip of knee	♂ 1.01 (0.82-1.18) ♀ 0.93 (0.82-1.00)	♂ 0.95 (0.85-1.09) ♀ 0.87 (0.78-0.95)	♂ 1.75 (1.24-2.19) ♀ 1.35 (1.14-1.63)
number of stridulatory pegs	♂ 163 (135-189) ♀ 148 (122-176)	♂ 107.6 (95-122) ♀ 79.5 (70-90)	♂ 127 (109-149) ♀ 102 (90-108)

or transitional forms. Assuming that the song has not been known or noticed by these authors, the diagnosis commonly has been missed. An exception is Ramme's (1951: 107) record of *vagans* from Plagusa Planina, SE Jugoslavian Makedhonia that belongs to the SW Bulgarian Struma river area where the species is common (pers. comm. D. Chobanov). This identification problem is well demonstrated by the material from Bulgaria listed above but in the past commonly assigned to *mollis* or *brunneus* (*e.g.* Popov *et al.*, 2001).

Previous records from Greece that may refer to *v. dissimilis* are not unequivocal. Brunner's record of *vagans* from Mt. Taiyetos is (1888: 118) can be correct but needs re-examination. Jannone (1936: 165, 222) and Salfi (1937: 4) recorded *vagans* from Rodhos and some adjacent Aegean islands. Jannone (l.c.) included also material from Rodhos, originally identified as *Stenobothrus bolivari* Brunner v. W. in Giglio-Tos (1914: 2). From Jannone's comments his identification was based on unreliable colour characters. It is likely that he was dealing with two forms, figs 4-7 agreeing with *v. dissimilis*, figs 1-3 with *bornhalmi*. Re-examination of this material would be welcome. Weidner's record (1959: 34) of *vagans* from the island of Kerkira is interesting and his material should be re-examined to know which taxon it represents. Willemse (1984: 146, map 198, partim) stated that he didn't believe *vagans* to occur in Greece (without studying the song). Therefore he synonymized several old records (discussed above) under *lesinensis* and *crassiceps*. In the same paper he recorded *mollis* from Greece, noting that his "*mollis*" material from all over Greece was not uniform. The current study has shown that all his Peloponnesean material uniformly belonged to *v. dissimilis* and not to *mollis* while those of the Greek mainland represent the slender, long winged, nominate form of *mollis*.

Most of the records under *mollis* and *bornhalmi* in Popov & Chobanov (2004) from Bulgarian and Greek eastern Thraki will prove to be correct but it might be that a few refer to *v. dissimilis*.

Distribution and ecology.— Common in the northern and central part of the Peloponnese and known from a number of localities scattered all over central, western and northern Greece, southern Bulgaria, the eastern Aegean islands from Samothraki to Rodhos and some localities in western Anatolia (distribution in Greece, fig. 261). The habitats range from the lowlands up to 1500 m, in open forest, along forest edges and clearings, in the shade of isolated trees in cultivated land or on dry slopes with numerous bushes. In one locality the habitat is deforested areas overgrown by *Quercus* sp. Sometimes it is living on the litter of dead leaves devoid of any green vegetation. Remarkable is the preference for shaded places.

The life cycle in Greece is not precisely known. In mountain areas of the Peloponnese adults have been observed from late July to mid October. However, in the lowlands of Attiki adults appeared a month later, not before the end of August, living in the shade of coniferous trees of cultivated gardens. In the Aegean islands both juvenile and adult specimens were found in May and June but also in July, August and even September, in agreement with Jannone's observations (1936). Whether juveniles and/or adults hibernate is not known. These observations might suggest that the life cycle of *v. dissimilis* has much in common with that of *bornhalmi* but lack of sufficient data leaves this question still open.

Chorthippus vagans cypriotus **Uvarov, 1936 stat. nov.**

(figs 15, 29-30, 81, 149, 179, 204, 226; tables 1, 20-21, cd 4)

Chorthippus cypriotus Uvarov, 1936: 512-513, fig. 4 (♂ holotype Cyprus, Mt. Troodos, vii.1935, G.A. Mavromoustakis, BMNH); Harz, 1975: 827, 845, 851, 855, 888, figs 3106, 3330-3347 (description). Tumbrinck, 2006: 123, 144 (several localities).

Chorthippus (Chorthippus) cypriotus: Storozhenko, 2002: 11 (taxonomic status).

Material studied.— CYPRUS: Mt. Troodos, 5600 ft, 1-8.vii.1948 (1 ♂, 1 ♀) & 5500-6000 ft, 21.vi.1937 (1 ♂) G.A. Mavromoustakis (CW); Troodos, Mt. Olympos, 36S VD87836413, 1930 m, 24.vii.2001, B. Odé (3 ♂) (CO); Troodes, Mt. Olimpus, Schwarzkieferzone, 21.viii.1996, Helmut Kriegbaum (1 ♂) (CKr) (all topotypes); Lefkosia district, Machairas forest, 10 km SE Lazanias, 1100 m, 2.x.2005, WGS84 N34°54′94.9″ E033°11′51.9″, J.M. Tilmans & J.F.R. Tilmans-Smid (1 ♂, 1 ♀) (CT).

Recognition.— Already given in the original description and that presented in Harz (1975). Habitus male and female as in figs 29-30. Pronotal sulcus just in front of the middle of the pronotal length (fig. 149). Tympanal aperture relatively narrow, minimum distance between the edges 1/3 to 1/4 of maximum distance (fig. 179). Fore wing as in fig. 81. Number of stridulatory pegs low, about 115-119, in female about 107, file comparatively short, ratio between length of file and distance between distal peg to tip of hind knee, in ♂ about 0.77-0.91 (mean 0.83), in ♀ about 0.89. Abdominal terminalia as in nominate subspecies. Biometric data for the male and female in tables 20-21.

Bioacoustics (figs 15, 226, cd 4).— The song, previously unknown, very much resembles that of the nominate form. The available recording of the calling song shows an echeme of about 4,5 s, with 21 syllables, repeated at the rate of about 5/s. The echeme begins quietly and reaches maximum intensity halfway the echeme. Syllables show the distinct pattern of movement for the nominate subspecies. Syllables consist of a weak upstroke hemisyllable and a strong downstroke hemisyllable with 3-4 clear gaps that coincide with short pauses in the downward movement of the legs.

Differential diagnosis.— This subspecies is near *v. dissimilis* but differs clearly from the latter and the other subspecies in its smaller general appearance (figs 27-30), by the more pronounced bow of the costal areas of the fore wing in the male (figs 78-81) and in the relatively shorter stridulatory file and low number of pegs in both sexes (table 1).

The distinction between syntopic *bornhalmi* and *v. cypriotus* is clearly shown by the larger habitus, longer fore wings, wider hind margin of pronotum and commonly more hairy ventral side of the thorax in *bornhalmi* and quite evidently by their distinct songs.

Discussion.— Only six males and two females have been studied and the biometric and bioacoustic data given above do certainly not cover its complete range of variation. The shorter stridulatory file and lower number of pegs may be associated with the shorter length of the hind femur.

Although Uvarov (1936) already noticed that *cypriotus* comes near *vagans*, the narrower tympanal aperture and the location of the pronotal sulcus apparently convinced him that he was dealing with a distinct species.

More material is needed to describe this taxon in full detail.

Distribution and ecology.— Known from the highest parts of Cyprus, Mt. Troodos and some other localities summarized in Tumbrinck (2006): Lazanias (Tilmans), Cape

Greco, region of Protaras, plateau of Rayies (all Zickendraht). Adults have been found between 18 April and 2 October (Tumbrinck, 2006). The habitat in Mt. Troodos is a mosaic of rocks, patches of grass, dwarf shrubs and scattered trees (pers. comm. B. Odé & J. Tilmans) and consist in Machairas forest, 10 km SE Lazanias, 1100 m, of conifers, rockroses and oaks (pers. comm. J. Tilmans).

The subspecies lives syntopic with *bornhalmi*, the only other member of the *Chorthippus* group with angled pronotal keels known from Cyprus.

***Chorthippus willemsei* Harz, 1971**

(figs 31-32, 82-84, 141, 152-153, 183-184, 227-229, 262, tables 5, 22-23, cd 5, 6, 7)

Chorthippus willemsei Harz, 1971: 335, figs 8-11 (♂ holotype, ♀ allotype, Mt. Chelmos 1.viii.1970, Willemse & Scherpbier in CW; additional material between 1100-2000 m in Mt. Erimanthos, Mt. Kyllini, Mt. Taiyetos, Sparti-Kalamata, Mt. Timfristos).

Chorthippus (Glyptobothrus) willemsei: Harz, 1975a: 866, figs 3104-3105, 3156, 3226-3232 (description, faunistics); Willemse, 1979c: 157 (Mt. Tomaros); 1984: 147, map 200 (full references & localities); 1986: 75, figs 993-997 (identification); Schmidt, 1990: 248 (song, Mt. Oiti 1800 m, but see discussion below).

Chorthippus (*Chorthippus*) *willemsei*: Storozhenko, 2002: 12 (taxonomic status).

Material studied.— ♂ holotype, ♀ allotype & 29 ♂, 30 ♀ paratypes labelled: "Hellas (Peloponnisos), Kalavrita Mt., Chelmos (Aroania Or.), 1700-2000 m, i.viii.1970, Willemse & Scherpbier" "*Chorthippus willemsei* K. Harz det. 1971" (in CW, except 1 ♂, 1 ♀ paratype BMNH/L & 1 ♂, 1 ♀ paratype in ZI/P).
Additional material, all from Greece:
IPIROS: Ioannina: Mt. Tomaros above Variadhes, 1200-1600 m, 2.viii.1978 & 1450-1900 m, 12.viii.2004, between plateau at S slopes and summit (1974 m), slopes, low vegetation, WGS84 N39°28′18.4″ E20°47′02.8″ (CW) & Mt. Tomaros oberhalb Variadhes, Schotterhalden unterhalb Gipfels mit wenig Vegetation, 19.viii.1986 (CvH); Arta: Mt. Tzoumerka, south of Theodhoriana, 1400-1800 m, 24.vii.1987. THESSALIA: Kardhitsa: Mt. Voutsinaki, eastern slopes, SW of Filakti, 1720 m, 29.vii.2000 & S slopes near M. Revma, 1620 m, 29.vii.2000; Mt. Karava (= Schizokarevo, 2184 m) (W of lake Plastira), below summit Koulkoutsari (2016 m), 3 km W of pass A. Nikolaos betw. Pefkofito-Petrilo, above timberline, 1560 m, 16.vii.2002, WGS84 N39°19′20.7″ E21°34′49.5″; border with Evritania, pass Tria Sinora between Petrilo-Trovato, 1420 m, 16.vii.2002, WGS84 N39°14′57.2″ E21°07′18.5″, grassy slope, dry; Elatos, W of techn. Lake Tavropou (= Plastira), along road to Vrangiana, 1480 m, 28.vii.2000, grazed mountain slope; Fteri Range, Mt. Avgo (2162 m), below summit Kokkinolakes (1911 m), 1 km W of pass Tria Sinora betw. Petrilo-Trovato, 1575-1820 m, 17.vii.2002, stony ground, WGS84 N39°14′37.3″ E21°36′55.3″. CENTRAL GREECE: Aitolia-Akarnania: Khaliki, southern slopes of Mt. Panaitolikon, 900 m, 1.viii.1975; N of Ambelakiotissa, pass betw. Mt. Ardhinis & Mt. Tsekoura, 1260 m, 7.viii.2004, forest clearing, WGS84 N38°37′52.9″ E21°52′39.6″; Mt. Tsakalakis near Eleftheriani, 1100 m, 6.viii.2004, *Abies* forest, WGS84 N38°32′78.2″ E21°50′30.9″ & 900 m, 6.viii.2004, forest, WGS84 N38°32′31.8″ E21°51′03.3″ & S of Ano Chora & Kendriki (Ano Chora after 2 km branch to Nafpaktos, after 7 km branch to Kendriki, after 5 km branch to A. Kiriaki, after 3.5 km collecting site), 1200-1560 m, 7.viii.2004, WGS84 N38°33′36.7″ E21°53′26.9″, steep stony slope with bushes, trees and open places; Evritania: Mt. Panaitolikon, Xerovouni above Proussos, 1400-1650 m, 2.viii.1975 & pass betw. Proussos & Ladikou, local name Arkoudhotripa, 1450-1550 m, 7.vii.2003, clearings along *Abies* forest road & E slopes, below summit Mt. Triandhafillia (1817 m), SE of Proussos, betw. Kastania & Aghiro Pighadhi, 1380-1460 m, 9.viii.2004, stony ground, sparse vegetation, scattered coniferous trees, WGS84 N38°42′36.2-34.1″ E21°41′35.3-19.5″; Bachtal zwisschen Kleistos & Vracha (Karpenision), 15.viii.1981, O. von Helversen (CvH); Mt. Timfristos above Karpenision, 1800-2100 m, 29.vii.1971, F. Willemse c.s. (paratypes) & 1700-1800 m, 4.viii.1975 & near ski resort, 1650-1900 m, 18.vii.2002, WGS84 N38°56′37.4″ E21°48′26.5″, stony ground, grazed, above timberline & 1790 m, 10.viii.2004; Karpenisi, 500 m (?), *Abies* forest, 28.ix.1989, Schmalfuss; Mt. Helidona

above Palaio Chori (SW of Karpenisi), 1420-1650 m, 21.vii.2002, WGS84 N38°50′12.6″ E21°41′22.0″, from below to above timberline; Mt. Kaliakoudha, between Megalo Chori-Stournara (= Dholiana), near branching to Aniada, 1350 m, 20.vii.2002, *Abies* forest, WGS84 N38°48′25.8″ E21°45′59.8″; Mt. Oxia, Stavli-Gardiki, 6.5 km E of branch to Abliani, 1720 m, 19.vii.2002, WGS84 N38°46′51.1″ E21°55′36.3″, southern slope; N of A. Theodhoros (S of Karpenisi), 1500 m, 19.vii.2002, small clearing in *Abies* forest, WGS84 N38°50′56.3″ E21°50′35.8″. Fthiotis: above Timfristos village, 1100 m, 5.viii.1975; Mt. Oiti, 18.iii.1981, O. von Helversen (3 ♂) (CvH) & plateau below summit, 1750 m, 24.vii.1991 & central part below Katavothra (1775 m), near cave and spring, 1550 m, 22.vii.2002, about N38°46′29″ E22°18′50″, rich vegetation & near EOS Refuge, 1760 m, 6.viii.2004, WGS84 N38°49′91.4″ E22°16′31.2″ & Mt. Oiti, between Kastania-Pavliani, 1300-1700 m, 19.ix.1989 & 10 km W of Pavliani, 1750 m, 5.viii.1972 & above Ipati-Neokhori, 1500 m, 13.viii.1973 & near refuge above Ipati 1800-1900 m, 5-7.viii.1972 (series of which 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P) & summit Koriphin, 2158 m, 7.viii.1972. Fokis: Mt. Vardhousia above Mousounitsa, 1600-2000 m, 7-9.viii.1978; Mt. Giona, SW of Kaloskopi, 2 km S of Mnimata, 1290 m, 23.vii.2002, open places, *Abies* forest, WGS84 N38°40′21.5″ E22°18′19.4″. PELOPONNISOS: Korinthia: Mt. Killini above Trikala, 1200-1700 m, Willemse & Scherpbier (paratypes) & (= Mt. Ziria) above Katafigio B, 1500-1850 m, 24.vii.2005, N37°35′50.0″ E22°24′50.6″; lake Dhastion, 1500 m, 24.vii.2005, N37°58′50″ E22°25′30″; E side of Mt. Aroania, to and at Feneos Pass, 1100-1400 m, 17.vii.1991, *Quercus* forest and open site & at border Korinthos-Akhaia district, Feneos Pass between Likouria & Kalivia, 1000-1200 m, 17.vii.1991, large forest clearing; Mt. Oliyirtos above Lavka, 950-1050 m & 1200-1500 m, 18.vii.1991 & Mt. Oliyirtos, 15.viii.1998 (1 ♂, 1 ♀, alcohol) (CM); Akhaia: Mt. Chelmos (= Mt. Aroania) above Kalavrita & above Kato Lousoi, 1400 m, 30.vii.1988 & near ski centre, 30.vii.1988, plateau and slopes near ski centre & near ski resort Souvardo, 1520 m, 26.vii.2005, N38°01′51.3″ E22°12′36.3″ (topotypes); Mt. Panakhaikon above Zastova, 1000-1800 m, 30.vii.1975; Mt. Panakhaikon oberhalb Souli, alpinen Matten, stark beweidet, 21.viii.1986, O. von Helversen (CvH); Mt. Erimanthos, above Kalentzi, 1100-1700 m & 1700-2000 m, 3-4.viii.1970, Willemse & Scherpbier (paratypes) & above Kalentzi, 900-1100 m, 16.vii.1987 & above Mika, 1250 m, 18.vii.1987. Arkadhia: 4 & 8 km west of Khrisovitsi, 1100 & 1150 m, 28.vii.1978 & 11.ix.1989, forest clearing; N (forest) & S (dry slope) of Valtesiniko (N of Vitina), 1200 m, 10.ix.1989; Elati & 4 km S of Elati (S of Vitina), 1200 m, 11.ix.1989, dry small slope and forest clearing; Ilia: Mt. Lambia above Lambia village, pass betw. Lambia-Astras above Monasteri Dhivris, forest with clearings, 1000-1200 m, 15.vii.1991. Messinia: Sparti-Kalamata, just W of Langadha Pass, 1500 m, 3.viii.1988, wayside forest road; Lakonia: Sparti-Kalamai (= Kalamata) (Mt. Taiyetos), 1200 m, 24.vii.1970, Willemse & Scherpbier (paratypes); Taygetos Osthang ZW Kalamata & Sparta, 1300 m, Kieferwald, 25.viii.1986, O. von Helversen (CvH, alcohol vial 6/0068); Mt. Taiyetos above Anoiya, from Toritza to near refuge EOS-club and below summit Profitis Ilias, 1700-2200 m, 23.vii.1971, Willemse & Scherpbier (paratypes) & 1250-1550 m, 1.viii.1991, clearings along forest road; Mt. Taiyetos, forest road between Yeoryitsi and pass between Sparti-Kalamata, 1450 m, 28.vii.1991, clearing; Mt. Parnon, 14 km NE Vamvakou, 1300-1500 m, 25.vii.1998, J. Tilmans & J. Tilmans-Smid. (number of specimens together 295 ♂, 231 ♀, unless otherwise stated collected by the Willemse's and in CW).

Recognition.— Male. Small but comparatively robust (fig. 31). Head not inflated, fastigium verticis wide, very slightly impressed, ridges meeting each other at the tip in an angle just more than 90°, ridges and foveolae obtusely rounded, interocular distance relatively wide (0.9-1.0 mm).

Prozona of pronotum longer than metazona, ratio 1.22 (1.12-1.38); shortest distance between lateral keels about in the middle of the prozona, lateral keels not or slightly intersected by reduced first two transverse sulci. Tympanal aperture widely open, narrowest part slightly more than half the largest diameter.

Fore wing short, reaching from 7th tergite to commonly the base of supra-anal plate and about two thirds as long as hind femur, membrane half transparent, fore and hind margin about parallel, precostal lobe commonly well indicated, C, Sc and R usually straight throughout their length, sometimes slightly bowed, Sc and R divergent, Sc area measured along the line of greatest width of C area, one third to almost half as wide as C area; apex of wing obtusely rounded, R reaching apical margin just in front of the tip, stigma lacking (fig. 82-84). Abdomen and its terminalia comparatively robust.

Hind femur strong, length of stridulatory file almost one third of length of hind femur, average number of pegs 94, about 32 per mm, distance between terminal peg and tip of hind femur more than length of file.

Coloration commonly dark brown, pattern as usual in this group of species but darker. Hind femur of general colour, hind knee and very base of hind tibia dark brown to black, remainder of hind tibia red, also the lower side, sometimes brown, hind tarsus brown or reddish.

Female (figs 32, 152-153, 183-184), as male. Interocular distance wide, 1.2-1.3 mm, apex of fastigium verticis obtusely angled, slightly more than 90°. Fore wing short, reaching begin of 2nd to end of 3rd tergite, less than half hind femur length, left and right wing slightly separated from each other medially; fore margin, after precostal lobe, commonly straight and converging towards the narrowly rounded apex, hind margin slightly rounded (fig. 141). Coloration as male, transverse fasciae of hind femur commonly well distinct. Biometric data for the male and female in tables 22-23.

Bioacoustics (figs 227-229, cd 5-7).— Song was previously unknown. The calling song (fig. 227) is an echeme, repeated at irregular intervals. Each echeme lasts about 1 s and consists of 9-13 syllables, repeated at the rate of about 10/s. Syllables consist of a weak upstroke hemisyllable and a strong downstroke hemisyllable. The downstroke hemisyllable may - as in *vagans* - show 2-4 clear gaps that coincide with short pauses in the downward movement of the legs, but these gaps may also be missing as shown in a recording from Mt. Tomaros.

The courtship song (fig. 228) starts with irregular movements of both legs with low amplitude, producing almost no sound. These movements are followed by an echeme that may last up to 20 s and shows similarities with the calling song. Syllable repetition rate is lower, about 5/s, with the upstroke syllable less pronounced and the downstroke with more pronounced gaps.

During rivalry short echemes are produced, lasting less than 1 s (fig. 229).

Differential diagnosis.— This short winged species resembles other short winged species from Greece: *pulloides*, *sangiorgii* and *biroi*. While two of them occur allopatric, *biroi* in Kriti and the Kiklades and *sangiorgii* in some Ionian islands, *willemsei* and *pulloides* may live syntopic. Both are easily recognisable by their different tympanal aperture, widely open in *willemsei* and slit-like in *pulloides* (figs 199-201). Besides in *willemsei* the hind tibia is commonly bright red in both sexes whereas in *pulloides* it is yellow brown. However in the northernmost known population of the *pulloides* (Mt. Tsakalakis/Mt. Lakmos) the hind tibiae are as red as in *willemsei*, which may lead to confusion. Other differences refer to the length of the fore wing, in *willemsei* commonly shorter than in *pulloides* and the degree of transparance of the fore wing: in *pulloides* (figs ♂ 121-130, ♀ 139-140) glassy hyaline while the membrane of the fore wing in *willemsei* is less transparent and the network of transverse veinlets between the longitudinal veins apparently denser, particularly in the female.

The distinction between *willemsei* and the allopatric taxa *biroi* and *sangiorgii* is discussed under these species. Both share a slender habitus with relatively narrow fastigium verticis and interocular distance, yellow brown coloured hind tibiae, more transparent fore wings and in *biroi* a remarkable narrow Sc area of the male fore wing.

Some distinct characters of the short winged taxa are summarized in table 5.

In the Peloponnese, *willemsei* may also resemble morphologically atypical short-winged populations of *crassiceps*, *moreanus* and those mentioned below under *pulloides* as transitional ones. In all these cases *willemsei* differs by the wide open tympanal aperture, dark coloured hind knee, red hind tibia and the broadly rounded apex of the male fore wing while the other forms have narrower tympanal apertures, hind knee and tibia of general colour and the tip of the fore wing less broadly rounded, presenting what may be called a not yet fully reduced apical part (figs 107, 117, 133-138). Also the short fore wings of the female of *willemsei* (fig. 141) are quite distinct from the other taxa.

Table 5. Some data compared between *Chorthippus pulloides*, *C. sangiorgii*, *C. biroi* and *C. willemsei*.

		pulloides (throughout range except Mt. Akarnanika)		**pulloides** (population of Mt. Akarnanika)	
		♂	♀	♂	♀
habitus		robust (figs ♂ 60, ♀ 63)		robust (figs ♂ 64, ♀ 65)	
head	fastigium verticis	wide (figs ♀ 171-172)		wide (fig. ♀ 173)	narrow (fig. ♀ 170)
	interocular distance (mm)	0.83 (0.79-0.90)	1.23 (1.1-1.40)	0.78 (0.75-0.80)	1.06 (1.0-1.16)
tympanum	aperture	narrow (figs ♀ 199, 201)		narrow to very narrow (fig. ♀ 200)	
	ratio max. / min. diam. tympanum	6.3 (3.0-13.1)	11.4 (5.6-24)	8.8 (6.8-10.8)	17.1 (7.0-46.6)
hind tibia	colour	yellow brown to red, ranging from S. to N. part of range respectively		yellow brown to pale red	
pronotum	ratio length prozona / metazona	1.06 (0.93-1.16)	1.12 (1.0-1.55)	1.04 (0.94-1.12)	1.08 (1.0-1.25)
	figures		171-172		173
fore wing	ratio length / width fore wing	3.41 (2.17-3.89)	2.98 (2.67-3.33)	3.33 (3.1-3.57)	2.41 (2.15-2.84)
	length fore wing (mm)	7.52 (6.2-8.8)	7.22 (6.5-8.0)	6.48 (5.6-7.1)	4.93 (4.0-5.7)
	ratio length fore wing / length hind femur	0.82 (0.71-0.99)	0.61 (0.50-0.65)	0.67 (0.62-0.74)	0.44 (0.38-0.53)
	width Sc area (mm), measured along line of widest C area	0.29 (0.20-0.37)		0.27 (0.24-0.30)	
	ratio widest C / Sc area, along same line	1.72 (1.26-2.50)		1.44 (1.17-1.87)	
	membrane betw. veins	hyaline, glassy		hyaline, glassy	
	figures	121-124, 126-130	139	125	140
additional data	altitude of localities	middle altitudes up to far above timberline		700-1400 m (almost highest part of the locality)	
	song, ♂	molloid pattern (figs 248, 250-251)		molloid pattern (fig.249)	
	sympatry	sympatric with *willemsei*		allopatric	
range	geographic area	Peloponnese and western mainland of Greece		only Mt. Akarnanika in extreme southwestrn mainland of Greece	

Discussion.— Based on morphology and song it is evident that *willemsei* is closely related to *biroi* and less so to *vagans*. While *willemsei* and *biroi* live allopatric, syntopic occurrenc of *willemsei* and *v. dissimilis* has been observed in Mt. Oiti, Central Greece.

Analysis of songs of additional localities is needed to describe the variation of song characters more precisely.

The oscillogram figured as *willemsei* in Schmidt (1990: fig. 1) does not refer to that species but has been erroneously exchanged with that of another species (pers. comm. G. Schmidt).

Distribution & ecology.— Known from a number of mountains in the Peloponnese, Central Greece, Ipiros and West Thessalia but not from any island (fig. 262).

sangiorgii (Island of Kefallinia)		***biroi*** (throughout range)		***willemsei*** (throughout range)	
♂	♀	♂	♀	♂	♀
slender (figs ♂ 66, ♀ 67)		slender (figs ♂ 33-34, ♀ 35)		robust (figs ♂ 31, ♀ 32)	
narrow (figs ♀ 154-156)		wide (figs ♀ 152-153)			
0.62 (0.54-0.69)	0.92 (0.80-1.01)	0.65 (0.60-0.71)	0.91 (0.80-1.0)	0.90 (0.80-1.0)	1.23 (1.1-1.3)
intermediate (figs ♀ 202-203)		wide (figs ♀ 185-187)		wide to very wide (figs ♀ 183-184)	
4.7 (3.5-6.25)	5.4 (3.0-7.5)	3.0 (1.9-5.5)	2.6 (2.0-3.2)	2.6 (2.3-2.6)	2.4 (2,0-2.6)
yellow brown		various shades of brown, often with black flush		bright red, exceptionally brown (in female)	
1.03 (0.93-1.16)	1.07 (1.0-1.22) 170	1.16 (1.07-1.25)	1.16 (1.05-1.25) 154-156	1.21 (1.11-1.38)	1.24 (1.14-1.61) 152-153
3.78 (3.33-4.46)	2.98 (2.1-3.6)	3.03 (2.6-3.9)	2.47 (2.16-2.80)	3.17 (2.0-3.5)	2.0 (1.66-2.28)
6.48 (5.6-7.1)	6.16 (4.9-7.1)	5.28 (4.4-6.1)	5.20 (4.4-6.10)	6.52 (5.9-7.4)	4.95 (4.4-5.7)
0.78 (0.74-0.84)	0.56 (0.47-0.61)	0.64 (0.56-0.79)	0.50 (0.44-0.56)	0.69 (0.57-0.83)	0.41 (0.36-0.47)
0.23 (0.20-0.28)		0.13 (0.09-0.10)		0.21 (0.17-0.25)	
1.97 (1.75-2.5)		3.36 (2.27-4.53)		2.22 (1.6-2.7)	
hyaline, glassy to slightly opaque		hyaline, glassy		semitransparent, brownish smoked	
131-132	142	85-87	143	82-84	141
sea level up to 1300 m (highest part of range)		sea level up to above timberline		middle altitudes up to above timberline	
intermediate pattern (?) (fig.252)		*vagans* pattern (figs 230-231)		*vagans* pattern (figs 227-229)	
allopatric		allopatric		sympatric with *pulloides*	
known only from Ionian Islands of Kefallonia, Ithaki & Lefkas		known only from Crete and Aegean islands the Kiklades		mountains of Peloponnese, central and western mainland Greece	

In the mainland of Greece *willemsei* has been found together with *bornhalmi*, *m. mollis*, *b. euhedickei*, *apricarius* and on Mt. Tzoumerka (Arta) and Kakardhitsa (Ioannina) with *pulloides* and on Mt. Oiti (Fokis) with *v. dissimilis*. In the Peloponnese it may occur syntopic with *bornhalmi*, *moreanus*, *pulloides* and the group of short winged forms assigned to atypical populations of *crassiceps*, *moreanus* and transitional ones bridging the latter with *pulloides*.

This species lives from 700 m to above the timberline, in open forests and its clearings and edges but also on sunny slopes with stony ground and low vegetation of grasses and herbs. Adults appear from mid July.

Chorthippus biroi **(Kuthy, 1907)**

(figs 2, 33-35, 85-87, 143, 154-156, 185-187, 230-231, 262, tables 5, 22-23, cd 8, 9)

Stenobothrus spec.? Griffini, 1894: 92. (discussed in Willemse & Kruseman, 1976).
Stenobothrus petraeus [nec Brisout]: Werner, 1903: 65, 66. (discussed in Willemse & Kruseman, 1976).
Stenobothrus biroi Kuthy, 1907: 552, 554 (description, 10 ♂ & 9 ♀ syntypes, "Omalos die 18.Augusti", from Crete, Mt. Aspro-Vuna (= Leuka Ori), 1050 m, Omalos, 18.viii.1906 in HNHM/B; in Harz (1975a) & OSF (2005) said to be deposited in NHMV/W; lectotype here selected, see below).
Stauroderus biroi: Ramme, 1927: 194. (Omalos, 1 male/female "types" in HNHM/B).
Chorthippus (Glyptobothrus) biroi: Harz, 1975a: 876, figs 317-3158, 3285-3291 (description; Omalos & Lakki, Psychro); Willemse & Kruseman, 1976: 148, pl. 10 figs 47-48 (full references & localities); Willemse, 1984: 147, map 201 (idem; Naxos?); 1986: 75, 275, figs 998-1001 (identification); Nadig, 1985: 328 (Omalos).
Chorthippus (Chorthippus) biroi: Storozhenko, 2002: 11 (taxonomic status).

Material examined.— Lectotype female (here designated): labelled "Creta Biró" "Omalos 18.viii.06" (HNHM/B); topotypes: Mt. Lefka, Omalos plateau, 1000 m, 4.viii.1973, F. Willemse & J. Scherpbier (15 ♂, 10 ♀) (CW)) & 23.viii.1989, R. von Helversen (1 ♂) (CvH).
KRITI: Chania: Mt. Lefka, Linoseli above Xiloskalo, 1600-1800 m, 6.viii (14 ♂, 21 ♀, of which 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P) & near refuge Koukoule, 1600-1800 m, 6.viii (5 ♂, 2 ♀) & Vasiliana, W of Omalos, 700 m, 7.viii (2 ♀) & Lakki-Omalos, 30 km S of Chania, 750 m, 4.viii (13 ♂, 4 ♀) & Lakki, 25 km S of Chania, 450 m, 3.viii.1973 (1 ♀); Askyfou, 750 m, N of Chora Sfakion 2.viii.1973 (3 ♂, 3 ♀); 3 km N of Anopoli, 600 m, 13.vi.2000, WGS84 N35°14′34.7″ E024°04′57.1″, J.M. Tilmans & J.F.R. Tilmans-Smid (2 ♂, 1 ♀); 4 km E of Anidroi, 400 m, 17.vi.2000, WGS84 N35°15′40.5″ E023°44′31.2″, J.M. Tilmans & J.F.R. Tilmans-Smid (1 ♂). Gavdos Is: 300 m, between Kastri & Ambelos, 24.vi.2000, WGS84 N34°50′14.0″ E024°04′07.5″ (1 ♀) & 250 m, Karave, 11.vi.2000 [as juvenile], WGS84 N34°51′00.3″ E024°07′23.6″, (1 ♂, 1 ♀) J.M. Tilmans & J.F.R. Tilmans-Smid (CT). Rethimni: A. Galini, N of Timbaki, 0-40 m, 31.vii.1973 (1 ♂); Selia, 85 km S of Rethimni, 450 m, 2.viii.1973 (1 ♂); Mt. Kedros, S of Amari, Chordakion (= Kardakion), 450 m, 1.viii.1973 (13 ♂, 10 ♀); Ano Meros, 500-700 m, 1.viii.1973 (2 ♂, 2 ♀); Mt. Idhi, Zominthos, 12.ix.1999, O. von Helversen (1 ♂) (CvH) & Kamares-Kolita, 520-1650 m, 28-29.vii.1973 (3 ♂, 1 ♀) & Kolita-Psiloritis, 1700-2100 m, 28-29.vii.1973 (2 ♂, 1 ♀) & above ski centre Anogia, 1550 m, 12.viii.1989, J.M. Tilmans & J.F.R. Tilmans-Smid (2 ♂, 1 ♀). Iraklion: Malia, 32 km E of Iraklion, 10 m, 9.viii.1973 (1 ♀) & 29.x.1972 A.C. & W.N. Ellis (1 ♂, 1 ♀). KRITI: Lasithi: 11,6 km N.E.N. Palaikastro, WGS84 N35°16.719′ E026°17.049′, 50 m, 31.v.2008 (5 ♂, 5 ♀), J.M. Tilmans & J.F.R. Tilmans-Smid. KIKLADES: Andros Is., 1 km N of Vourkoti to Achia, 600 m, 28 & 30.vii.2004, WGS84 N37°52′17.7″ E024°53′30.1″ (2 juveniles); Tinos Is., 250-450 m, Mt. Tsiknias, WGS84 N37°34′36.2″ E025°13′15.4″, 1.viii.2004, (4 ♂, 2 ♀) & pass E of Koumaros, WGS84 N37°35′00.8″ E025°10′26.8″, 360 m, 31.vii.2004, (3 ♂, 3 ♀) & 5.5 km N of Tinos town, to Komi, 250 m, 31.vii.2004 (1 ♂); Naxos Is., Moutsouna, 15.vii.1982 (1 ♀) & 7.xi.1981 (1 ♀), collector unknown. (Unless otherwise stated collected by the Willemse's and in CW).

Recognition.— Male (figs 2, 33-34). Slender and small. Head not inflated, fastigium verticis narrow, slightly impressed, left and right ridge meeting each other at the tip in about 90°, ridges and foveolae distinct, interocular distance narrow (0.6-0.7 mm). Prozona of pronotum slightly longer than metazona, their length ratio 1.16 (1.08-1.25); shortest distance between lateral keels just beyond middle of prozona, keels usually not intersected by first two weak tranverse keels. Tympanal aperture widely open, narrowest diameter more than one third of the largest diameter.

Fore wing very short, never reaching base of supra-anal plate but 4th to 6th tergite and about two thirds as long as hind femur; fore and hind margin about parallel, precostal lobe commonly well indicated, C, Sc and R from straight to slightly bowed towards the tip, Sc and R very slightly divergent, Sc area narrow, measured along the line of greatest width of C area, only one quarter to at most one third as wide as C area; apex of wing regularly rounded, R reaching apical margin just in front of the tip, stigma lacking, membrane transparent (figs 85-87). Abdomen and its terminalia slender.

Hind femur slender, length of stridulatory file about one third of hind femur, number of pegs low, ranging from 43-84, average 72, about 27 per mm, the last distal pegs slightly more widely spaced; distance between terminal peg and tip of hind knee always more than length of file. Coloration and pattern consists of, as usual in this group of species, diverse shades of brown and yellow, quite exceptionally with green flush on dorsum of thorax and fore wing. Hind femur, knee, tibia and tarsus of general colour, keels of hind femur sometimes with series of dark dots, crescent of hind knee dark brown and lower side of hind tibia commonly dark brown or black.

Female (fig 35). As male, fastigium verticis relatively narrow, ridges of fastigium meeting at the tip at 90° or slightest more, interocular distance 0.8-1 mm (figs 154-156). Tympanal aperture (figs 185-187) from almost one third to half as narrow as largest diameter. Fore wing short, reaching 2nd to 3rd tergite, about half hind femur length or slightly less, left and right wing slightly separated from each other medially; fore margin, after precostal lobe, slightly bowed to straight and converging towards the apex, hind margin slightly rounded, apex narrowly rounded (fig. 143). Coloration as male. Biometric data for the male and female in tables 22-23.

Bioacoustics (figs 230-231, cd 8-9).— The song was previously unknown. This description is based on a few recordings. The calling song (fig. 230) can be described as an echeme of about 1 s, consisting of about 12-14 syllables. This echeme may be repeated more or less regularly. Except for the first 1-3 syllables, all syllables are equally loud and repeated at the rate of about 10/s. The synchronous upward movement of the hindlegs produces a weak sound whereas the downward movement produces a loud sound, irregularly with 1-2 gaps. In the rivalry song (fig. 231), echemes are shorter and often preceded by a strong but silent upward movement of the hind legs. The song seems to be related to the songs of the other species of the *vagans*-group (including *willemsei*). Yet, the syllable repetition rate is higher and the presence of gaps is less clear than in *vagans*. The syllable repetition rate equals that of *willemsei*, but *biroi* shows fewer and less clear gaps.

Differential diagnosis.— The species is well defined by its slender habitus, quite short wings, wide tympanal aperture and its song. While the short wings, wide tympanal aperture and song of *biroi* all are very close to *willemsei*, both taxa differ in habitus: *biroi* slender with narrow fastigium verticis and small interocular distance (♂ 0.6-0.71,

♀ 0.8-1.0 mm), *willemsei* more robust with wider fastigium verticis and larger interocular distance (♂ 0.8-1.0, ♀ 1.1-1.3 mm). Another difference is found in the length of the fore wings, in *biroi* shorter than in *willemsei*, but particularly in the width of the Sc area of the male fore wing. While the width of the C area both of *biroi* and *willemsei* is about equal (0.4 mm), that of the Sc area in *biroi* (0.1 mm) is about half that in *willemsei* (0.2 mm). An additional difference is the colour of the hind tibia, from yellowish to brownish with or without black flush in *biroi* against bright red in *willemsei*.

Other species which resemble *biroi* are *pulloides* and *sangiorgii*, both also short winged but with allopatric ranges. The distinction with *pulloides* is apparent: habitus robust, wide fastigium verticis, interocular distance wider (♂ 0.79-0.90, ♀ 1.0-1.4 mm), slit-like tympanal aperture, commonly longer fore wings and wider Sc area of male fore wing (0.20-0.37 mm). The distinction with *sangiorgii* refers to slightly narrower tympanal aperture, location of pronotal sulcus more in the middle of the pronotal length, slightly longer fore wings and wider Sc area of male fore wing (0.20-0.28 mm). These four short winged Greek members can be distinguished by using table 5 or by comparison of figs 31-35, 60-67, 82-87, 121-132, 139-143, 152-156, 170-173, 183-187, 199-203.

The longer fore wings of all other Greek congenerics are obviously distinct from *biroi*.

Discussion.— Though *biroi* and *willemsei* are well recognisable, they appear very closely related, sharing a wide tympanal aperture and resembling bioacoustic characters. At the same time, song and leg movements of these species indicate that they are related to *vagans* (s.l.), which is underlined by the relatively wide tympanal aperture, at least in nominate *vagans*. Further studies on this item, including the sing-alike *reissingeri* from Spain would be most welcome.

Previous records from Kriti both in Griffini (1894) and Werner (1903) surely refer to *biroi* as it is the only known short-winged *Chorthippus* species from the area.

According to Harz (1975a) and OSF (2005) the (syn-)types are deposited in NM/W. In the original paper, it is clearly stated that Biró's material belongs to the National Hungarian Museum. As no holotype has yet been designated, we select herewith a lectotype, a well-preserved female syntype and the only original specimen that could be traced in the Budapest Museum.

Morphology and currently available bio-acoustics from the Kikladhes islands and Gavdos (satellite island of Kriti) indicate that these populations are conspecific with *biroi* from Kriti. However this conclusion is based on a small series of specimens and one poor sound recording only. Considering the fact that there are quite a few examples of short-winged species that have evolved into separate taxa in Kriti as compared to adjacent islands (Gavdos) or islands groups (Kikladhes), it is worthwhile to re-examine larger samples of *biroi* from islands outside Kriti and include more bio-acoustic data.

Distribution and ecology.— The range of *biroi* covers Kriti and its adjacent islets, at least that of Gavdos and extends into a number of the Kiklades islands, such as Naxos, Tinos and Andros (fig. 262).

The species was found in stony patches, often with sparse vegetation but also with grasses and shrubs, both in lowlands (100 m) and in Kriti even up to above the timberline (2000 m). Adults were found in July and August but are believed to live longer.

The only observed syntopic congeneric is *bornhalmi*.

BRUNNEUS GROUP

typical species: *Gryllus brunneus* Thunberg, 1815: 256
(holotype female; Sweden, ZIU/L)

Chorthippus brunneus brunneus (Thunberg, 1815)

(tables 6, 24-25, cd 39)

Gryllus brunneus Thunberg, 1815: 256 (holotype female; Sweden, ZIU/L).

For a general account of the species see Ragge & Reynolds (1988, 1990 & 1998). The calling song is included on the cd with this paper (cd 39).

Chorthippus brunneus is a common species, widespread over large parts of western and central Europe. It is recognised by its slender habitus and long fore wings with a long apical part, the distance between stigma and tip of fore wing in the male is more than 5 mm and in the female more than 6 mm. The nominate form is easily recognised by its smal number of stridulatory pegs, fewer than 80-90 in both sexes. Other subspecies are *b. brevis* from Finland (Klingstedt, 1939) and the recently described *b. raggei* from Sicily (La Greca *et al.*, 2002). These taxa differ morphologically from the nominate form mainly in a larger number of stridulatory pegs. Until a few decades ago, it was supposed that the range of nominate *brunneus* extended as far south as Spain, North Africa and the Balkans including Greece. Now, by means of phonotaxonomy, we know that it is absent from these regions except for the north of the Iberian Peninsula and parts of the Balkan. In the former it is replaced by *C. jacobsi* Harz, 1975 (Ragge *et al.*, 1988, 1990, 1998) and in the latter by *bornhalmi*, see below.

Chorthippus bornhalmi Harz, 1971

(figs 1, 17, 36-37, 88, 157-159, 188, 205, 207-208, 232, 263, tables 3, 6-7, 24-25, cd 10)

Chorthippus (*Glyptobothrus*) *bornhalmi* Harz, 1971: 336, figs 12-14, 16, 18, 20 (description, male holotype: Dubrovnik, Sommer 1969, leg. D. Bornhalm; in CH-MHN/G); 1972: 132 (number of stridulatory pegs 121-128); Harz, 1975: 890, figs 3108, 3161, 3357-3360; Ingrisch & Pavicevic, 1985: 69, fig. 9 (first record

Table 6. Biometric data which may be useful to separate typical *Chorthippus bornhalmi* from typical *C. brunneus*. Measurements of *C. brunneus* were taken of specimens from Austria, a few from central Italy and a number from the northern Balkans, those of *C. bornhalmi* from Yugoslav Makedonia and all over Greece.

	bornhalmi (typical)	*brunneus* (typical)
number of stridulatory pegs	♂ 124 (105-153)	♂ 71 (55-89)
	♀ 103 (83-118)	♀ 57 (45-78)
length of stridulatory file (mm)	♂ 4.00 (3.25-4.50)	♂ 2.78 (2.35-3.30)
	♀ 5.11 (4.80-6.10)	♀ 3.8 (3.2-4.2)
distance from end of file to tip of knee (mm)	♂ 4.10 (3.75-4.50)	♀ 5.60 (5.00-6.50)
	♂ 4.62 (3.75-5.66)	♀ 6.57 (5.80-7.30)
ratio length of file / distance end of file to tip of knee	♂ 0.96 (0.81-1.12)	♂ 0.61 (0.49-0.72)
	♀ 0.91 (0.83-1.00)	♀ 0.58 (0.50-0.72)
number of pegs per mm	♂ 31.2 (25.5-36.6)	♂ 26.1 (21.7-31.8)
	♀ 20.2 (16.6-22.3)	♀ 14.9 (11.8-18.5)

from Greece; as *bornhalmi*, oscillogram, biometrics; *lagrecai* as synonym; list of localities); Willemse, 1986: 77 (replacing *brunneus* in Greece?); Nadig, 1985: 328 (as *bornhalmi*, Crete, Lassithi: Hochebene, 800 m & Adravasti, 350 m; eastern Greek Macedonia); Schmidt, 1990: 248, fig. 1 (oscillogram male Mt. Olimbos 1100 m); Szijj, 1992: 19, 20 (Acheloos delta); Paul, 1995: 221 (first song record from Crete: Phaistos & Georgopolis); Kati & Willemse, 2001: 15 (Thraki, Dadia Forest Reserve).

Chorthippus (*Glyptobothrus*) *lagrecai* Harz, 1975: 889, figs 3109, 3348-3356 (description, male holotype: Delphi, 18.x.1959, Ch. Walther leg. (CH-MHN/G; additional material from Greece: Taiyetos, Tripolis, Mistras, Levadia, Tirgus, Paralia Astros, 20 km N Athens, Asprovalta, Mt. Vermion, Chorbiatis & Karpathos, Chios, Samos, Mytilini, Cyprus); 1983: 40 (as a synonym of *bornhalmi*); Ingrisch & Pavicevic, 1985 (idem).

Chorthippus bornhalmi: Ragge *et al.*, 1990: 243, figs 10, 14 (oscillogram, Mt. Mainalon above Kardhara); 1998: fig. 15 (map); Popov & Chobanov, 2004: 284 (discussion of previous records, faunistics of Bulgarian and eastern Greek Thraki).

Chorthippus brunneus brunneus [nec Thunberg]; Kočárek & Vrabec, 2005: 8-10 (Kerkira, first record).

Chorthippus (*Glyptobothrus*) *brunneus brunneus* [nec Thunberg]; Willemse, 1984: 143, map 196 (as *brunneus brunneus*, full Greek references & distribution in Greece; partim?); 1985: 27 (in Greece no *brunneus*); 1986: 77, figs 1033-1038 (idem, identification); Ponel & Hébrard, 1988: 10 (Aetopetra near Ioannina); Szijj, 1992: 51 (as *brunneus*?, Acheloos & Nestos delta).

Chorthippus (*Chorthippus*) *bornhalmi*: Storozhenko, 2002: 11 (comb. nov.) (taxonomic status).

Chorthippus (*Glyptobothrus*) sp.: Tilmans *et al.*, 1989: 27 (Mt. Athos, *bornhalmi* ?).

Material studied.— *C. bornhalmi*: paratype 1 ♂, 1 ♀, labelled: "Jugoslavien, Dubrovnik, Sommer 1969, Bornhalm", "*Chorthippus bornhalmi* Harz, det. K. Harz" (CW).
C. lagrecai: holotype ♂, allotype ♀, paratype 1 ♂, labelled: "18.10.59, Delphoi, leg. Chr. Walther", "*Chorthippus lagrecai* spec. n. K. Harz det." & labels holo-, allo- and paratype; paratype 1 ♂ labelled: "25.9.1959, Taiyetos, leg. Chr. Walther"; paratype 1 ♂ labelled: "20.ix.59, Tripolis, Chr. Walther", identification and type-labels as above (CH-MHN/G).

Additional material from Greece, specified down to department/district and locality:
THRAKI: Evros: 5 & 8 km NNW of Aisimi (CI) & 6 km N of Aisimi; Gianouli, N of Dhadhia; Kallithea, 36 km W of Dhadhia; Dhadhia-Lefkimi-Soufli Forest reserve; 13.5 & 18 km SW of Dadhia; 19 km E of Nea Sandha; Valtos; Rodhopi: 8 km E of Nea Sandha; Xanthi: Xanthi & 8 km W of Xanthi (CI); MAKEDHONIA: Drama: Mt. Falakron; Volax (CI); Kokkinogia (CI); Xiropotamos (CI); Polinerion (CI); Sterna (CI); Rodhopi Reserve: Elatia Centre & 3 km & 9 & 25 km NE of Elatia; 10 km S of Sidheronero; Serrai: 5 km N of Sidherokastro; Mt. Kerkini; Mt. Vrondhous; Lalas (CI); Chrisopigi (CI); Orini (CI); Skepaston (CI); Kavalla: Mt. Pangaion above Akrovounion; Paleo Kavalla (CI); Lekani (CI); Khalkidhiki: Mt. Kholomon; Taxiarchis (CvH); Stratonkon (CI); Arnea (CI); Thessaloniki: Mt. Vertiskos; Kilkis: Platania; Evzoni; Pieria: Katerini; Leptokaria-Karia; Litochoron; Mt. Olimbos, Refuge A (Prioni-Mitikas) & Stavros & Stavros-Prioni; Mt. Pieria above Katafygion; Fteri; 10 km NW of Fteri; Kozani: Servia; Velvendhos-Katafygion; Velvendhos; 5-10 km E of Dheskati; Mt. Vourinos near A. Pandhelimon; Imathia: Naoussa; Seli; Mt. Vermion near refuge Tria Pigadhia; Kastanea; Grevena: Mt. Smolikas, 10-12 km S of Samarina; Mt. Vasilitsa, W of Smixi; Kastoria: Kastoria town; Eptakhorion; Klisoura; Florina: Mt. Vernon 10 km NE of Gavros & 3 km S & 4 km E of Pissodherion & 6 km W of Dhrosopiyi; Mt. Varnous (= Mt. Bela Voda) near pass Pissodherion; Klidhi; THESSALIA: Larissa: Ag. Dhionysios; 1 km SE of Gonnoi; Kallithea; Mt. Olimbos above Sparmos & refuge B; Mt. Ossa above Anatoli & Dhimitri-Anatoli; 11 km W of Tirnavos; Kardhitsa: Mt. Avgo below Kokkinolakes; Mt. Karava below summit Koulkoutsari; Kazarma below summit Moutsiara; Neokhori, W of Lake Tavropou (= Plastira); Mt. Voutsikaki, Neraidha-Karitsa & near M. Revma; Magnisia: Chorefto; Mt. Othris above Kokkotoi; Mt. Pilion above Portaria & Portaria-Zagora; Neochorion (CI) Trikala: Mt. Avgo above Nea Pefki; Mt. Chatzi above Spitia; Gropa, pass between Vathiremma and Stournareika; Khrisomilia; Mt. Neraidha above Neraidhochori; Pyli; Trigon; IPIROS - Ioannina: Plagia (Sarandaporos river); Mt. Timfi above Papigon; 1-2 km S of Aristi; 15 km W of Eptakhorion; Fourka-Samarina; Mt. Gionistra above Elataria; 8 km N of Kalentzion; Mt. Dhokimi, 10 km SE of Metsovon; Katara Pass & Katara Pass-Lake Aoou & 5 km S of Katara Pass; Konitsa-Elefteron; Mikro

Peristeri-Rahoula; Mt. Lakmos above Mikro Peristeri-Rahoula; Mt. Mavrovouni (N of Metsovon) between Flega and Tri Sinora & W of Milia; Metsovon; 3 & 6 km E of Metsovon; Milea-Metsovon; Mt. Mitsikeli, Lingiadhes & above Lingiadhes; Mt. Tomaros; Arta: Mt. Gavrogo below summit Yerabi; Katarraktis; Mt. Tzoumerka above Katarraktis & above Vourgareli; Thesprotia: Mt. Soulion above Souli; Plakoti (E of Igoumenitsa) (CvH); IONIAN IS.: Kerkira, Almyros; Kefallonia, Mt. Ainos; CENTRAL GREECE: Aitolia-Akarnania: Mt. Akarnanika; Acheloos Delta, Koutsilaris hill; Mt. Tsakalakis near Elefteriani & S of Ano Chora; Mt. Valtou above Perdhikaki; Evritania: Mt. Agrafa, Kamaria; Mt. Helidona above Palaio Mikrochori; Mt. Kaliakoudha, Megalo Chori-Stournara; Karpenisi; Megalo Khorio; Mt. Oxia, Stavli-Gardiki; Mt. Panaetolikon, 5 km W pass Proussos-Labiri & pass Proussos-Labiri; Mt. Timfristos above Karpenission & surr. refuge; Fokis: Eptalofos; Mt. Giona, 2 km S of Mnimata & Lakkes Lyritsa; Itea; 6 km SE of Physkeis; Polidrosos; Mt. Vardhousia above Moussonitsa; Fthiotis: Mt. Kallidromo, 1.5 km E of Elefterochori; Mt. Oiti above Ypati & near refuge above Ypati; Mt. Oiti, 6 & 10 km NW of Pavliani; Mt. Oiti, Pavliani-Kastania; Mt. Oiti, summit Korifin; Mt. Parnassos, ski centre Kelaria & Fterolakas; Thermopilai; Voiotia: Mt. Helikonas below summit Paliovouna & Kiriaki-Ag. Anna; Mt. Parnassos above Arakhova & Livadhi plateau & Livadhi plateau-Gerondho Vrachos & ski centre Gerondho Vrachos; Attiki: Mt. Yerania, W of Megara; Mt. Imittos; Nea Makri; Mt. Parnis; 20 km N of Athens (CH, paratype *lagrecai* in Ingrisch & Pavicevic, 1985); Evvoia: Mt. Dirphys above Steni; PELOPONNISOS: Akhaia: Mt. Aroania (= Chelmos) above Kalavrita & above Feneos & ski resort; Aroania village, W of Klitouria; Mt. Erimanthos above Kalentzi; Kalavrita town; Kastelli; Kato Lousoi; Livartzi-Lekhouri (Psofida); Mt. Panakhaikon above Romanou & above Zastova & above Katafigio; Sella-Pititsa; Argolis: A. Eleni; Methana above Kounoupitsa; Arkadhia: Elatia, S of Vitina; 3 & 4 & 5 & 8 & 11.5 km W of Khrissovitsi; Mt. Mainalon above Kardhara; Mt. Parnon above Kastanitsa & Vouvoura; Platanos-Charadros; Thisoa; 5 km W of Tripolis; Valtesinikon; 6 km W of Vitina; Ilia: Mt. Lambia above Lambia & 6 km E of Ag. Triadha; Korinthia: Mt. Killini above Trikala & above Katafigio B; Mt. Oliyirtos above Lavga; Korinthia/Akhaia: Feneos pass; Lakonia: 1 km W of Foutia; 3 km W of Nomia; Mt. Parnon above Vamvakou; Polidrosos & 5 km W; Mt. Taiyetos above Yeoryitsi & below summit Prof. Ilias; 1 km S of Yithion; Messinia: 4 km E of Kalama; Nedhoussa (CvH); Sparti-Kalamai, Langhadha pass; Andhikithira Isl, 0.6 km E of Potamos (not included in fig.263); KIKLADHES: Santorini: Santorini (CW) & summit Mt. Profitis Ilias & 2.7 km E Ia & 1.7 km SE Fira (all CT); Sikinos, 4.5 km SW Kastro (CT); Ios: 7.5 km WSW Psathi, road to Manganari & 0.4 km SE Homer's Tomb, 8.7 km NEN Epano Kambos & 9.9 km SW Psathi, road to Manganar & Mt. Pyrgos, 7.8 km SW Pathi (all CT); Andiparos, 0.1 km SS summit Profitis Ilias (CT); Paros: 0.3 km W summit Ayioi Pandhes, 7 km WSW Lefkes & 6.8 km NE Angairia & Monastiri Ayios Theodhoron, 3.5 km NEN Angairia (all CT); Mikonos, Ano Mera & Kalafati & Kalafati-Tigani & Panormos; Andros, Achia & Ay. Petros & 3.5 km S of Palaiopolis & 1 km N of Vourkoti; KRITI: S. Kriti, Lentas (CvH); Khania, 1 km N Souyia; 1 km N Epanokhori; Ayia Irini; Kaleryi Refuge above Omalos; 4 km E Palaiohora; 1 km N Ayia Roumeli (all CT); Mt. Lefka, Omalos plateau (CW); Lasithi: 1 km S Maronia; 7 km W Orino, Mt. Thriptis, below Afebdis (all CT); NE AEGEAN IS: Lesvos: Mt. Lepetimnos, NW of Stipsi & Mytilini town; S SPORADHES: Samos: A. Kiriaki & Pyrgos. Number of specimens together about 700 (most of this material collected by the Willemse's in CW, some duplicates in BMNH/L & ZI/P and partly by others and in CvH, CI & CT).

Additional material from Northeast Italy, former Yugoslavia, Albania, Bulgaria, Anatolia and Cyprus, not specified, ca 90 specimens (partly in CW, CT, HNHM/B & NMNH/S).

Recognition.— The discovery of *bornhalmi* was based on the observation that, though morphologically similar to *brunneus*, the song differs from that of *brunneus*. In its original description it is clearly noticed that morphological distinction between *bornhalmi* and *brunneus* is quite limited (compare table 24 and 25), distinctive features only being found in particulars of the stridulatory file, *e.g.* length of file and number of pegs (table 6). However it is noted here that these numbers both of *brunneus* and *bornhalmi* as given in table 6 do not fit all specimens throughout their range. Specimens of *brunneus* from Finland (*b. brevis* Klingstedt, 1939), some parts of the Alps or from Corsica, Sardinia and the recently described *b. raggei* La Greca *et al.* from Sicily have either a larger number of stridulatory pegs or longer file or both (Ingrisch, 1995; Ragge & Reynolds, 1998). It is also noticed here that in the region of Trieste, Northeast Italy, where the ranges of *bornhalmi* and *brunneus* meet, songs and biometrics of both species come very close to each other, even with some overlap, probably resulting from hybridisation (Kleukers *et al.*, 2004). Important characters are figured: figs 36-37, 88, 157-159, 188. Biometric data for the male and female in tables 24-25.

Bioacoustics (fig. 232, cd 10).— The song of *C. bornhalmi* has been described before *e.g.* in Ragge *et al.* (1990), Ingrisch & Pavicevic (1985) and Kleukers *et al.* (2004). As the song varies throughout its geographic range the particulars of the song of *C. bornhalmi* in Greece are summarized here.

The calling song consists of a single echeme of 2-4 s. Echemes are rarely produced in short series with the first echeme of about 3 s and the following ones decreasing in duration, down to about 1 s (fig. 232). Echemes typically consist of 10-30 syllables, starting weak, but reaching maximum loudness after the first 3-10 syllables. Syllables are repeated at the rate of about 8-10/s. Both the upward and downward movement of the legs is loud. The downward movement is more or less regularly interrupted, resulting in 1-3 not so clear gaps (of about 2-3 ms) in the syllables. Gaps are not as sharply defined as in *vagans* (s.l.).

Differential diagnosis.— The species belongs to the long-winged species, with wings extending well beyond the tip of the abdomen and hind knees, which in Greece also includes *biguttulus euhedickei* (figs 38-41), *vagans dissimilis* (figs 27-28) and *mollis mollis* (figs 50-53). All of them have a highly characteristic and easily recognisable song.

The morphological distinction between *bornhalmi* and *b. euhedickei* is quite apparent in the male by the strongly bowed fore margin of the elytron with rather expanded costal areas in *b. euhedickei* (figs 88 against 93-96) as well as the relatively long stridulatory file in both sexes in *b. euhedickei* (table 7, fig. 208).

Its distinction from *m. mollis* is apparent by the shorter fore wings with relatively shorter apical part (beyond the stigma) in both sexes of *m. mollis* (table 7, figs 36-37 against 50-53, fig. 88 against 110- 113). However, the distinction between *bornhalmi* and *v. dissimilis* is sometimes difficult and discussed under the latter, including their bioacoustics (table 3, figs 205, 207).

An additional feature distinct from all other Greek members of *Chorthippus* is the maximum width of the pronotal disc (measured as in fig. 3), which is largest in *bornhalmi* and particularly obvious in the female (figs 157-159).

Discussion.— The type-series of *lagrecai*, including holo- and allotype, have been examined to be sure whether its synonymy with *bornhalmi* is correct and whether *v. dissimilis* was not involved (see under *vagans*). The synonymy of *lagrecai* and *bornhalmi*, proposed in Harz (1983) and Ingrisch & Pavicevic (1985), was fully confirmed by biometric data.

Chorthippus bornhalmi is quite common in the southern Balkans, replacing the widely distributed *brunneus*. The southern extension of the range of *brunneus* in the Balkans is badly known. Among material from former Yugoslavia the southernmost localities of *brunneus* are south of Nis, even as far south as Vranje and reaching Kumanovo where it may occur syntopic with *bornhalmi* (material in CW). In Bulgaria we studied *brunneus* from the plain of Sofia (Tsarichina near Kostinbrod) and in the east from several locali-

Table 7. Biometric data which may be useful to distinguish *Chorthippus bornhalmi* from *C. biguttulus euhedickei* and Greek *C. mollis mollis* (fig. 208).

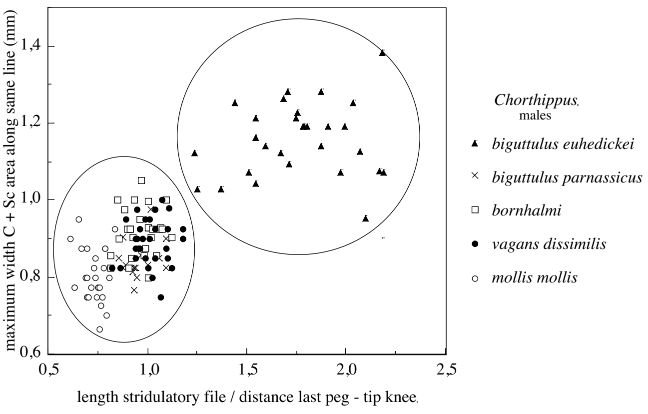
	bornhalmi	*biguttulus euhedickei*	*mollis mollis* (Greece)
maximum width of pronotal disc (mm)	♂ 2.39 (2.15-2.70)	♂ 2.09 (1.84-2.27)	♂ 1.90 (1.7-2.1)
	♀ 3.36 (3.0-3.9)	♀ 2.96 (2.8-3.1)	♀ 2.69 (2.4-3.0)
length of fore wing (mm)	♂ 15.3 (13.4-16.9)	♂ 13.3 (11.0-15.5)	♂ 10.7 (8.7-12.7)
	♀ 19.4 (18.0-20.9)	♀ 16.4 (15.1-18.2)	♀ 13.6 (12.1-16.0)
distance of stigma to tip of fore wing (mm)	♂ 6.29 (5.38-7.30)	♂ 5.11 (4.3-6.0)	♂ 3.46 (2.8-5.0)
	♀ 7.99 (7.4-8.8)	♀ 6.53 (5.6-7.4)	♀ 4.77 (4.0-5.7)
ratio distance of stigma to tip of fore wing / length of fore wing	♂ 0.41 (0.36-0.44)	♂ 0.38 (0.34-0.49)	♂ 0.32 (0.28-0.39)
	♀ 0.43 (0.40-0.44)	♀ 0.39 (0.35-0.45)	♀ 0.35 (0.31-0.39)
length of hind femur (mm)	♂ 9.9 (8.4-10.7)	♂ 9.7 (8.5-11.4)	♂ 8.9 (7.7-11.1)
	♀ 13.4 (11.6-14.8)	♀ 12.4 (11.1-13.1)	♀ 11.7 (10.2-13.2)
ratio length of fore wing / length of hind femur	♂ 1.55 (1.38-1.73)	♂ 1.37 (1.17-1.58)	♂ 1.19 (1.09-1.40)
	♀ 1.45 (1.35-1.58)	♀ 1.32 (1.22-1.43)	♀ 1.16 (1.01-1.31)
width of combined C & Sc area (mm)	♂ 0.92 (0.80-1.05)	♂ 1.15 (0.95-1.38)	♂ 0.80 (0.67-0.95)
ratio width of comb. C & Sc areas × 100 / length of fore wing	♂ 5.96 (5.33-6.49)	♂ 8.69 (7.55-9.75)	♂ 7.55 (5.95-8.67)
length of stridulatory file (mm)	♂ 4.00 (3.25-4 .5)	♂ 5.12 (4.2-5.77)	♂ 3.07 (2.6-3.65)
	♀ 5.11 (4.8-6.0)	♀ 5.71 (5.2-6.3)	♀ 4.13 (3.8-4.6)
ratio length of stridulatory file / distance of last peg to tip of knee	♂ 0.96 (0.81-1.12)	♂ 1.75 (1.24-2.19)	♂ 0.72 (0.61-0.83)
	♀ 0.91 (0.83-1.00)	♀ 1.32 (1.22-1.43)	♀ 0.72 (0.67-0.80)

ties in the district of Varna, the northern Black Sea coast (St. Konstantin and Elena resort & Pobiti Kamani, 15 km west of Varna & Ludogorski Plateau, Valchidol in the eastern Danubian plane). *Chorthippus brunneus* is also known to occur north of the Stara Planina and west of Sofia (Pernik and Kyustendil districts). Both *brunneus* and *bornhalmi* were found syntopic or close together in the area of Kyustendil in West Bulgaria and along the Black Sea coast in East Bulgaria, near the village of Staro Oryahovo between Burgas and Varna (pers. comm. D. Chobanov and V. Vedenina, material in NMNH/S).

Most previous records of *brunneus* from Greece refer to *bornhalmi* (Ingrisch & Pavicevic, 1985; Willemse, 1985; Ragge *et al.*, 1989; Schmidt, 1990; Szijj, 1992; Paul, 1995). However, some previous records may refer to *vagans dissimilis*, particularly from the Eastern Aegean Islands and the Southern Sporadhes, see the discussion under the latter. The distribution map under *brunneus brunneus* given in Willemse (1984) includes also all previous records and therefore may not always be reliable.

Noteworthy is some material at hand from Mt. Athos, a difficult accessible and rather isolated mountain of the peninsula of Khalkidhiki, Greek Makedhonia (Tilmans *et al.*, 1989): Greece, Khalkidhiki, Mt. Athos: below Panaya, 900-1200 m, vii.1983, J. Tilmans & 1200-1500 m, vii.1986, L. Willemse & Panaya, 1500 m, vii.1983, J. Tilmans & above Panaya, 1500-2000 m, vii.1986, L. Willemse (together 44 ♂, 30 ♀, CT & CW). This material strongly resembles *bornhalmi* but differs in: pronotal lateral keels less angled, due to relatively larger minimum distance; fore wings relatively short (length in male 12.6-14.2 mm; ratio length fore wing/length hind femur in male 1.28-1.41) with length of apical part also relatively short (length stigma to tip of fore wing in male 4.4-5.4 mm, ratio of tbis length to length of fore wing 0.33-0.30) and integument of thorax, abdomen and legs very densely

Fig. 208. Scatter diagram showing a plot of the ratio of the length of the stridulatory file to the distance from the terminal distal peg to the tip of the knee against the maximum width of the combined C and Sc areas of the fore wing measured along the same line (mm) of *Chorthippus biguttulus euhedickei*, *C. b. parnassicus*, *C. bornhalmi*, *C. vagans dissimilis* and *C. mollis mollis*.



pubescent. We refrain from identifying this population as the song is still unknown.

Distribution and ecology.— From the material examined, the range of *bornhalmi* extends from extreme Northeast Italy (Kleukers *et al.*, 2004) southward along Istria and western former Yugoslavia, covering Albania, Yugoslav Makedhonia, all the mainland of Greece, some off-shore islands, the Peloponnese and some islands of the Kiklades, extending eastwards into Greek Thraki, southern Bulgaria (Popov & Chobanov, 2004), European Turkey, Anatolia, many Aegean islands, Crete and Cyprus. The first record of *bornhalmi* from Cyprus is not in Tumbrinck (2006) but in Harz (1975) who included one male from this island ("Pentedactylos, Olymbos, Ende v.1972, H. Eckerlein") under *lagrecai*, which is synonymous with *bornhalmi*.

Opportunity is taken here to give a revised distribution map of *bornhalmi* in Greece but now restricted to recently examined and reliably identified material (most of it preserved in CI, CT, CvH, CK and CW) (fig. 263).

Being quite common, *bornhalmi* may occur syntopically with almost all other known congeneric species.

Adults are found from spring to far into autumn, most abundant in late spring to early summer. In August the number of adults is commonly low but in September-October fresh subadults and adults are found again. Its life cycle is at least in some populations bivoltine, depending on change of day length for diapause induction (Ingrisch, 1987). The species has a wide range of habitats, ranging from open forests to bare rocky ground, from lowlands up to far above the timberline reaching their summits. Mountain areas are preferred.

***BIGUTTULUS* GROUP**

typical species: *Gryllus* (*Locusta*) *biguttulus* Linnaeus, 1758: 433
(lectotype male, locality unknown, LS/L)
(figs 16, 89-92, 209-210, 233, tables 8, 26-27)

***Chorthippus biguttulus*-complex**

Nominate *C. biguttulus* is a well-known species. For convenience of the reader figures are given of the male fore wings (figs 89-92), the male song (figs 16, 233, cd 11, 12, 13, 14) and some biometric data are included (tables 26-27).

Table 8. Characters which may be useful to separate *Chorthippus biguttulus biguttulus* from *C. biguttulus parnassicus*, *C. biguttulus euhedickei* and Greek *C. mollis mollis* (figs 208-211).

	biguttulus biguttulus	*biguttulus parnassicus*	*biguttulus euhedickei*	*mollis mollis* (Greece)
length of fore wing (mm)	♂ 13.1 (12.0-14.8)	♂ 11.3 (10.6-12.1)	♂ 13.3 (11.0-15.5)	♂ 10.7 (8.7-12.7)
	♀ 15.6 (14.7-16.2)	♀ 14.4 (14.1-14.8)	♀ 16.4 (15.1-18.2)	♀ 13.6 (12.1-16.0)
width of C area (mm)	♂ 0.74 (0.67-0.83)	♂ 0.62 (0.56-0.67)	♂ 0.84 (0.64-0.97)	♂ 0.52 (0.44-0.60)
width of Sc area (mm)	♂ 0.47 (0.42-0.56)	♂ 0.23 (0.19-0.30)	♂ 0.44 (0.28-0.62)	♂ 0.28 (0.22-0.35)
ratio width of C / Sc area	♂ 1.57 (1.26-1.84)	♂ 2.68 (2.21-3.25)	♂ 1.94 (1.36-3.14)	♂ 1.85 (1.53-2.22)
width of combined C & Sc area (mm)	♂ 1.21 (1.12-1.30)	♂ 0.84 (0.76-0.97)	♂ 1.15 (0.95-1.38)	♂ 0.80 (0.66-0.95)
ratio width combined C & Sc areas × 100 / length of fore wing	♂ 9.27 (8.27-9.89)	♂ 7.49 (6.74-8.55)	♂ 8.69 (7.55-9.75)	♂ 7.55 (5.95-8.67)
length of stridulatory file (mm)	♂ 3.24 (2.85-3.70)	♂ 3.51 (3.20-3.75)	♂ 5.12 (4.20-5.77)	♂ 3.07 (2.6-3.65)
	♀ 3.9 (3.7-4.4)	♀ 4.5 (4.3-4.7)	♀ 5.71 (5.2-6.3)	♀ 4.13 (3.8-4.6)
distance of end file to tip knee (mm)	♂ 4.45 (4.00-5.03)	♂ 3.68 (3.20-4.05)	♂ 2.95 (2.30-3.58)	♂ 4.23 (3.55-5.20)
	♀ 5.54 (5.1-6.1)	♀ 5.16 (4.7-5.5)	♀ 4.27 (3.6-5.0)	♀ 5.61 (5.0-6.1)
ratio length of stridulatory file / distance end of file to tip knee	♂ 0.73 (0.63-0.88)	♂ 0.94 (0.85-1.09)	♂ 1.75 (1.24-2.19)	♂ 0.72 (0.61-0.83)
	♀ 0.72 (0.61-0.83)	♀ 0.87 (0.78-0.95)	♀ 1.35 (1.14-1.63)	♀ 0.72 (0.67-0.80)
number of stridulatory pegs	♂ 98 (84-114)	♂ 107.6 (95-122)	♂ 127.2 (109-149)	♂ 112.5 (94-134)
	♀ 93.4 (84-105)	♀ 79.5 (70-90)	♀ 102.8 (90-118)	♀ 109 (92-120)
number of stridulatory pegs per mm	♂ 30.2 (26.5-35.3)	♂ 30.7 (26.4-35.8)	♂ 25.0 (20.2-31.4)	♂ 36.1 (28.5-40.0)
	♀ 23.5 (21-25)	♀ 17.7 (14.8-20.9)	♀ 17.9 (16.6-20.3)	♀ 27.1 (23.4-32.1)
(male fore wing) R & Sc veins and Sc area	R more divergent to Sc; Sc area slightly widened at bifurcation of Rs (figs 89-92)	R more divergent to Sc; Sc area slightly widened at bifurcation of Rs (figs 98-102)	R more divergent to Sc; Sc area distinctly widened at bifurcation of Rs (figs 93-97)	R more parallel to Sc; Sc area not or slightest widened at bifurcation of Rs (figs 110-113)

Originally Ramme (1942) described *Stauroderus hedickei* from Romania, Macedonia and Hungary as a distinct species. But later and based on allopatric occurrence and closely resembling song, Ramme (1951: 75) considered his taxon as a subspecies of *biguttulus*, replacing the nominate form from Hungary southwards into the Balkan. The type-locality of *hedickei* is Mt. Szechenyi, near Budapest.

Von Helversen (1989) discovered that the song of the *hedickei* populations from Jugoslav Macedonia, Greek mainland and northwestern Anatolia are not identical to nominate *biguttulus* from Central Europe (figs 16, 233). The song of these populations is typically characterized by one or more remarkable aftersongs (figs 234-235). However, the song of topotypical *hedickei* (Budapest, Hungary) proved to be almost similar to that of nominate *biguttulus*. Therefore a new taxon had to be created for which the well fitting name *euhedickei* was proposed. This taxon was known to occur from Yugoslav Makedhonia throughout the Greek mainland but absent in the Greek islands and the Peloponnese.

It became apparent that in part of the range of *b. euhedickei*, like the summit area of Mt. Parnassos and probably other high mountains of the southwestern Balkan, another *biguttulus* "sing-alike" occurs. It is described below as *biguttulus parnassicus* subspec. nov.

Apart from that the Peloponnese is inhabited by yet another form of which the stridulation, particularly the movement pattern of the hind leg, shows a close alliance with that of *biguttulus* (s.l.). It is described below as *moreanus* spec. nov.

Chorthippus biguttulus euhedickei **von Helversen, 1989**

(figs 38-41, 93-97, 160-161, 189-190, 208-209, 234-235, 264, tables 4, 7-8, 26-27, cd 12, 13)

Stauroderus hedickei Ramme, 1942: 333 (partim, only Macedonia).

Chorthippus biguttulus hedickei: Ramme, 1951: 75, 85, 107, 115, Pl. 2 figs 11-13 (only fig. 13, nec figs 11-12) (partim).

Chorthippus (*Glyptobothrus*) *biguttulus hedickei* [nec Ramme]: Willemse, 1984: 144, map 197 (full references and distribution); 1986: 77, figs 1027-1032 (identification); Ingrisch & Pavicevic, 1985: 71 (number of localities in eastern Greece); Ponel & Hébrard, 1988: 10 (Mt. Olimbos; Imatha, Mt. Vermion, Kastania; Metsobon).

Chorthippus biguttulus euhedickei von Helversen, 1989: 28, figs 5-6 (description, holotype ♂: Mt. Pangaion, 8.ix.1986, leg. H. Kriegbaum, CvH)

Chorthippus Taxon B: Ragge *et al.*, 1990: 244, fig. 12 (oscillogram, Greece, Ioannina, plateau north of Metsobon, 1300 m).

Chorthippus biguttulus Form X (in map *graecus*): Schmidt, 1990: 249, figs 3-4 (oscillogram, Perivolion, Greece).

Chorthippus porphyropterus euhedickei: Benediktov, 1999: 44, fig. 1/2, 2/2 (comb. nov., file length, faunistics); Popov & Chobanov, 2004: 284 (discussion; faunistics of Bulgarian and eastern Greek Thraki).

Glyptobothrus biguttulus hedickei: Storozhenko, 2002: 4. (partim) (taxonomic status)

Material examined.— *C. biguttulus euhedickei*: holotype ♂, labelled: "Mt. Pangaion, 8.ix.1986, leg. H. Kriegbaum" & 7.ix.1986, Pangaion Gipfelregion, H. Kriegbaum (1 ♂ paratype, alcohol vial 6/0035) (both in CvH).

Greek material, specified down to district and locality:

THRAKI: Evros: Aisimi; 13 km W Dhadhia; Komotini: Nea Sandha. MAKEDHONIA: Drama: Khiropotamos; Mt. Falakron, Volax; Sidheronero; Skaloti; Rodhopi Forest Reserve: Elatia Centre, Betula forest; Kavalla: Korifes; Mt. Pangaion above Akrovouni (topotypes); Mt. Lefkanis, Polinero; Serrai: Mt. Vrondhous, Lalias & Orini; Kilkis: Kilkis town; Thessaloniki: Mt. Vertiskos, Sokhos & Vertiskos village; Mt. Kerdhilio, Skepasto; Khalkidhiki: Mt. Kholomon & near Taxiarchis, K.-G. Heller (CvH); Florina: oberhalb Pissodherion Pass, O. von Helversen (CvH) & Dhrosopiyi; Kastoria: Eptakhori; Grevena: Mt. Vourinos near Ag. Panthelimon; Venetikos river, 10 km S of Grevena town; Mt. Vasilitsa near Smixi; Mt. Smolikas, 7 km E (& CvH) & 10 km S of Samarina; Kozani: Pendalophos, O. von Helversen (CvH) & Polimilos; Mt. Pieria, Velvendhos-Katafiyi; Imathia: Mt. Vermion near refuge Tria Pigadhia; Pieria: Fteri; Mt. Olimbos, Stavros, Stavros-Prioni, Prioni-refuge A; Litokhoron; Leptokaria-Karia. THESSALIA: Larissa: Mt. Olimbos above Sparmos, refuge B (some duplicates in BMNH/L & ZI/P); Mt. Ossa above Anatoli; Magnisia: Mt. Pilion; Mt. Othris above Kokkotoi; Trikala: Mt. Neraidha, W of Pertouli; Mt. Chatzi, SE of Mesochora; Mt. Avgo, NE of Mesochora; pass between Vathirema & Stournareika; Khrisomilia, Pili; Kardhitsa: mount between Oxia and Argithea, below summit Pr. Ilias; Mt. Karava; S of Neokhori, W of lake Tavropou; Mt. Voutiskaki; Mt. Fteri, Avgo below summit Kokkinolakes. IPIROS: Thesprotia: Mt. Chionistra, N of Paramithia; Ioannina: Mt. Grammos, Kefalochori-Aetomilitsa; surroundings Ambelochori; surroundings Metsobon (duplicates in BMNH/L & ZI/P); Katara Pass; Mt. Mavrovouni, N of Metsobon; Mt. Peristeri above Sirako, N of Ag. Athanasios; Mt. Lakmos; Mt. Kakardhitsa (= Athamanika) above Pramandha; Kotstitsi, halfway between Serviana & Pramandha; Milea-Metsobon; Mega Peristerion; Zagora, Vrisokhorion & Vitsa & K. Pedina; Mt. Timfi above Papigon; Papigon; Aristi; Mt. Smolikas above A. Paraskevi; Fourka; Konitsa-Elevtheron; Elevtheron; Mt. Mitsikeli, Marasis-Dikorifo; Kalentzion near Arakhthos river; Mt. Tomaros above Varyiadhes; Arta: Mt. Tzoumerka, Milea-Katarraktis; Mt. Tzoumerka above Theodhoriana (& CvH); Vourgareli; Sgara-Ramia, turn-off to Grekiko; Mt. Gavrogo above Megalochari.

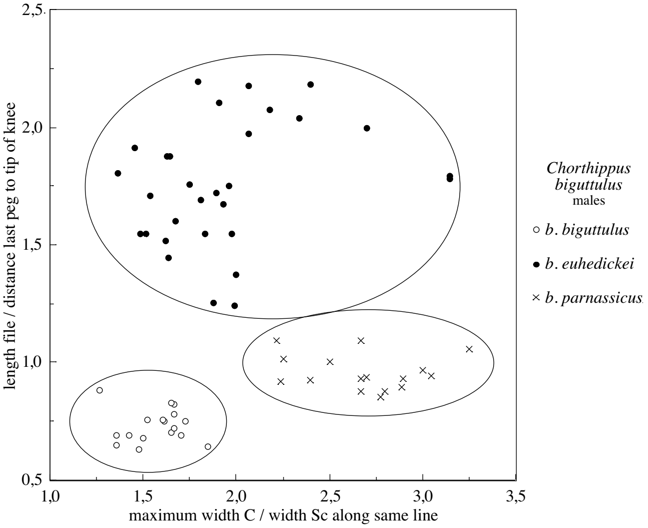


Fig. 209. Scatter diagram showing a plot of the ratio of the maximum width of the C area to the width of the Sc area measured along the same line against the ratio of the length of the stridulatory file to the distance from the terminal distal peg to the tip of the knee in males of *Chorthippus biguttulus biguttulus*, *C. b. euhedickei* and *C. b. parnassicus*.

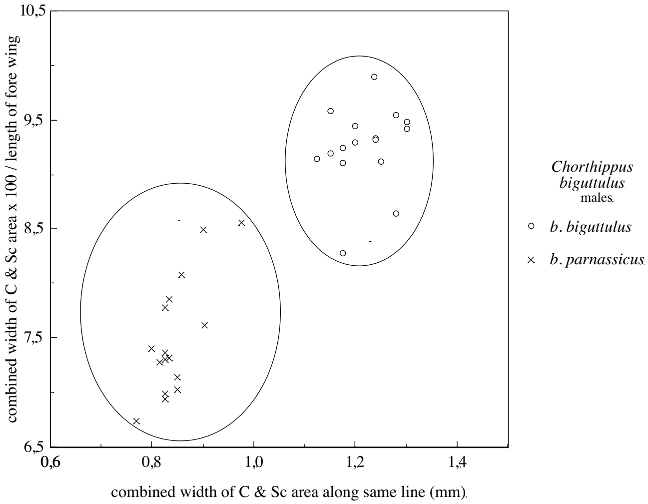


Fig. 210. Scatter diagram showing a plot of the ratio of the maximum width of the C and Sc area to the width of the Sc area measured along the same line (mm) against the ratio of the maximum width of the C area and Sc area to the length of the fore wing in males of *Chorthippus biguttulus biguttulus* and *C. b. parnassicus*.

CENTRAL GREECE: Aitolia-Akarnania: Mt. Panaitolikon, Drimon & Khaliki; Mt. Valtou above Perdhikaki; Ambelakiotissa, pass betw. Mts. Ardhinis & Tsekoura; Mt. Tsakalakis near Elefteriani & S of Ano Chora and Kendriki. Evritania: Mt. Panaitolikon above Proussos; Mt. Triandhafillia, betw. Kastania & Arghiro Pighadhi, SE of Proussos; Mt. Kaliakoudha, Megalochorion & Megalochorion-Stoumera; Mt. Oxia, Stavli-Gardiki; Mt. Timfristos above Karpenision (& CvH); Fthiotis: Timfristos village; Mt. Oiti above Ipati, above Kastanea, from Kastanea to Pavliani; Pavliani; Mt. Kalidromo, Elefterochori-Drimea; Fokis: Mt. Vardhoussia above Mousounitsa; Voiotia: Mt. Parnassos above Arakhova & A. Nikolaos & Livadhia to ski centre & near Gerondhovrachos & near Keralia, 1400-1600 m.

Number of Greek specimens together 790 (unless otherwise stated collected by the Willemse's and in CW).

Additional material from Yugoslav and Bulgarian Makedonia: 45 ♂, 93 ♀ (CW & Bulgaria 5 ♂, 2 ♀ in NMNH/S).

Recognition.— This form strongly resembles nominate *biguttulus* but the C areas of the male fore wing are more expanded (figs 93-97 against 89-92 of the nominate form) and the stridulatory file is remarkably longer, extending far distad to near the base of the hind knee (table 8, fig. 209). Besides the distal pegs of the stridulatory file are over an unusual long distance increasingly more widely spaced. This character is usually also well recognisable in the female. Biometric data for the male and female in table 26-27.

Bioacoustics (figs 234-235, cd 12-13).— A summary of the biacoustics of this species can be found in Ragge *et al.* (1990) - as taxon B - and Schmidt (1990) but a more comprehensive description is given in Von Helversen (1989). The calling song of *Chorthippus biguttulus euhedickei* (fig. 235) consists of 1-3 very typical loud rattling "whizzing metallic" echeme-sequences, similar to the echeme-sequence of the nominate form, that are followed by 1-5 shorter aftersongs. The number of rattling echeme-sequences and aftersongs varies among individuals and among populations, but is quite constant for individual specimens. The rattling echeme-sequences last 1,5-5 s and - as in the nominate form - start quietly, gradually reaching maximum intensity. They consist of echemes that are repeated at the rate of about 10-12/s. An individual echeme consists of about 2-4 syllables. This number varies throughout the distribution area (Von Helversen, 1989), but may even vary within an echeme-sequence. Both upstroke and downstroke produce sound, and hemisyllables are visible in the oscillogram of a male with one fore wing removed, thus producing sound with only one leg (fig. 235).

Aftersongs have to be considered to be echemes, lasting about 0.5-1 s and usually consisting of a clear pattern of syllables, produced at a low position of the legs and repeated at the rate of about 20/s. Presumably the distal stridulatory pegs on the hind legs are used during the aftersong. A downstroke hemisyllable and upstroke hemisyllable of one leg is followed by the same two hemisyllables of the other leg, producing a clicking or fluttering sound in contrast to the more musical, metallic timbre of the main song. Occasionally the leg movement of the aftersong does not seem to be this clear for a part of the echeme.

During courtship the song (fig. 234) changes slightly. The number of echeme-sequences in a series usually decreases until only one long echeme-sequence remains. The crescendo during this echeme-sequence is usually more gradual and begins hesitating, with short broken song starts. Typical aftersongs as described with the calling song may also follow the courtship song.

Differential diagnosis.— Both the *biguttulus* song followed by one or more typical aftersongs and the length, shape and venation of the male fore wing as well as the length of the stridulatory file in both sexes are most helpful to separate *b. euhedickei* from all other taxa of this genus occurring in Greece (tables 4, 7-8, figs 208-209). The distinction with *b. parnassicus* is discussed below (table 8, figs 208-209).

Discussion.— Part of the type-series of Ramme's *C. biguttulus hedickei* have been examined. The specimens are labelled as follows: (♂) "Holo-type" (round label with red circle) and "Budapest, 3.ix.1927, Hedicke"; same locality label (1 ♀); Rumanien, Oberhalb Herculesbad, 400 m, 19.ix.1942, Ramme (1 ♂, 1 ♀); Rumanien, Cozia bei Calimanesti, 15-1800 m, 5.ix.1941 [sic 1942!] Ramme (1 ♂); Rumanien, Oberhalb Sinaia, 900 m, 10.ix.1942, Ramme (1 ♂) (all in ZMHU/B).

The male holotype agrees fully with Ramme's notes (1942, 1951) that the expansion of the Sc area is limited mainly to its distal part where R shows a bend at the bifurcation of Rs. This is, indeed, a slight difference with males from West Europe. Further examination of the stridulatory file reveals that its length (± 4.1 mm) and the distance from the terminal distal peg to the tip of the hind knee (± 4.2 mm) are almost equal to each other and similar to the nominate form rather than to *b. euhedickei*. Also the spacing of the last distal pegs is limited and restricted to the terminal 5 to 8 ones, almost as in nominate *biguttulus*. Further biometric data are as follows (length in mm): prozona 1.5, metazona 1.6; elytron 12.9, stigma to tip 4.6, maximum width C area 0.9 and of combined C + Sc area 1.2, maximum width Sc area 0.47; tympanal aperture 0.23 & 1.13; tip subgenital plate 0.7; hind femur 10.1, file 4.1, terminal peg to tip knee 4.2, number of stridulatory pegs 123. The Romanian specimens listed above, agree fully with the holotype of *hedickei* and thus are closer to nominate *biguttulus* rather than to *b. euhedickei*. It can be confirmed now that the morphological difference between *b. euhedickei* and *b. hedickei* is restricted mainly to characters of the stridulatory file.

In the context of this study our observations on *biguttulus* populations from the northern border of the range of *b. euhedickei* are worth mentioning. Part of this border refers to the region of Peč and Mt. Hajla, western Kosovo (former Yugoslavia). In this zone of contact some specimens have a stridulatory file as long as in typical *b. euhedickei* but in most specimens it is shorter, sometimes even as short as nominate *biguttulus*. Although the available acoustic data are insufficient, we expect that in this area transitional forms occur. A closer study of this region would be most welcome.

The extraordinary length of the stridulatory file and the widely spacing of the distal pegs of *b. euhedickei* probably play an important role in sound production (see above under bioacoustics). These morphological particulars of the stridulatory file seem to be shared with *maroccanus* Nadig, 1976. But this species, as far as known, produces no "aftersongs" (Ragge & Reynolds, 1988).

Benediktov (1999) synonymized *euhedickei* with *C. porphyropterus* (Vorontsovsky, 1928), which also has an extraordinary long stridulatory file. Although bioacoustics had not been involved, he considered *euhedickei* the western subspecies of *porphyropterus*. A few years later the same author (Benediktov, 2005) published oscillograms of nominate *porphyropterus* (synonimising it with *brunneus mistshenkoellus* Oliger). From this figure it appears that the song of nominate *porphyropterus* lacks typical biguttuloid elements and is different from both nominate *biguttulus* and *euhedickei*. For this reason and because the length and number of stridulatory pegs of the file in itself is useless below species level (*e.g. C. brunneus brunneus* against *brunneus brevis* and *brunneus raggei*, see Ragge & Reynolds (1998) & La Greca *et al.* (2000); also the file of *C. maroccanus* is remarkably long) preference is given to stabilise the current taxonomic nomenclature and to combine *euhedickei* under *biguttulus*.

Distribution and ecology.— The range extends from Yugoslavian Makedhonia, throughout southern Bulgaria into northwestern Anatolia (Von Helversen, 1989; Benediktov, 1999; Popov & Chobanov, 2004). In Greece (fig. 264) it is common throughout the northern part of the Greek mainland, from Thraki to Ipiros, extending south but increasingly scarce in Central Greece. Apparently it is lacking in extreme southeastern Central Greece beyond Mt. Parnassos, the district of Attiki and throughout the Peloponnesean Peninsula. It has not yet been found in any Greek island, not even in offshore islands of continental Greece. In Greece this taxon has been found together with *C. bornhalmi, m. mollis, willemsei, v. dissimilis* and *pulloides*. The occurrence of *b.*

euhedickei and *b. parnassicus* is discussed under the latter taxon.

This form occurs in open grassland, waysides, forest edges and sunny slopes with sufficient grasses. It is scarce in lowlands and more abundant in uplands to above the timberline. Adults are most abundant from July to September.

Chorthippus biguttulus parnassicus **subspec. nov.**

(figs 42-43, 98-102, 162, 191, 206, 208-211, 236, 265, tables 4, 8-9, 14, 18, 26-27, cd 14)

Chorthippus (*Glyptobothrus*) *lesinensis* [nec Krauss]: Willemse, 1984: 145, map 198 (faunistics, partim).
Chorthippus biguttulus: von Helversen, 1989: 30 (as local populations in continental Greece).
Chorthippus (*Glyptobothrus*) *mollis mollis*: Ponel & Hébrard, 1988: 10 (partim, only Mt. Liakoura (= Mt. Parnassos), 1900 m).

While typical *b. euhedickei* occurs from the lowlands up to far above the timberline (*e.g.* Mt. Olimbos), in Mt. Parnassos this subspecies lives locally throughout this mountain but below the timberline and is completely absent at higher altitudes. It is replaced here by a population producing *biguttulus*-like songs but without typical aftersongs as in *b. euhedickei*. Besides the males of these high altitude populations lack the conspicuously widened costal areas of the fore wing, a key character both of *b. euhedickei* and the nominate subspecies.
Because of morphological as well as song differences both with nominate *biguttulus* and *b. euhedickei*, in combination with its parapatry along a quite narrow zone of contact with the latter, the high mountain populations of Mt. Parnassos are treated here as a separate taxon (see discussion below).

Material studied.— ♂ holo-, ♀ allo-, 24 ♂, 12 ♀ paratypes, Central Greece, labelled: "Hellas (Fthiotis), Mt. Parnassos, 1750 m, 10.viii.1988, F. Willemse" "rocky slopes above timberline near ski centre Fterolakas" (CW except 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1♀ in ZI/P).
Additional paratypes: Mt. Parnassos (Voiotia) [straight] above Arakhova, 1800 m, 26.vii.1971 (1 ♂) & 1500 m, 22.vii.1978 (2 ♂, 1 ♀) & 1600-1700 m, 4.ix.1989, above timberline rocky slope with grasses and low shrubs (5 ♂, 3 ♀); Mt. Parnassos (Voiotia) [below summit] [near EOS-Club refuge] 1900-2200 m, 1.viii.1972 (10 ♂, 2 ♀) & below summit, 1900 m, 22-23.vii.1978 (10 ♂, 3 ♀) & L. Willemse & J. Tilmans (7 ♂, 5 ♀) & 9.viii.1988, near EOS-Club refuge Gerondhovrakhos (4 ♂, 1 ♀) & 1750 m, stony slopes above timerline, few grasses, low prickly shrubs, some herbs, 20-24.vii.2000 (19 ♂, 11 ♀, of which 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P); Mt. Parnassos (Fthiotis), 1900 m, above ski centre Fterolakas, 3.ix.1989, above timberline, stony ground with shrubs and grasses (25 ♂, 10 ♀); Mt. Parnassos (Fthiotis), 1680 m, between Fterolakas and Kelaria, pine forest wayside clearing, 2.ix.1989 (15 ♂, 4 ♀); Mt. Parnassos (Fthiotis), 2000 m, above ski centre Kelaria, above timberline, stony ground, low shrubs and grasses, 2.ix.1989 (11 ♂, 9 ♀) & 1950 m, 22.vii.2000 (29 ♂, 18 ♀); Mt. Parnassos, 1750 m, main road to ski centre at exit to Keralia, above exit to Gerondhovrakhos near branching to either Keralia or Fterolakis, road verge in open pine forest, 25.vii.2000 (3 ♂, 1 ♀); Parnass-Gebirge, 1700 m, 20.viii.1981, Heller/Volleth (1 of 3 ♂ in alcohol vial 6/0154, other 2 ♂ are *m. mollis*) (CvH) (unless otherwise stated collected by the Willemse's and in CW).
Additional material tentatively arranged under this taxon is recorded below.

Description.— Male and female. General appearance small but robust (figs 42-43). Integument moderately to strongly hairy. Head capsule slightly inflated. Thorax, pronotum and tympanal aperture as in nominate form (figs 162, 191). Fore wings relatively short, extending a little beyond the tip of the hind knee in the male and commonly just reaching the tip of hind knee in the female. General shape of elytron slender. Male fore wing (figs 98-102) with fore margin moderately bowed, C and Sc areas moderately expanded, maximum width of combined C and Sc area 0.76-0.97 mm and less than 0.085 times the length of the fore wing; R and Sc veins slightly divergent; Sc area measured at the point of the maximum width of C area, relatively narrow, less than half as wide as C area; maximum width of Sc area more distally, commonly at the bifurcation of Rs; length of apical part (beyond the stigma) as in nominate form. Spacing and number of pegs of stridulatory file as in nominate form, but file relatively longer but not as long as in *b. euhedickei*. Distance between terminal distal peg and tip of hind knee from 0.85-1.09, mean 0.95 times the length of the stridulatory file. Abdominal terminalia and coloration as in nominate form.

Measurements (mm): body ♂ 13.1-14.9, ♀ 18.0-21.2; pronotum ♂ 2.5-2.9, ♀ 3.7-4.2; elytron ♂ 10.6-12.1, ♀ 14.1-14.8; hind femur ♂ 8.4-9.2, ♀ 11.4-12.4. Biometric data for the male and female in tables 26-27.

Bioacoustics (fig. 236, cd 14).— The calling song (fig. 236) is very similar to that of the nominate form (figs 16, 233), with series of 1-3 echeme-sequences, lasting about 1-2,5 s. Echemes are repeated at the rate of about 15/s and consist of about 2-4 syllables. Occasionally echemes consist of 5-8 syllables. Aftersongs are very rare in our recordings and only seem to be of the type known from the courtship song of the nominate form, with the legs in a high position. This is in contrast with the aftersong of *b. euhedickei* that is produced with the legs in a low position.

Differential diagnosis.— This taxon is characterised by its nominate *biguttulus*-like song and thus without typical aftersongs as in *b. euhedickei*, in combination with poorly expanded costal areas of the male fore wing, a more thickset habitus and other morphological particulars as described above. A morphological key character of *biguttulus* (s.l.) refers to the strongly bowed fore margin of the male fore wing, resulting from strongly expanded costal areas, greatest width of combined C and Sc area 1 mm or more. However, *b. parnassicus* lacks this character, the greatest width of the combined C and Sc area being less than 1 mm (table 8, figs 98-102). Further distinct features between *b. parnassicus* and the nominate form are given in the description above and also shared by *b. euhedickei* (table 8, fig. 209). Both taxa also differ, with very few exceptions, in the length of the stridulatory file (table 8, fig. 208).

Chorthippus b. parnassicus differs from *bornhalmi* and *v. dissimilis* a.o. by the shorter elytra with shorter apical part (beyond the stigma), (compare figs 88 or 78-80 against 98-102 respectively) and the larger number of stridulatory pegs in *v. dissimilis* (fig. 206).

On the other hand, the morphological distinction between *b. parnassicus* and *m. mollis* is difficult, particularly with the small mountain form of the latter which occurs also in Mt. Parnassos. The distinction is even more difficult than between *b. euhedickei* and *b. parnassicus*. In the forested slopes of Mt. Parnassos *b. parnassicus* occurs above the timberline and *mollis mollis* at lower altitudes. Syntopic occurrence of both species was found only along a narrow zone of overlap at the timberline. The R and Sc veins are slightly divergent in *b. parnassicus* (figs 98-102) while these are more parallel to each other in *mollis* (figs 110-113). Besides the R vein in *b. parnassicus* commonly presents a slight bend at the bifurcation of Rs, which is lacking or scarcely indicated in *mollis*. The Sc area of the male, measured along the same line of the maximum width of the C are, is compared with *mollis* slightly narrower in *b. parnassicus*, ratio width C/Sc area 1.53-2.22 against 2.21-3.25 respectively (table 8). Another character was found in the relatively slightly shorter stridulatory file in *mollis*: distance between terminal distal stridulatory peg and tip of knee relatively longer in *mollis* than in *b. parnassicus* (fig. 211). The spacing of the stridulatory pegs appear also different, those in *m. mollis* more closely set than in *b. parnassicus*. However, all these morphological differences are subtle. The most reliable character and easiest means of identification is the quite different song between *b. parnassicus* and *m. mollis*.

Morphological and acoustical differences between *b. parnassicus* and the also relatively long winged allopatric taxa *crassiceps* (typical form) (table 14), *parnon* (table 18) and *moreanus* (typical form) (table 9) are clear and shortly discussed under these three species.

Discussion.— In Mt. Parnassos *b. euhedickei* occurs locally, from its lower parts up to 1600-1700 m near the timberline while the higher slopes and pastures, especially above the timberline, are occupied by huge populations of *b. parnassicus*. The zone of contact is narrow, locally limited to a slight difference of altitude, ranging locally from 20-50 m: below this zone uniformly inhabited by typical *b. euhedickei* (figs 95-96), above this zone by typical *b. parnassicus* (figs 99-102). In this narrow zone of overlap, according to our observations, some males produce a typical aftersong of *b. euhedickei* but other males do not. Morphologically, most specimens in this overlap zone agree with typical *b. euhedickei* but a few are a little more thickset with shorter stridulatory file and venation of fore wing like *b. parnassicus*. In one locality (N38°32′35″ E22°33′48″, Voiotia, Mt. Parnassos, 1600 m, road to a small ski refuge, 2 km after exit to Gerondhovrachos, 23.vii.2000, road verge with abundant vegetation of *Stipa* grass in pine forest) we found these forms even syntopic, comparing venation and shape of the fore wings (fig. 97 resembles *b. euhedickei*, and fig. 98 that of *b. parnassicus*). Whether hybridisation occurs in this locality is unknown and if so, whether hybrid specimens are fertile is another open question. Clear mosaic dispersal of both forms was not observed.

The question arose whether this situation in Mt. Parnassos is shared with other high mountains in Greece and adjacent areas. Observations on the following material are noteworthy:

GREECE: Ioannina, Mt. Timfi, Papigon, 1000 m & above Papigon, 1800-2100 m, 1.viii.1971 (12 ♂, 17 ♀); Ioannina, Mt. Tomaros above Varyiadhes 1200-1600 m, 2. viii.1978 (4 ♂, 6 ♀) & 1180-1300 m & 1250-1450 m & 1450-1900 m, 11/12.viii.2004 (10+18+6 ♂, 7+17+1 ♀); Evritania, Mt. Panaetolikon above Proussos, Xerovouni, 1400-1650 m, 2.viii.1975 (1 ♂) & 1400-1650 m, 5 km W of pass Proussos-Labiri, 21.vii.2002 (1 ♂) &

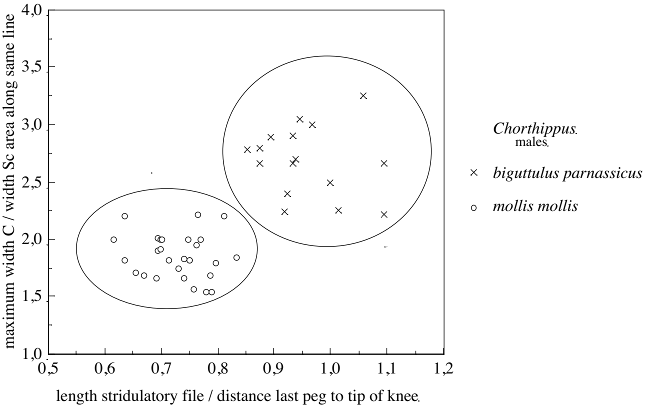


Fig. 211. Scatter diagram showing a plot of the ratio of the length of the stridulatory file to the distance from the terminal distal peg to the tip of the knee against the ratio of the maximum width of the C to the width of the Sc area of the fore wing, measured along the same line, in males of *Chorthippus biguttulus parnassicus* and *C. mollis mollis*.

Table 9. Biometric data useful to separate males of typical *Chorthippus moreanus* from *C. biguttulus parnassicus*.

	moreanus (typical)	*biguttulus parnassicus*
ratio length of prozona / length of metazona of pronotum	1.02 (0.94-1.07)	0.86 (0.81-0.95)
distance stigma to tip of fore wing (mm)	2.89 (2.7-3.3)	3.96 (3.4-4.43)
ratio distance from stigma to tip / length of fore wing	0.26 (0.33-0.29)	0.35 (0.32-0.38)
length of hind femur (mm)	9.98 (9.4-10.6)	8.79 (8.4-9.18)
ratio length of file / distance from end of file to tip of knee	0.73 (0.67-0.82)	0.95 (0.85-1.09)

Proussos-Ladhikou, 1450-1550 m, 7.viii.2003 (1 ♂, 2 ♀); Evritania, Mt. Timfristos above Karpenision, below summit 1500 & 1800-2100 m, 29.vii.1971 & 5.viii.1975 (31 ♂, 35 ♀) & 1650-1900 m, 18.vii.2002 (5 ♂, 1 ♀).

YUGOSLAVIA: Macedonia, Mt. Bistra above Mavrovi, 1800 m, 16.vii.1969 (2 ♂, 1 ♀) (all collected by the Willemse's and in CW).

It was observed in Mt. Timfristos (Central Greece) and Mt. Tomaros (Ipiros) that the number of individual males of *b. euhedickei* producing typical aftersongs changes from almost always below the timberline up to about 1500 m to almost never from 1500-1600 m altitude up to the summit. At the same time it was observed that with increasing altitude also morphologically the specimens are slightly smaller, shorter winged and with shorter stridulatory file and thus closer though not similar (male fore wing) to typical *b. parnassicus* from Mt. Parnassos. Also material before us from high altitudes of other high mountains *e.g.* Mt. Panaetolikon (Central Greece), Mt. Timfi (northern Pindhos) and Mt. Bistra (Yugoslav Macedonia) resemble morphologically somewhat *b. parnassicus* but unfortunately their songs have not or insufficiently been recorded. In all these cases, however, the abrupt transition of *b. euhedickei* into typical *b. parnassicus* like in Mt. Parnassos has not been observed.

The southeastern distribution limit in Greece of *b. euhedickei* is Mt. Parnassos (fig. 263). Song and morphology of *b. parnassicus* indicate a close relationship both with nominate *biguttulus* and *b. euhedickei*. A suggestion could be that *b. parnassicus* represents an archaic form of *biguttulus* (s.l.) which survived in high altitude areas of the southern Balkans. This could explain why *b. parnassicus* comparatively much better survived and is recognisable in Mt. Parnassos and less so in more northern and commonly less isolated localities.

Our conclusion is that, at least in Mt. Parnassos, two closely related but distinct forms occur, *b. euhedickei* and *b. parnassicus*. We do neither know what the exact nature of the genetic distance between these forms is, nor between each of them and nominate *biguttulus*. Although there are arguments that, at least in Mt. Parnassos, the populations are genetically sufficiently separated to prevent broad hybridisation and to preserve their identity, we classified the new form for the time being as a subspecies. Further studies are needed.

Previously *b. parnassicus* has been recorded (Willemse, 1984) as a taxon related to *mollis* (under the name *lesinensis*). The cumbersome morphological distinction between *b. parnassicus* and *mollis* in combination with their slight overlapping occurrence at the timberline and particularly the lack of recorded songs explain why the separate taxa have been missed in the past.

Distribution and ecology.— *Chorthippus b. parnassicus* (fig. 265) lives in the highest parts of Mt. Parnassos. The occurrence in a number of other high mountains of central Greece, the Pindhos range, Ipiros and further north in Albania and Yugoslav Macedonia requires confirmation. On Mt. Olimbos and further eastwards (Mt. Pangaion), typical *b. euhedickei* occurs from the lowlands to far above the timberline. This may indicate that the range of *b. parnassicus* is more west, extending roughly from the Albanian and West Macedonian mountains through the Pindhos range southeasternwards reaching Mt. Parnassos.

In Mt. Parnassos the new taxon occurs syntopic with *bornhalmi* and at or just below the timberline with *m. mollis* in the zone of contact. The parapatric occurrence with *b. euhedickei* is mentioned above.

Scarcely occurring in more open pine forests close but just below the timberline at about 1600 m, huge populations were found at higher altitudes up to more than 2000 m, all over the open, sunny, rocky slopes with mixed sub-alpine vegetation of grasses and herbs.

Chorthippus moreanus spec. nov.

(figs 16, 44-45, 103-107, 163, 192, 212-215, 220-222, 237-238, 256-257, 268, tables 9-10, 17, 19, 28, 29, cd 15, 16)

Chorthippus bozdaghi [nec Uvarov]: Harz, 1975: 866, figs (partim, "Taygetos").

Chorthippus crassiceps [nec Ramme]: Willemse, 1984: 145, map 198 (faunistics, partim); 1985: 28; 1986: 76 (identification, partim).

Chorthippus taxon "A": Ragge *et al.*, 1990: 243, fig. 11, 14 (oscillogram, Messinia, E of Kalamata, Kardhamili); Ragge & Reynolds, 1998: fig. 76 (map).

Material examined (all Greece, the Peloponnese).— ♂ Holo-, ♀ allo-, 37 ♂, 23 ♀ paratypes, labelled: "Hellas, Peloponnisos, Ilia, ruins of Bassae, 1100 m, stony ground, scattered shrubs, grassy patches, 7. ix.1989, F. Willemse" (in CW except 1 ♂, 1 ♀ paratypes in BMNH/L & 1 ♂, 1 ♀ paratypes in ZI/P).
Additional paratypes: Ilia: as holotype, 27.vii.1970, Willemse & Scherpbier (6 ♂, 4 ♀) & 30.vii.1978, L. Willemse & J. Tilmans (1 ♂, 1 ♀) & Tempelbereich von Vassai, 23.viii.1986, O. von Helversen (1 ♀, alcohol vial 6/0072) (CvH) & NE von Vassai, 23/24.viii.1986, O. von Helversen (5 ♂, alcohol vial 6/0073) (CvH) & Bassae, 1995 & Bassae, Umgebung Tempelgelaende, 27.viii.1989, both O. von Helversen (3 ♂) (CvH);
Additional material including also morphologically atypical populations: Ilia: Andritsaina, 1000 m, 29.vii.1978, L. Willemse & J. Tilmans (4 ♂, 1 ♀); 3 km N of Andritsaina, Sikies, 1000 m, surroundings tresh floor, scarce vegetation, 7.ix.1989 (4 ♂, 4 ♀); E of Andritsaina, W of Thisoa, 600 m, stony slope, 9. ix.1989 (2 ♂, 2 ♀). Messinia: 5 km N of Nedha, 1000-1100 m, stony slope, scattered shrubs, 8.ix.1989 (13 ♂, 15 ♀); 3 km N of Nedha, 900 m, stony slope, scattered shrubs, 8.ix.1989 (1 ♂); Nedhia, 800 m, cultivated ground with apple trees, 8.ix.1989 (2 ♀); Petra-Kakaletri, 600 m, wayside, stony grassy slope, 8.ix.1989 (11 ♂, 13 ♀); above Agrilovouno, 600 m, stony plateau with *Quercus* tree, 8.ix.1989 (5 ♂, 4 ♀); S of Aryirovouni [Agrilovouno], 600 m, 8.ix.1989 (1 ♂); S of Kalamata, Kambos, 400-700 m, 21.vii.1971, Willemse & Scherpbier (11 ♂, 8 ♀); Kardhamili, 100 m, 13.vii.1987 (3 ♂, 2 ♀); S of Pilos, between Palaioneri & Varakes, 140 m, stony hill, 31.vii.2001, WGS84 N36°53'32.8" E021°42'06.5" (2 ♂). Lakonia: above Areopolis, 300 m, 12.vii.1987 (1 ♂); Mt. Taiyetos above Anoyeia via Toritza, forest road to Refuge Alpine Club EOS, 1200 m, 22.vii.1971 (12 ♂, 6 ♀, including 1 ♂, 1 ♀ in ZI/P) & 1250-1550 m, clearings, 1.viii.1991 (26 ♂, 8 ♀, including 1 ♂, 1 ♀ in BMNH/L) & Taiyetos Geb., 8.viii.1998, F. Mayer (7 ♂, 7 ♀, alcohol) (CM); Mani peninsula, between Tsikkali & Lagia, 380 m, phrygana, 31.vii.2001 (1 ♂). Arkadhia: E of Andritsaina, E of Thisoa, 500 m, 9.ix.1989 (1 ♂, 1 ♀); S of Dhimitsana, N of Elliniko, 1100 m, stony slope, 9.ix.1989 (5 ♂, 2 ♀); Elliniko, 1050 m, trockenes Macchia in Kalkfelsen, 28.viii.1989, O. von Helversen (4 ♂) (CvH); Zygovitsi bei Dhimitsana, 1100 m, trockene Haenge, 28.viii.1989, O. von Helversen (2 ♂, 1 ♀)

(CvH); SE of Dhimitsana, Ipsous, 800 m, 27.vii.1970, Willemse & Scherpbier (11 ♂, 9 ♀). (unless otherwise stated collected by F. Willemse and in CW)

Since the late 1980s it has been known that males of populations ranging over the central southern part of the Peloponnese produce a song that differs from any other taxon in Greece (Ragge *et al.*, 1990). This song was not described until now and we consider these populations to belong to a not yet described taxon. At the same time it became clear that across the populations there is a clinal shift towards smaller specimens with shorter wings resulting into an increasing similarity with *pulloides*. Therefore we selected as type locality a population with uniform and quite typical characters both bioacoustically and morphologically: to wit the surroundings of the ruins of Bassae, southwest of Andritsaina, for historical reasons a preserved area. The description below refers to this form of the taxon.

Recognition (typical form).— Male and female, general appearance as *biguttulus* (figs 44-45). Fastigium verticis, interocular distance and proportions of head normal, greatest width of the head not exceeding the pronotal length, ratio between pronotal length to maximum width of the head always more than 1. Metazona of pronotum commonly only slightly shorter than prozona, sulcus almost in the middle of pronotal length (fig. 163). Tympanal aperture usually narrow, ratio maximum to minimum diameter 3.5-7.1, mean value 5 (fig. 192). Fore wings (figs 103-106) reaching hind knees, extending just beyond tip of abdomen in male and slightly shorter in female; stigma well indicated, ratio between distance from stigma to tip of fore wing to length of fore wing in the male 0.24-0.29, mean 0.26; fore edge in male moderately bulging, C and Sc area relatively wide, maximum width of C area average 2.2 times width of Sc area measured along same line. Stridulatory file of usual length, not conspicuously extending towards the hind knee, number of pegs in male 100-136, average 116, spacing about 34 pegs per mm.

Measurements (mm): body ♂ 13.1-14.9, ♀ 18.0-21.2; pronotum ♂ 2.5-2.9, ♀ 3.7-4.2; elytron ♂ 10.6-12.1, ♀ 14.1-14.8; hind femur ♂ 8.4-9.2, ♀ 11.4-12.4. Biometric data for the male and female in tables 28-29.

Bioacoustics (figs 16, 237-238, cd 15-16).— The calling song (fig. 237) consists of an echeme-sequence of 1-3 s, sometimes up to 8 s, starting very weak, gradually becoming louder. About 2-4 loud ticks sometimes precede the echeme-sequence. As pointed out above under terminology (figs 15-16), the echemes are interpreted as a biguttuloid element (Eb), each echeme consisting of 3-5 syllables, one loud (S1) followed by 2-4 weak sounds (S2), corresponding with the first strong and the following weaker to-and-fro movements of the hind legs. Echemes last 90-120 ms (commonly about 100 ms) and are repeated at the rate of about 7-12/s (commonly 9-11/s), without visible intervals. Based upon analysis of the song of one-legged specimens, both the upstroke and downstroke of the legs produce sound. Downstrokes produce the loudest sounds. The leg movement is slightly out of phase, thus making individual syllables often hard to recognise in oscillograms of two-legged specimens. As pointed out in Elsner (1974; pattern I & II) for nominate *biguttulus*, a slight difference in movement of the left and right hind leg also explains the absence of an inter-echemic interval.

Sometimes the echeme-sequence ends with a series of less pronounced echemes with a slower repetition rate, less pronounced than in the courtship song.

The courtship song (fig. 238) commonly lasts longer than the calling song (up to 20 s) and basically has the same structure as the calling song. At its start, it may be interrupted some times before fully sung. Echemes may consist of up to 6 syllables. The echeme-sequence of the courtship song often is followed by a series of less pronounced and in loudness decrescendo echemes with usually a slower repetition rate. We consider this series of echemes an aftersong, although included in the echeme-sequence. It is worthwhile mentioning that in the contact zone with *pulloides* on Mt. Taiyetos aftersongs in *moreanus* are most explicit. A possible explanation could be that the pronounced aftersong offers females a means (a.o. the difference in echeme repetition rate) to discriminate males from the two species.

Variability.— Adjacent to the type-locality in extreme southern Ilia, adjacent Messinia, the western parts of Mt. Taiyetos including the lowlands around Areopolis and the Mani peninsula in the extreme southwestern Lakonia, populations occur that are fairly consistent, morphologically as well as bioacoustically, with the topotypical population of *C. moreanus*. At the edge of its range, more to the east at the Arkadhia high plateau, west of Tripolis and southeast on the forested slopes below the timberline in the central parts of Mt. Taiyetos near the refuge of the Alpine Ski Club EOS populations differ from topotypical populations in being smaller in size and having shorter wings (*e.g.* figs 106-107, 221-222). However, because the bioacoustics in these populations still closely resemble those of the topotypical populations, they have also been assigned to C. *moreanus*. On the other hand the populations occurring around Petralona (& Sekoula?) and Nedhoussa closely resemble topotypical *C. moreanus* morphologically but do show a distinctive variation in bioacoustics where the long lasting echeme-sequence tends to look and sound as a series of echeme-sequences (figs 256-257). These populations are discussed as atypical *moreanus* under "Atypical and transitional populations " (see after *C. pulloides*).

Differential diagnosis.— The taxon *moreanus* is well defined by its song which is different from all other taxa, at least in Greece. Its morphological differentiation is sometimes not so easy.

Distinction between *moreanus*, both the typical and morphologically atypical shorter winged populations, and the syntopic occurring species *willemsei*, *bornhalmi* and *v. dissimilis* is very clear: *willemsei* (figs 82-84, 183-184) is characterised by shorter wings, red colored hind tibiae and much more open tympanal aperture, *bornhalmi* (figs 88, 157-159) by much longer wings and wider pronotum with the sulcus in front of the middle of pronotal length and *v. dissimilis* (figs 78-80, 150-151) by relatively longer pronotal metazona, apparently longer wings and a much larger number of stridulatory pegs.

Also the difference between typical *moreanus* and Greek *biguttulus* is obvious: *b. euhedickei* is characterised by the fore wing being longer and with remarkably enlarged C & Sc areas in the male (figs 93-96) and much longer stridulatory file in both sexes, *b. parnassicus* by the pronotal sulcus being more in front of the middle of the pronotal length (fig. 162), the longer distance between stigma and tip of fore wing (figs 99-102) and the relatively shorter hind femur (table 9).

However, the morphological difference between typical *moreanus* and typical *crassiceps* is subtle: the latter has the head capsule remarkably inflated, pronotal metazona slightly shorter with transverse sulcus located slightly less in front of the middle, the tympanal aperture wider, the distance of the stigma to the tip of the elytron relatively longer (table 10, figs 114-115, 168, 197, 212).

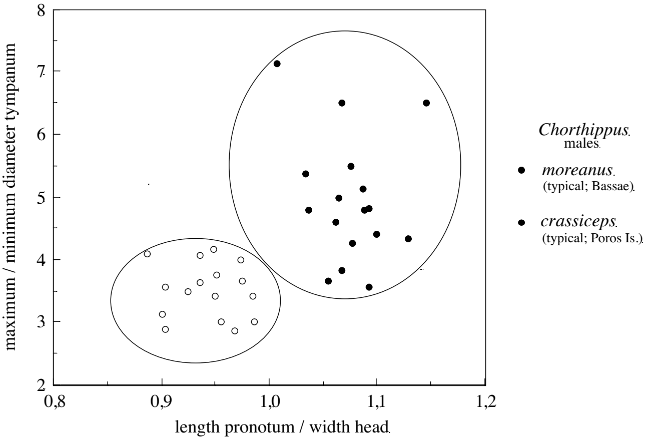


Fig. 212. Scatter diagram showing a plot of the ratio of the length of the pronotum to the maximum width of he head against the ratio of the maximum to minimum diameter of the tympanum in males of typical *Chorthippus moreanus* and typical *C. crassiceps*.

For the differentiation between typical *moreanus* and *parnon* similar characters can be used but instead of the location of the pronotal sulcus, the sometimes relatively broader Sc area in the male fore wing of *moreanus* is more helpful (table 10, 17, see *parnon* figs 118-120, 198, 213-214).

Nominate *mollis*, particularly the small mountain form of Central Greece, differs from *moreanus e.g.* in the much more slender habitus, particularly shown by head, thorax and wings (see *mollis*: figs 50-53, 110-113, 165-167).

The distinction between typical *moreanus* and typical *pulloides* is evident by *pulloides* having shorter fore wings often without stigma, with narrower C area (in the male of *moreanus* mean 0.58 against 0.47 mm in *pulloides*) and widely rounded tip (figs 103-107 against figs 131-140), shorter hind femur and fewer number of stridulatory pegs in the latter (mean number in the male of *moreanus* 116 against 89 in *pulloides*) (partly in table 17, figs 215, 220).

However, differentiation between the morphologically atypical, shorter winged populations of *moreanus* and the morphologically and bioacoustically transitional populations between the *C. pulloides* complex and *moreanus* is arbitrary (table 19, figs 221-

Table 10. Biometric data useful to separate males of typical *Chorthippus moreanus* from both typical *C. crassiceps* and *C. parnon* (figs 212-214).

	moreanus (typical)	*crassiceps* (typical)	*parnon*
ratio length of pronotum / maximum width of head	1.07 (1.01-1.14)	0.95 (0.88-0.99)	0.96 (0.83-1.02
ratio length of prozona / length of metazona of pronotum	1.02 (0.94-1.07)	1.09 (1.04-1.15)	1.07 (0.93-1.23)
ratio maximum / minimum diameter of tympanum	4.95 (3.57-7.14)	3.51 (2.87-4.17)	3.12 (2.5-3.83)
ratio distance of stigma to tip of fore wing / length of fore wing	0.26 (0.23-0.29)	0.31 (0.29-0.33)	0.31 (0.27-0.33)
ratio width of C / width of Sc area measured along same line	2.23 (1.69-2.67)	2.42 (1.91-3.0)	2.91 (2.0-4.0)

Fig. 213. Scatter diagram showing a plot of the ratio of the length of the pronotum to the maximum width of he head against the ratio of the maximum to minimum diameter of the tympanum in males of typical *Chorthippus moreanus* and typical *C. parnon*.

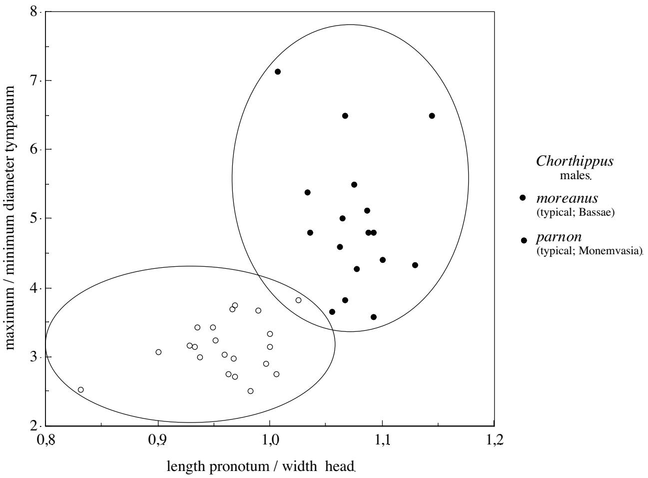
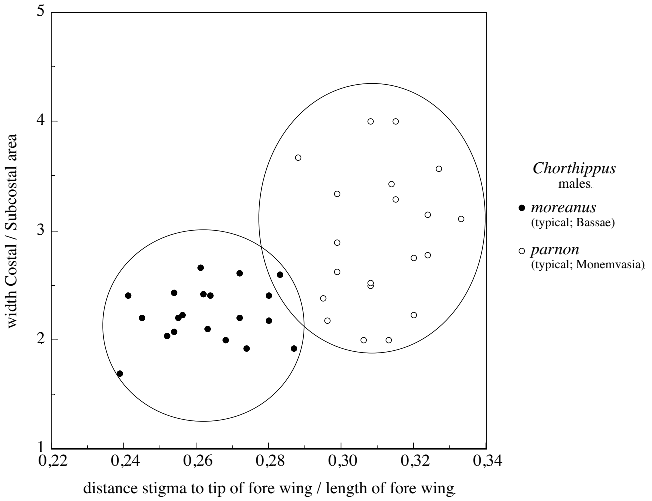


Fig. 214. Scatter diagram showing a plot of the ratio of the distance of the stigma to the tip of the fore wing to the length of the fore wing against the ratio of the maximum width of the C to the width of the Sc area, measured along the same line in males of typical *Chorthippus moreanus* and typical *C. parnon*.



222). Concluding, *C. moreanus* can be recognised most reliably by means of the song, but compare also the heading of these transitional populations of *C. pulloides*.

Discussion.— The typical form of *moreanus* is well defined. However, because of the occurrence of parapatric atypical forms and particularly of bioacoustically transitional populations presenting a mixture of characters both of *moreanus* and *pulloides-crassiceps*, we do not know how far genetic divergence has been developed between *moreanus* and *pulloides*. The exact nature of the relationships between all these populations is still an open question (see also below under heading "Atypical and transitional populations" of *C. pulloides*).

Previous records of *moreanus* are found in Willemse (1984, as *crassiceps* partim) and in Harz (1975, as *bozdaghi*). The last diagnosis was based on specimens from Langadha Pass over Mt. Taiyetos, connecting Sparti and Kalamata. Harz forwarded this material to Uvarov, who found the specimens close but not identical with his *bozdaghi* from Tur-

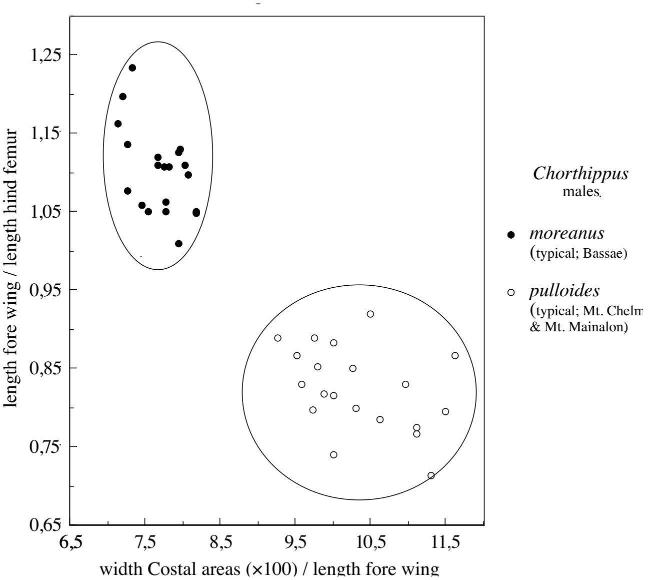


Fig. 215. Scatter diagram showing a plot of the ratio of the width of the combined C areas to the length of the fore wing against the ratio of the length of the fore wing to the length of the hind femur in males of typical *Chorthippus moreanus* and typical *C. pulloides*.

key (pers. comm. K. Harz, 1974). The bioacoustics of these Langadha Pass populations have now been studied and are clearly transitional, bridging the biguttuloid characters of *moreanus* and the molloid ones of *pulloides-crassiceps*. The song of the Westanatolian species *bozdaghi*, is clearly molloid (Mol *et al.*, 2003) and could be related to *pulloides-crassiceps* but certainly not to *moreanus*. However, there is another Anatolian congeneric possibly related to *moreanus*, to wit *ilkazi* Uvarov (Mol *et al.*, 2003). The latter occurs in central north Anatolia, but the relationship of both taxa is not clear.

Distribution and ecology.— The range of *moreanus*, including its morphologically atypical forms but excluding transitional situations to the *pulloides* complex, is restricted to the southern part of the central Peloponnese, covering Messinia and southwestern Arkadhia and Lakonia (fig. 268). In Lakonia it extends into the southern and western slopes of the Taiyetos range, while the northeastern parts of this mountain range are inhabited by populations intermediate between *moreanus* and *pulloides-crassiceps*. Interesting is the observation that in Mt. Taiyetos *moreanus* occurs from sea level to the timberline at about 1600 m but is absent above this altitude which is inhabited by a *pulloides*-like population which, in its turn, does not occur in the forested slopes below the timberline (see also below under heading "Atypical and transitional populations"). Syntopic occurrence of *moreanus* has been observed with *bornhalmi* and *willemsei*.

The habitat consists of dry and stony open ground with low to moderately high vegetation mixed with grasses, open forests with low undergrowth or forest clearings. The species ranges from the lowlands up to the mountains. As far as the range extends, these mountains are all of middle altitudes, except for Mt. Taiyetos. Here the species occurs in the forested slopes up to 1600 m but was not found in the zone above the timberline, extending between 1600-1700 m to the summit of 2404 m. Adults appear in the second half of July or slightly later, depending on altitude or other local factors, and are most abundant in the second half of August and during September.

Etymology.— The name *moreanus* is derived as adjective of Morea, the Latin name of the Peloponnese.

MOLLIS GROUP

typical species: *Gryllus mollis* Charpentier, 1825 (lectotype ♂, "Silesia", ZIL/L).

Chorthippus mollis is strongly defined by its highly characteristic song (cd 17-20. It is widely spread over Europe, from Denmark to the northern Iberian Peninsula and from France eastwards into temperate Asia. Based upon slight differences in morphology and song an Alpine form is recognized, *C. m. ignifer* (Ramme, 1923), occurring mainly in the southern Alps, while the populations of the northern Alps are more intermediate between nominate *mollis* and *m. ignifer* (*e.g.* Ingrisch, 1995; Ragge & Reynolds, 1998).

The situation in the Balkans is more complicated. The nominate subspecies is known from the Balkans, extending southwards into the mainland of Greece and a few offshore islands, but absent from the Peloponnese.

Karaman (1975) described a subspecies, *mollis pechevi*, from Bulgaria. Because its song is unknown, the classification is not yet settled but its morphology very much resemble nominate *mollis*.

Chorthippus lesinensis (Krauss, 1888) was described from the Dalmatian Island of Hvar (= Lesina). Morphologically, this taxon differs slightly from nominate *mollis*. Its song was unknown but is related to that of *mollis*, particularly of *m. ignifer*. *Chorthippus lesinensis* is treated here as a subspecies of *mollis*.

Another group of Greek "sing-alikes" of *mollis* are *C. crassiceps* and *pulloides* (both Ramme, 1926) and a closely related newly discovered taxon described below as *parnon*. However, their morphology and bioacoustics are more or less distinct from *mollis* (s.l.). While *pulloides* may occur syntopic with nominate *mollis* and therefore is considered a distinct species, the position of *crassiceps* is not fully understood as will be pointed out below. Another doubtful case concerns the position of *C. sangiorgii* (Finot, 1902), reminiscent of *pulloides* though maybe related to the *vagans* group (stridulation movements).

The taxa in Greece and adjacent areas closely related to *mollis* are treated below in the following sequence: 1) the *mollis*-complex, representing some intraspecific forms of that species: nominate *mollis*, *m. lesinensis* and *m. pechevi*; 2) the *pulloides-crassiceps* complex including *parnon* and *sangiorgii* (uncertain state) and 3) finally some data on Peloponnesean morphologically and bioacoustically atypical forms of *pulloides-crassiceps* and transitional populations bridging *pulloides* and *moreanus*.

Chorthippus mollis-complex

Chorthippus mollis lesinensis (Krauss, 1888) stat. nov.

(figs 46-47, 108, 164, 193, 216, 241-242, tables 11-12, 30-31, cd 19, 20)

Stenobothrus lesinensis Krauss, 1888: 117-118 (description of female, syntype females Lesina (= Hvar), surr. Brusje & Humac, ix-x.1887, D. Novak, SMN/S).

Chorthippus lesinensis: Ramme, 1951: 119 (Hvar, Brusje).

Chorthippus lesinensis lesinensis: Mařan, 1965: 654 (description of male; faunistic details).

Chorthippus lesinensis svarci Mařan, 1965: 654 (description, male holotype Korčula, Vela Luka, 28.viii.1961, V. Svarc, NM/P).

Chorthippus lesinensis lastovensis Mařan, 1965: 655 (description, male holotype Lastovski Ostrvi, 17.ix.1961, V. Svarc, NM/P).

Chorthippus (*Glyptobothrus*) *lesinensis*: Harz, 1975: 888, figs 3135, 3183, 3334-3339 (description, Adriatic area of Yugoslavia); Willemse, 1984: 145 (faunistics, partim); 1985: 28 (further research needed); 1986: 76, figs 1019-1022 (identification).

Glyptobothrus lesinensis lesinensis: Storozhenko, 2002: 4 (comb. nov.). (taxonomic status).

Glyptobothrus lesinensis svarci: Storozhenko, 2002: 4 (comb. nov.). (taxonomic status).

Glyptobothrus lesinensis lastovensis: Storozhenko, 2002: 4 (comb. nov.). (taxonomic status).

Material studied.— Topotypes: Croatia, Hvar (= Lesina I.), rocky grassy slope 500 m south of Pitve, altitude c. 300 m, (17 ♂, 10 ♀) & rocky slope, 500 m east of Vrisnik, altitude c. 150 m (2 ♂, 1 ♀) & hillside 500 m north of Starigrad, altitude c. 50 m (7 ♂, 2 ♀) & rocky hillside, 1 km east of Velo Grablje, altitude 350 m (3 ♂) & hillside, 3 km southwest of Starigrad, altitude 80 m (4 ♂) (all viii.1996, R. Kleukers, song recordings and in CW).

Additonal material: Dalmatien, Kučiste, Ende Sept. (22 ♂, 6 ♀); Gravosa [Dubrovnik] 17-30.x.[19]32 Coll. Wagner Wien (2 ♀, CW); I. Brač, Supetar, 18-30.ix.67, leg. Adolf Cejchan (1 ♂, 1 ♀, CW). Montenegro: Lovcen, 1999 (1 ♂) (CvH).

Recognition.— As nominate *mollis* but general appearance more robust and head more inflated, especially shown in the female sex where the greatest width of the head exceeds slightly the pronotal length (figs 46-47, 164). Fore wings relatively short and slender, just slightly longer than hind femur, reaching the tip of abdomen but not that of the hind knee (fig. 108). Biometric data for the male and female in tables 30-31.

Bioacoustics (figs 241-242, cd 19-20).— The number of available recordings of this taxon is quite limited. The calling song (fig. 241) is closely related to the song of *m. mollis* and *m. ignifer*. It consists of an echeme-sequence of about 4-6 s, with about 12-17 echemes. Echemes are repeated at the rate of about 3-4/s. They consist of a buzzing part with a molloid pattern of leg movement (Em, see fig. 15) that is preceded by a tick sound, commonly produced by both hind legs. The ticks are usually less loud than in *m. mollis* and *m. ignifer*, but unlike in *m. mollis* and like in *m. ignifer* also present in the final echemes. There is no indication of an aftersong.

Rivalry song (fig. 241) is similar to the calling song but lasts shorter and starts louder.

Courtship song (fig. 242) lasts longer, up to about 10 s, consisting of about 20-30 echemes, repeated at the rate of about 2/s. It is less pronounced than the calling song, with weaker tick sonds and a gradual increase of loudness. Echemes seem to be repeated with longer intervals.

Differential diagnosis.— The typical populations of the Dalmatian islands are distinct from nominate *mollis* by the enlarged head and shorter fore wings which do not or scarcely extend beyond the tip of the abdomen (table 11). Compared with Greek *m. mollis* it is noticed that relatively short fore wings also occur in the small mountain form of the latter but that these specimens do not have the strongly enlarged head of ***C. m.*** *lesinensis* (figs 46-47 against 50-53 and fig. 164 against 165-167).

The difference between *m. lesinensis* and typical *crassiceps* is restricted to slightly wider open tympanal aperture (figs 193 against 197), wider C area (not Sc area, compare ratio C/Sc) and even more inflation of the head in *crassiceps* (table 12, fig. 216). These distinct characters with *m. lesinensis* are shared also by *parnon*.

The distinction with *m. ignifer* is less clear and discussed below.

Table 11. Biometric data useful to separate typical *Chorthippus mollis lesinensis* from Greek *C. mollis mollis*.

	mollis lesinensis (typical)	*mollis mollis* (Greece)
ratio length of pronotum / maximum width of head	♂ 1.04 (1.01-1.06) ♀ 0.97 (0.89-1.07)	♂ 1.13 (1.02-1.2) ♀ 1.07 (1.03-1.16)
ratio length of fore wing / length of hind femur	♂ 1.08 (0.96-1.15)	♂ 1.20 (1.09-1.40)

Table 12. Biometric data useful to separate typical *Chorthippus mollis lesinensis* from typical *C. crassiceps* (fig. 216).

	mollis lesinensis (typical)	*crassiceps* (typical)
ratio length of pronotum / maximum width of head	♂ 1.04 (1.01-1.06) ♀ 0.97 (0.89-1.07)	♂ 0.95 (0.89-0.99) ♀ 0.93 (0.88-0.98)
ratio maximum / minimum diameter of tympanum	♂ 5.98 (4.80-7.19)	♂ 3.51 (2.87-4.17)
width of costal area (mm)	♂ 0.46 (0.41-0.50)	♂ 0.56 (0.50-0.62)
ratio width costal / subcostal area	♂ 1.86 (1.46-2.18)	♂ 2.42 (1.91-3.00)

Discussion.— The differences between nominate *lesinensis* and the subspecies *svarci* and *lastovensis* described by Mařan (1965), from each of the islands of Hvar, Korčula and Lastovo, are subtle. We consider them as local races resulting from geographic isolation and of intra subspecific value because the main characters of these populations are comparatively uniform. Also specimens from the coastal strip of the opposite continental part of Dalmatia (*e.g.* Gravosa, surroundings of Dubrovnik in CW) agree well with the topotypical ones. However, those from sites more inland, *e.g.* Titograd, Cetinje, Bioce, Mostar-Nevesinje (CW) have the size of head and length of fore wings intermediate between *m. lesinensis* and nominate *mollis*. While the populations throughout the mainand inland of former Yugoslavia agree with the slender form of nominate *mollis*, the intermediate forms extend along the Adriatic coast. The populations farther northwards from Istria and northeastern Italy are assigned by most authors to *m. ignifer*.

We propose to restrict the name of *m. lesinensis* only to the typically large headed and shorter winged populations from these Dalmatian islands and the coastal stripe of opposite continental Dalmatia.

Previous records of *m. lesinensis* from Greece (Willemse, 1984), discussed below under *m. mollis*, do not refer to this taxon as defined here.

In Harz (1975) the types of Krauss are said to be in Ludwigsburg (Germany) albeit with a question mark. The largest part of Krauss' collection there moved to the SMN in Stuttgart. There are at least a number of syntypes deposited, maybe that some other specimens are deposited in the NM in Vienna. A lectotype has not yet been selected (pers. comm. S. Ingrisch, 2004).

Distribution.— Known from the Dalmatian islands of Brač (Brazza), Hvar (Lesina), Korčula (Curzola), Lastovo (Lagosta), some other adjacent islets, peninsula Peijesac (Sabbioncello) and the opposite coastal stripe of Dalmatia and Montenegro. Part of the previous records under *lesinensis* will certainly prove to refer to transitional forms between typical *m. lesinensis, m. ignifer* and nominate *mollis*. The subspecies occurs, at least in the island of Hvar, on stony, dry and sunny slopes with mixed vegetation of grasses, herbs and shrubs, locally together with *C. bornhalmi* (pers. comm. R. Kleukers, 1996).

Chorthippus mollis pechevi Karaman, 1975

(figs 48-49, 109, table 30)

Chorthippus mollis pechevi Karaman, 1975: 55, figs 2, 4 (description, 13 ♂, 1 ♀ syntypes from Bulgaria, Rogatchevo and Kranevo at Varna, 1.viii.1967, M. Karaman) (lectotype male designated here: Bulgaria-Varna, Kranevo 12.viii.1967, leg. M. Karaman, CK)

Glyptobothrus mollis pechevi: Storozhenko, 2002: 4 (comb. nov.) (taxonomic status)

Material studied.— Type series: Bulgaria-Varna, Kranevo, 12.viii.1967, leg. M. Karaman (♂ lectotype designated here, 4 ♂, 1 ♀ paratypes, CK).

Additional material, tentatively arranged under *mollis pechevi* : Bulgaria, E Stara Planina Mts, road from Sliven to Byala (Sliven distr.), xeromesic grass community, N42°42″13.9′ E026°13″76.4′, 610 m alt., D. Berger & D. Chobanov leg. (2 ♂, 1 ♀) (NMNH/S).

Recognition.— As nominate *mollis* but fore wings slightly more slender, in the male with narrow Sc area (figs 48-49, 109). Male subgenital plate and apex of phallus robust as in *mollis*. Biometric data of male in 30.

Bioacoustics.— Unknown.

Differential diagnosis.— From the biometric data it is clear that *m. pechevi* does not belong to *brunneus* (pronotal sulcus more in front, shorter stridulatory file, lower number of stridulatory pegs), *bornhalmi* (pronotal sulcus more in front, metazona wider), nominate *vagans* (tympanal aperture more open, longer stridulatory file), *v. dissimilis* (pronotal metazona longer, longer stridulatory file, larger number of pegs, male subgenital plate and apex of phallus less robust). Among the additional material listed above, one male and the female agree perfectly with the type series. In the other male, however, the fore wings are less slender, the distance stigma to tip of fore wing is relatively shorter and the costal areas are slightly more bulging. This male is almost identical to nominate *mollis*. The taxon *pechevi* appears to be very close if not synonymous with nominate *mollis*.

Discussion.— Karaman (1975) compared *pechevi* with material he considered belonging to *m. mollis* (l.c. fig. 1, elytron, Pristina, Yugoslavian Macedonia; fig. 3, apex of phallus, ibidem) and *m. ignifer* (fig. 5, apex of phallus, Holland). The "Holland" specimen originated from The Netherlands, collected and granted to him by one of us, representing nominate *mollis* but erroneously assigned by Karaman to *m. ignifer*. A reasonable explanation of Karaman's conclusion that his *pechevi* differs from *m. mollis* could be that his "Pristina" material from Yugoslav Macedonia represented *vagans dissimilis* instead of *m. mollis* (his figures 1 and 3, indeed, could refer to *v. dissimilis*). But as long as its song is unknown, the status of *m. pechevi* is uncertain.

As there was no holotype, a lectotype now has been designated and labelled.

Distribution.— Known from the type series, Kranevo and Rogatchevo, both near Varna, the northern Black Sea coast and from a locality east of Sliven, both Bulgaria.

***Chorthippus mollis mollis* (Charpentier, 1825)**

(figs 12-14, 15, 18-19, 50-53, 110-113, 165-167, 194-196, 205-206, 208, 211, 217, 239-240, 266, tables 2, 7-8, 11, 13, 16, 30-31, cd 17, 18)

Gryllus mollis Charpentier, 1825: 164. (lectotype ♂, Silesia in ZILU/L).

Chorthippus (*Glyptobothrus*) *mollis mollis*: Willemse, 1984: 145 (reference, faunistics, partim); 1986: 77, figs 1039-1044 (identification, partim); Ponel & Hébrard, 1988: 10 (partim, only Kastania = Mt. Vermion, 1360 m).

Chorthippus (*Glyptobothrus*) *mollis*: Schmidt, 1990: 248, fig. 2 (oscillogram, Perivolion, Pindhos range)

Chorthippus cf. *mollis*: Popov & Chobanov, 2004: 283 (discussion, Thraki, partim?).

Chorthippus lesinensis [nec Krauss]: Kočárek & Vrabec, 2005: 8-10 (from Kerkira).

Chorthippus (*Glyptobothrus*) *lesinensis* [nec Krauss] & *crassiceps* [nec Ramme]: Willemse, 1984: 145, map 198 (faunistics, partim); 1985b: 76 (identification, partim).

Chorthippus (*Glyptobothrus*) *lesinensis* [nec Krauss]: Ingrisch & Pavicevic, 1985: 75 (from Mt. Lidorikion, C. Greece).

Chorthippus crassiceps [nec Ramme]: Ragge *et al.*, 1990: 244, figs 13-14, table 1 (oscillogram, Mt. Parnassos, 1300 m); 1998: fig. 35 (map).

Glyptobothrus mollis mollis: Storozhenko, 2002: 4 (comb. nov) (taxonomic status).

Material studied.— MAKEDHONIA: Drama: Mt. Falakron above Volax, 1250-1800 m, 13.viii.1976 (1 ♂); Serrai: Mt. Vrondhous above Serrai, 1000-1150 m, 30-31.vii.1979 (6 ♂, 2 ♀); Kilkis: Evzoni, along highway, 150 m, 20.ix.1989 (1 ♂, 1 ♀); Imathia: Vermion Geb., Strasse Naussa-Kato Vermion 1330 m, F 298, 3.x.1974, O. von Helversen (1 ♂, 1 ♀ in alcohol vial 6/0025) (CvH); Florina: Mt. Vernon, 1500 m, 9.viii.1978, M. La Greca (1 ♂) & 3 km S of Pisodheri, 1500-1600 m, 13.viii.1988 (2 ♂, 1 ♀); Psaradhes, lake Mikro Prespa, 850-950 m, 14.viii.1988 (2 ♂); Kastoria: 10 km NE of Gavros, 1000 m, 19.vii.1969 (1 ♂); Grevena: Vourinos near Ag. Pandhelimon, 1200-1500 m, 17-18.viii.1985 (4 ♂, 2 ♀). THESSALIA: Trikala: Mt. Neraidha above Neraidhochori (W of Pertouli), below summit Boudhoura (2010 m), 1750-1800 m, 1.viii.2003 (5 ♂); Kardhitsa: N Agrafa Mts, between Mts. Oxia and Argithea, below summit Pr. Ilias (1761 m), 1600 m, 2.viii.2003, N39°21′ E21°34′ (1 ♂, 1 ♀).

IPIROS: Thesprotia: Mt. Chionistra (1644 m) above Elataria (N of Paramythia), 1400-1600 m, 25.vii.2003, N39°31′21.4″ E20°30′56.5″ (31 ♂, 9 ♀, of which 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P); Plakoti, E of Igoumenitsa, 600-800 m, 7.viii.1978, O. von Helversen (2 ♂, 1 ♀ alcohol vial 6/0010) (CvH); Pass between Ioannina & Igoumenitsa, 10.viii.1978, O. von Helversen (3 ♂, 3 ♀, alcohol vial 6/0013) (CvH); Ioannina: Mt. Grammos, Kefalochori-Aetomilitsa, 700-2000 m, 9.viii.2006 (1 ♂); Mt. Mavrovouni (N of Metsobon), 1800 m, 3.viii.1971 (1 ♂); 6 km E of Metsobon, 1500 m, 9.viii.1966 (2 ♂); Mt. Mitsikeli above Lingiadhes, 850-1650 m, 3.viii.1978 (6 ♂, 1 ♀) & 1200-1400 m, 25.viii.2001, V. Kati (6 ♂, 6 ♀) & 1100 m, 23.vii.2003, N39°41′44.8″ E20°53′37.6″ (8 ♂, 2 ♀); Zagora, Vrisokhorion, 1100 m, 18.viii.1978 (4 ♂, 1 ♀); Mt. Timfi above Papigon, 1800-2100 m, 1.viii.1977 (2 ♂); Armata, 1000 m, 12.vii.1977 (3 ♂, 3 ♀) & vii.1978, O. von Helversen (3 ♂ in alcohol vial 6/0001)(CvH); Mt. Lakmos above Kalarrites, 31.viii.2004, O. von Helversen (1 ♂) (CvH); Mt. Peristeri above Sirrako, N of Ag. Athanisios (Lakomata), 1800 m, 12.viii.2005 & 2.viii.2006 (2 ♂ & 1 ♂); surroundings Chouliaradhes, pine forest, 31.vii.2006 (1 ♂); Mt. Kakardhitsa (erroneously sometimes named Mt. Athamanika), above Matsaki (N of Pramandha), below summit Katarachias (2280 m), 1800-1850 m, 27.vii.2003, N39°35′13.0″ E21°10′37.5″ - N39°32′42.4″ E21°11′13.2″ (1 ♂, 1 ♀); Kotstitsi, halfway between Serviana and Pramandha, 26.vii.2003 (2 ♂, 1 ♀); Mt. Tomaros above Varyiadhes, 1200-1600 m, 2.viii.1978 (1 ♂) & Schotterhalden 1100-1200 m, 18.-19.viii.1986 (O. von Helversen 4 of 9 ♂ in alcohol vial 6/0089) (CvH) & 1250-1450 m, 12.viii.2004, N39°28′18.4″ E20°47′02.8″ (3 ♂, 1 ♀); Arta: Strana, north of Aghnadha, *Abies* forest mixed maquis, 3.viii.2006 (1 ♂); 2 km N of Ramia, *Quercus* forest, around church, 11.viii.2005 (2 ♂, 3 ♀); Mt. Tzoumerka (= Athamanika), 3 km W of Vourgareli (formerly Dhrosopiyi), 1000 m, 16.viii.1988 (3 ♂, 2 ♀) & road to summits Sklava & Tria Sinora, 1150-1250 m, 28-29.vii.2003, N39°22′43.4″ E21°10′07.5″ (2 ♂); Mt. Gavrogo above Megalochari, below summit Yerabi, 1500-1750 m, 3-4.viii.2003, N39°11-12′46.4-1″ E21°16-17′16.4-51.8″ (24 ♂, 8 ♀, of which 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P);

IONIAN IS.: Kerkira: Perithea, 300-450 m, 17.vii.1976 (1 ♂); Almyros, surroundings, 0-50 m, 9/17.ix.2003, P. Kočárek (2 ♂, 1 ♀ in CKo).
CENTRAL GREECE: Aitolia-Akarnania: Mt. Akarnanika above Thirion, 800-1380 m, 27.vii.1987 (2 ♂) & 18.viii.1990, O. von Helversen (2 ♂, 1 ♀ in CvH) & 19.viii.1998, F. Mayer (10 ♀, alcohol) (CM); Drimon, 700 m, 1.viii.1975 (5 ♂, 3 ♀); Evritania: Mt. Panaetolikon, above Proussos, 1100 m, 2.viii.1975 (1 ♂) & Xerovouni above Proussos, pass, 1400-1650 m, 2.viii.1975 (1 ♂) & 3 km W of pass between Proussos & Labini, 1360-1480 m, 8.viii.2004, N38°44′01.0″ E21°36′34.1″ (3 ♂); NE of Platanos, Ambelakiotissa, pass between Mts. Ardhinis & Xerovouni (Tsekoura), 1080 m, 8.viii.2004, N38°37′30.4″ E21°49′12.6″ (4 ♂, 1 ♀); E Agrafa Mts. (Kamaria village) pass about 10 km E of Agrafa, below summit Kornopi, 1650-1800 m, 6.viii.2003, N39°08′36.4″ E21°41′32.6″ (5 ♂, 4 ♀); Mt. Triandhafillia, between Kastania & Aghiro Pighadhi (SE of Proussos) below summit (1817 m), 1380-1460 m, 9.viii.2004 (4 ♂, 1 ♀); Mt. Timfristos above Karpenision, Abies forest, 500 m, 28.ix.1989, Schmalfuss (4 ♂, 5 ♀). Fthiotis: Mt. Oiti, 2 km W of Oiti village, 1000 m, 5.viii.1972 (1 ♂); Mt. Kallidromo, Eleftherochori-Drimea, 1250 m, 24.vii.2002, N38°45′27.9″ E22°32′33.0″ (7 ♂, 2 ♀) & 1.5 km E of Eleftherochori, 900 m, 24.vii.2002, N38°44′33.5″ E22°28′09.5″ (1 ♂, 1 ♀); Fokis: Mt. Giona above Amfissa, 1400 m, 13.viii.1973, M. La Greca (1 ♂, 1 ♀); Mt. Parnassos, Eptalofos, 1000 m, 2.ix.1989 (1 ♂, 1 ♀); Mt. Lidhorikiou (SW of Amfissa), 800-1000 m, 15. vii.1981, felsige Haenge, S. Ingrisch (2 ♂ in CI as *lesinensis*); Voiotia: Mt. Parnassos, 22.viii.1998, F. Mayer (20 ♂, 10 ♀, alcohol) (CM) above Arachova, 1500 m, 26.vii.1971 (1 ♂) & 1600 m, 1.viii.1972 (5 ♂) & 1400 m, 18.vii.1974 (1 ♂) & 1500 m, 22.vii.1978 (2 ♂); Mt. Parnassos, 10 km N of Arachova, 1300 m, 3.viii.1972 (4 ♂, 14 ♀); Mt. Parnassos, straight above Arachova, 1300-1600 m, 4.ix.1989 (13 ♂, 2 ♀); Mt. Parnassos, Stavros above Arachova, entrance of Livadhia plateau, 1200 m, 5.viii.2004 (2 ♂) & Livadhia plateau, 6-9 km N of Arachova, 1100 m, 20.vii.2000 (1 ♂, 1 ♀); Parnass Gebirge, 1700 m, 20.viii.1981, Heller/Volleth (2 of 3 ♂ in alcohol vial 6/0154, other male *b. parnassicus*) (CvH); Mt. Parnassos, Eptalofos-Arachova, 2.5 km after main exit to ski centre, pine forest, clearing, 1320 m, along road to Katafigion EOS club Gerondhovrachos, 9.viii.1988 (20 ♂, 21 ♀) & 2.ix.1989 (6 ♂, 2 ♀) & 20 & 24.vii.2000, N38°32′5.50″ E22°32′5.70″ (7 ♂, 5 ♀) & close to refuge EOS club Gerondhovrachos, 1600 m, 9.viii.1989 (1 ♂); Mt. Parnassos, Kefalari, 0.5 km after exit to Megali Vrisi-Kalavia, road verge, clearing pine forest, 1300 m, 21.vii.2000 (4 ♂, 1 ♀); Mt. Helikon, Paliovouna, 1100 m, 16.vii.1983, J. Tilmans & J. Tilmans-Smid (3 ♂, 3 ♀ in CT) & 1000-1300 m, 26 & 30.vii.2000 (14 ♂, 10 ♀) & below summit Paliovouna, 1220 m, 25.vii.2002, N38°18′31.5″ E22°50′05.7″ (8 ♂, 8 ♀) & from Kiriaki to A. Anna, 900 m, 25.vii.2002, N38°20′32.3″ E22°48′32.7″ (1 ♂, 2 ♀), all 25.vii.2002; Fthiotis: Mt. Othris, Yerakovouni, above Neraidha, 1000-1250 m, 21.viii.1983, J. Tilmans & J. Tilmans-Smid (3 ♂, 3 ♀ in CT); Evvoia: Mt. Dhirfis above Steni, 1100 m, 22.vii.1975 (18 ♂, 3 ♀) & 1300-1745 m (1 ♂, 2 ♀) & 900 m, 12.x.1980, Schmalfuss (3 ♂); 15 km NNW of Psachna, 500 m, 21.vii.1975 (1 ♂). (unless otherwise stated collected by the Willemse's and in CW)
Number of specimens together about 450.
Additional nominate material from rest of Europe, originating from The Netherlands, Belgium, N. France, Germany, Hungary, lower Austria, Czecho-Slovakia, Ukraine, Serbia, Bulgaria and Yugoslav Macedonia (excluding material from the Alps, the Adriatic coastal areas from NE Italy to Albania), about 230 specimens (CW).

Recognition (based on Greek material).— Habitus slender (figs 50-53). Head not remarkably enlarged, its greatest width slightly less than pronotal length. Pronotum with metazona as long as or commonly very slightly longer than prozona, transverse sulcus commonly in or just in front of the middle of pronotal length; lateral keels moderately angled (figs 165-167). Fore wings of male (figs 110-113) longer than hind femur (1.1-1.4, mean 1.2 times), reaching and commonly just extending beyond the tip of hind knee; comparatively slender, distance from stigma to tip of fore wing about 3-5 mm, or 0.3-0.4 times the length of fore wing; C and Sc areas slightly expanded, anterior margin of fore wing moderately bowed, maximum width of C area less than 0.6 mm, ± 1.5-2 times as wide as Sc area, ratio between greatest width of combined C & Sc areas measured along same line × 100 against length of the fore wing mean 7.5 times. Tympanal aperture intermediately wide, maximum diameter in male 3.4-7.3 (mean 4.9), in female 5.0-9.3 (mean 7) times more than minimum diameter (figs 194-196). Number of stridulatory pegs in male 94-134 (mean 112), in female 92-120 (mean 109); distal end of file not extending beyond the middle of hind femur, length of file in male 0.6-0.8 (mean 0.7) times the distance between the distal end of the file and the tip of the hind knee. Biometric data for the male and female in tables 30-31.

Bioacoustics (figs 15, 239-240, cd 17-18).— The song of nominate *mollis* from Greece resembles that from populations from Central Europe, that have been described by many authors (*e.g.* Elsner, 1974; Ragge & Reynolds, 1998). The calling song consists of a ticking/buzzing echeme-sequence lasting about 15-30 s. The first echemes are very quiet, only very gradually becoming louder, reaching maximum intensity near the end. The echeme repetition rate is about 2-4/s. After an initial tick, produced by one of the hind legs, the echeme begins and ends quietly, reaching maximum intensity in the middle. It consists of 16-20 syllables repeated at the rate of about 60-80/s. Echemes show a molloid pattern of leg movement (Em, see fig. 15). Unlike *m. mollis* from Central Europe, the ticks in Greek *mollis* are also produced in the last echemes of the sequence. The courtship song is not much different, but usually lasts longer. There is no aftersong.

Variation.— The variation in Greek *mollis* is mainly geographically and/or ecologically (altitude). Its range in Greece extends from Thraki (?) in the east to Ipiros in the west and from Macedonia in the north to the central mainland of Greece in the south. The few Greek populations studied from the lowlands (Vardar valley, northern Macedonia and Ionan Island of Kerkira) are identical to those from adjacent parts of former Yugoslavia and Bulgaria and fit well nominate *mollis* from central Europe (figs 50-51, 110-111). In the Pindhos range and southeastern Central Greece *mollis* occurs predominantly in mountain habitats. These specimens are smaller with relatively shorter wings and shorter songs (figs 52-53, 112-113). Specimens from extreme western mainland (Kerkira, Ipiros and southwestern Central Greece) differ slightly from the nominate form in somewhat more inflated head but by far not as conspicuously as in Dalmatian *m. lesinensis*. Noteworthy is the population of Mt. Elikon, the southeastern most known locality of *mollis* in Greece. The head is somewhat more inflated and resembles morphologically its geographical closest relative in eastern Argolis, typical *crassiceps*. However, biometrics and bioacoustics of these populations agree rather with the Greek mainland form of *mollis* than with *crassiceps*.

Though there are differences between the populations of the various areas of Greece, preference is given to treat all of them as nominate *mollis*. It is noticed that the biometric data presented here refer to Greek material that includes mainly the smaller form inhabiting the Pindhos range and the higher parts of Central Greece. Therefore some of these data are not representative for nominate *mollis* from the adjacent parts of Yugoslavia and Bulgaria.

Differential diagnosis.— Apart from the quite distinct song, the morphological differentiation of *m. mollis* from both its long winged syntopical congenerics *bornhalmi* and *b. euhedickei* is not difficult (table 7). Helpful are the wide pronotal metazona in both sexes of *bornhalmi* (figs 160-161) and in *b. euhedickei* the remarkably widened C areas of the male fore wing (figs 93-96) and the extraordinairy long stridulatory file (fig. 208). The distinction between *m. mollis*, particularly the slender lowland form, from *v. dissimilis* is not easy and discussed under the latter (table 2, figs 9-14, 205, 206).

Other syntopical species of *m. mollis* are *pulloides* and *willemsei*, both easily recognisable by their short fore wings.

More problematic, particularly in Mt. Parnassos, is the morphological separation of the local mountain form of *m. mollis* (figs 52-53, 112-113) and *b. parnassicus* (figs 42-43, 98-102). Their morphological distinction is quite subtle and discussed under *b. parnassicus* (table 8, fig. 211), the most reliable and distinct feature being the male calling song.

Nominate *mollis* does not occur in the Peloponnese. In this area occur also relatively long winged forms, recognized here as *crassiceps*, *parnon* and *moreanus*. Distinction between these taxa and *m. mollis* are discussed under the former and, except for *crassiceps* the calling songs of *parnon* and *moreanus* are quite distinct from that of *mollis*.

Discussion.— Previous records in Willemse (1984, 1985, 1986) were based upon morphological characters only. The inclusion of bioacoustic characters resulted in a number of changes in the identification for a number of populations. In Willemse (1984, 1985, 1986) the typical *mollis* form has been recorded correctly under *m. mollis*. However, the smaller mountain form from mainland Greece, here included under nominate *mollis*, as well as the material described here as *biguttulus parnassicus* (!) were previously recorded as *lesinensis*. Apart from that all material from the Peloponnese, mentioned under *mollis* in Willemse (1984) proved to belong to *vagans* (see under *v. dissimilis*)!

Distribution.— In the Balkans the species extends into Greece as far south as Mt. Elikon, southeastern Central Greece (fig. 266). The species is also known from the Ionian island of Kerkira (Corfu) and Mt. Dhikti of the offshore island of Evvia. It has not been found yet on any of the Aegean islands. Also, it appears to be absent from the southeasternmost part of Central Greece (Attiki), the land bridge (Isthmus) between the mainland and all of the Peloponnesean Peninsula. Its occurrence in eastern Thraki is doubtful.

As in large parts of its wide range, *m. mollis* in Greece is present rather locally. While *m. mollis* was found occasionally in lowlands (150 m, Vardar valley, Kilkis district in Makedhonia and at 300-450 m in the Ionian island of Kerkira), most localities are mountain slopes, from 500-1500 m, sometimes even up to above the timberline, except in Mt. Parnassos and Mt. Elikon, the southeastern most sites of its range. The species prefers clearings of forests or large open sites with grasses and low shrubs. Most adults are found from mid July to the end of September. In Greece *m. mollis* may occur syntopic with *bornhalmi*, *b. euhedickei*, *b. parnassicus* and with the short winged species *pulloides* and *willemsei*.

Chorthippus pulloides-crassiceps complex

While typical *pulloides* and *crassiceps* are well recognisable in morphology and song, it became clear that, due to transitional forms, the boundaries between *pulloides* and *crassiceps* could not be well defined, neither in morphology nor in bioacoustics. Apart from these two species, another group of populations has been found, morphological almost identical to typical *crassiceps* but in which the males produce a calling song well distinct from all others. These populations are described below under the name *parnon*. As the systematic position of *parnon*, particularly its ranking is not clear, we prefer to use only the first two taxa in naming the complex. Both *crassiceps* and *pulloides* have been described in the same paper. As *pulloides* was described first (Ramme, 1926: 275)

Fig. 216. Scatter diagram showing a plot of the maximum width of the C to the width of the Sc area, measured along the same line against the ratio of the maximum to minimum diameter of the tympanum in males of typical *Chorthippus crassiceps* and typical *C. mollis lesinensis*.

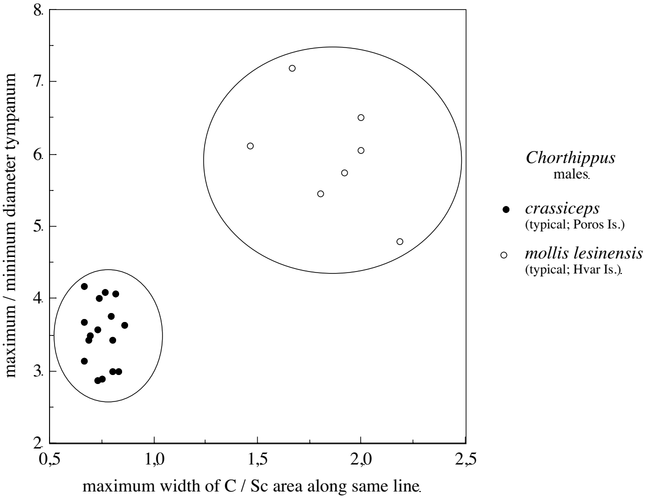
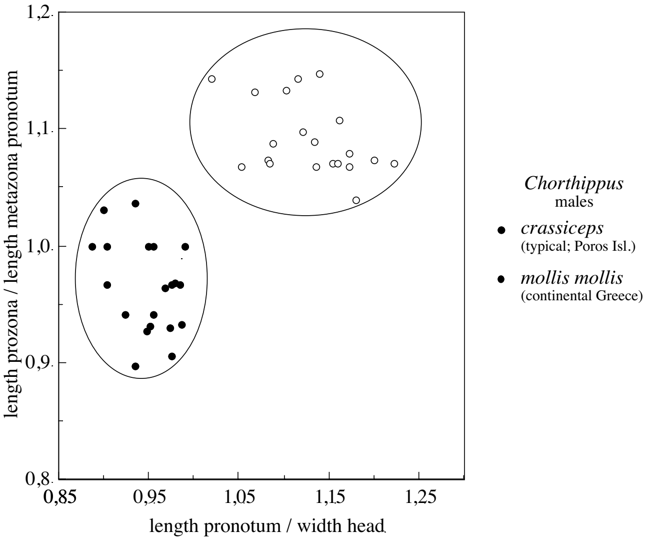


Fig. 217. Scatter diagram showing a plot of the ratio of the length of the pronotum to the maximum width of the head against the ratio of the length of the prozona to the length of the metazona of the pronotum in males of *Chorthippus mollis mollis* and typical *C. crassiceps*.



followed by that of *crassiceps* (l.c. 276) the name of the former is used here as the first one of this complex.

In this publication we treat these taxa as a closely related group naming them the *Chorthippus pulloides-crassiceps* group (compare also discussions under these taxa).

Chorthippus crassiceps (Ramme, 1926)

(figs 15, 54-57, 114-117, 168, 197, 212, 216-219, 243-244, 268-269, tables 10, 12-16, 32-33, cd 21, 22)

Stauroderus crassiceps Ramme, 1926: 276, pl. 2 fig. 5 (description, ♂ holotype; Poros, Th. Krueper, MNHU/B).

Fig. 218. Scatter diagram showing a plot of the maximum width of the combined C and Sc area measured along the same line (mm) against the length of the fore wing (mm) in males of typical *Chorthippus parnon* and typical *C. crassiceps* showing their large overlap.

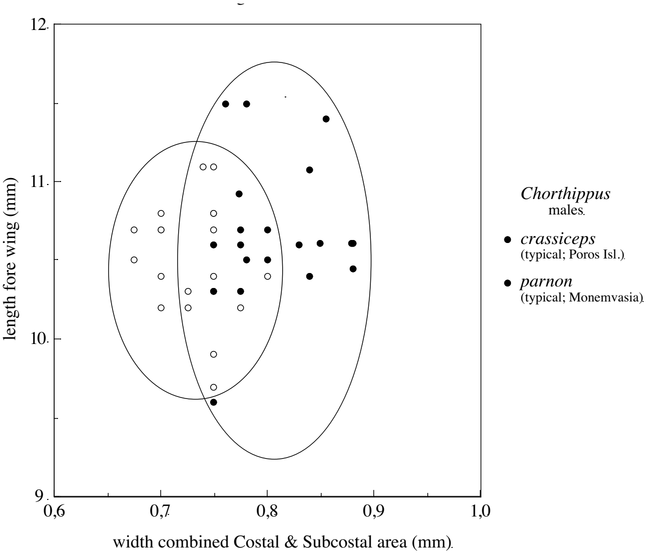
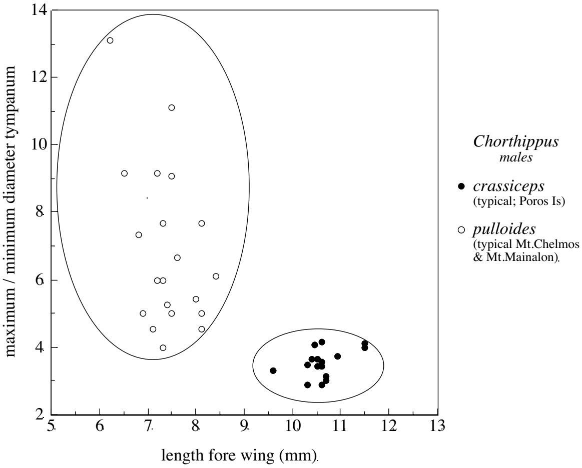


Fig. 219. Scatter diagram showing a plot of the length of the fore wing (mm) against the maximum to minimum diameter of the tympanum in males of typical *Chorthippus crassiceps* and typical *C. pulloides*.



Chorthippus (*Glyptobothrus*) *crassiceps*: Harz, 1971: 336; 1975: 891, fig, 3115, 3362-3365 (description; Poros); Willemse, 1977: 55 (Poros); 1984: 145, map 198 (partim, references and faunistics, only Poros Isl.); 1985: 28; 1986: 76, figs 1024-1026 (partim, identification); Ragge *et al.*, 1990: 244 (partim).

Chorthippus (*Glyptobothrus*) *sangiorgii* [nec Finot]: Ingrisch & Pavicevic, 1985: 75 (Sofikon).

Chorthippus (*Chorthippus*) *crassiceps*: Storozhenko, 2002: 11 (taxonomic status).

Material studied.— Topotypes: Greece, Argolis, Poros Island, 1896, Dr. Krüper (1 ♀, badly damaged, Zool. Mus. Athens) & 50-200 m, 8-9.vii.1974 (1 ♂, 3 ♀) & 4-5.viii.1988 & 13.ix.1989, pine forest, clearings along circuit of island (45 ♂, 22 ♀, in CW except 1 ♂, 1 ♀ in BMNH/L & 1 ♂ in ZI/P) (CW) & 9.viii.1979, W. Ellegast (6 ♂ dry & 4 ♂, 2 ♀ in alcohol vial 6/0022) (CvH).

Additional material: Greece, Argolis, Ano Fanari, 120 m, 5.viii.1988, cultivated land (1 ♂, 3 ♀) (CW); Argolis, Methana peninsula above Kounoupitsa, 100 m, 13.ix.1989, shrubs and trees near relict of pine

Table 13. Biometric data useful to separate typical *Chorthippus crassiceps* from Greek *C. mollis mollis* (fig. 217).

	crassiceps (typical)	*mollis mollis* (Greece)
ratio length of prozona / length of metazona	♂ 1.09 (1.04-1.15) ♀ 1.07 (1.00-1.18)	♂ 0.97 (0.89-1.11) ♀ 0.91 (0.76-1.06)
maximum width of head	♂ 3.13 (2.94-3.29) ♀ 4.03 (3.8-.4.2)	♂ 2.62 (2.45-3.0) ♀ 3.61 (3.4-4.0)
maximum diameter of eye	♀ 2.36 (2.3-2.48)	♀ 2.05 (1.97-2.16)
ratio length of pronotum / maximum width of head	♂ 0.949 (0.887-0.990) ♀ 0.935 (0.884-0.985)	♂ 1.127 (1.019-1.222) ♀ 1.066 (1.028-1.162)
ratio width costal / subcostal area	♂ 2.42 (1.91-3.00)	♂ 1.85 (1.53-2.22)
maxim.width of Sc area meas-red along same line of C area	♂ 0.23 (020-0.28)	♂ 0.28 (0.22-0.35)
ratio maximum / minimum diameter of tympanum	♂ 3.51 (2.87-4.17) ♀ 4.04 (3.3-5.5)	♂ 4.89 (3.38-7.33) ♀ 6.96 (5.0-9.33)
ratio length of fore wing / length of hind femur	♂ 1.07 (1.00-1.14) ♀ 1.07 (1.01-1.13)	♂ 1.19 (1.09-1.40) ♀ 1.16 (1.01-1.31)

forest (1 ♂, 2 ♀) (CW); Argolis, Mt. Dhidhimo near summit, 1050 m, 14.ix.1989, stony ground with shrubs (*Quercus*) & grasses much grazed by goats (13 ♂, 8 ♀, of which 1 ♂ in BMNH/L & 1 ♂, 1 ♀ in ZI/P); Argolis, above Palaio Epidhavros, 150 m, 5.viii.1988 & 15.ix.1989, pine forest, undergrowth of grasses and low shrubs (11 ♂, 9 ♀).

Atypical material (morphological): Korinthia, N & S of Sofikon, 200 m, 15.ix.1989, pine forest, undergrowth of low shrubs and grasses (4 ♂, 1 ♀) & Kiefernwald, 19.vii.1981, S. Ingrisch (2 ♂, 1 ♀ in CI, as *sangiorgii*); Argolis, Arachnaio Mts, Limnes-Ayionori, 600 m, 2.viii.1991, stony slopes with low shrubs and arid grasses (6 ♂, 3 ♀) (CW) & Arachnaio Mts., 26.viii.1998, F. Mayer (9 ♂, 6 ♀, alcohol) (CM); Argolis, Zonga (Mt. Ktenias, W of Argos), 25.viii.1998, F. Mayer (1 ♂, 6 ♀, alcohol) (CM). (unless otherwise stated collected by the Willemse's and in CW).

The diagnosis given here refers to its typical form, ranging from the island of Poros (type locality) and the opposite part of the northeastern Peloponnese (fig. 268).

Recognition (typical form).— Close to *m. mollis* from continental Greece but differing as noted in table 13. General appearance more robust (figs 54-55 against 60-63). Head capsule remarkably wide, inflated, greatest width as wide or usually slightly exceeding the length of the pronotum. Eyes relatively large, maximum diameter in male mean 2.0 against 1.8 mm, and in female 2.36 against 2.05 mm in Greek *m. mollis* respectively. Pronotum (fig. 168) with prozona slightly longer than metazona, sulcus commonly located just behind middle of pronotal length, while in Greek *m. mollis* prozona commonly shorter or of equal length as metazona (figs 165-167). Fore wing (figs 114-115 against 110-113) relatively shorter and more tapering distally, not extending but just reaching the hind knees, covering the abdomen of male and female or almost so; stigma present, apical part well developed; Sc area of male fore wing measured at maximum width of C area narrower. Tympanal aperture (fig. 197 against 194-196) relatively wide, slightly more open than in *m. mollis*. Male subgenital plate and phallus as robust as in *mollis* (figs 12-14). Biometric data for the male and female in tables 32-33.

Bioacoustics (figs 15, 243-244, cd 21-22).— The male calling song (figs 243-244) is an echeme-sequence, beginning quietly and gradually increasing in intensity. The clearly molloid echemes (Em, fig. 15) are repeated at the rate of about 2-4/s. All echemes begin with a characteristic "tick", produced by the downstroke of usually two hindlegs. In some specimens the legs don't move at exact the same time, thus resulting in a double tick. In general, the tick is less spaced from the following buzzing syllables than in *m. mollis*. The number of audible echemes in the sequence is variable, but usually within the range of 6-30; the sequence usually lasts for 2-5 s. The duration of individual echemes (including their intervals) increases slightly during the course of the sequence.

The 10-15 syllables after the initial tick are more or less equally loud and are repeated at the rate of about 40-55/s. Number of syllables per echeme slightly increases during the echeme-sequence. Apart from the tick, the left and right hind legs are usually in opposite phase. Both upstroke and downstroke produce a hemisyllable, visible in the oscillogram of an unilateral song (fig. 243). Both legs show a gradual, parallel and slow upward movement before the strong downstroke hemisyllable (the tick) of the next echeme, at the same time creating the inter-echemic interval.

A quiet aftersong is rarely following the typical echeme-sequence. It consists of 1-3 rustling echemes without a clear syllabic structure.

During courtship the song tends to be longer, echeme-sequences lasting up to about 5 s or longer.

During rivalry the song is short, whereas the characteristic crescendo is less pronounced.

The song of *crassiceps* can be discriminated from that of *mollis* (including *m. mollis*, *m. lesinensis* and *m. ignifer*) by the lower syllable repetition rate, the absence of a clear maximum loudness of syllables in the middle of each echeme and the shorter interval between the tick and the series of the vibratory molloid syllables. Also the duration of the echeme-sequence of the calling song is shorter in *crassiceps*. Especially the lower syllable repetition rate could be important, inducing inter-syllabic intervals probably long enough to be recognized by the female (45-50/s in *crassiceps* against 60-70/s in *mollis*) (Elsner, 1974; von Helversen, 1972; D. & O. von Helversen, 1983).

In *pulloides* the number of syllables and the syllable repetition rate are usually lower. A well-separated first syllable (the tick) is also usually absent in the echemes.

Variation.— Geographical variation is considerable. While populations in the Peloponnesean mainland opposite the island of Poros (Methana; Ano Fanari) agree perfectly with the topotypical form from Poros Island, those occurring somewhat remote from this area (Sofikon in E Korinthia; Epidhavros & Mt. Dhidhimo, both in central Argolis) agree fairly well except for a slightly smaller size and slightly shorter fore wings with the stigma closer to the tip. Specimens from localities at an even greater distance from the type locality (Limnes of the Arachneio Mts. in W Argolis; Zonga, Mt. Ktenias in extreme SW Argolis) are still smaller in size and their fore wings are still shorter (compare figs 55-57, 114-117). In fact they closely resemble *pulloides*, due to the small general size, the short fore wings that commonly lack a stigma, the relatively wide costal areas and the small number of stridulatory pegs (74-98). Other characters sometimes agree with typical *crassiceps* rather than typical *pulloides*, like the width of the head, the tympanal aperture and the spacing of stridulatory pegs. Yet, in these populations the overlap in characters is usually considerable. Apparently we are dealing with a clinal variation from the longest winged form (topotypical) in eastern Argolis to the shorter winged ones from western Argolis (*e.g.* Limnes, see table 19, fig. 32) to northeastern Arkadhia (fig. 268).

Table 14. Biometric data to separate males of typical *Chorthippus crassiceps* from *C. b. parnassicus*.

	crassiceps (typical)	*biguttulus parnassicus*
ratio length of pronotum / maximum width of head	0.95 (0.89-0.99)	1.0 or >1.0
ratio length of file / distance from end of file to tip of hind knee	0.64 (0.54-0.73)	0.95 (0.85-1.09)

The song of most of the mentioned populations agrees with those of topotypical *crassiceps* (figs 243-244). However, the songs of the shortest winged populations may present intermediate and transitional patterns, bridging typical *pulloides* and *crassiceps*. Biometric data of males of some morphologically atypical populations can be found in table 32.

Differential diagnosis.— The relatively long winged form of topotypical *crassiceps* comes close both to nominate *mollis* and particularly to *m. lesinensis*. The morphological distinction between typical *crassiceps* and Greek nominate *mollis* is given above under recognition (table 13, fig. 217). The thick head and relatively short fore wings of typical *crassiceps* are shared by *m. lesinensis*. In *crassiceps* however, the head is still more enlarged and the tympanal aperture slightly wider and besides the Sc area of the male fore wing relatively narrower (table 12, fig. 216; compare figs *crassiceps* 54-55, 168, 197, 114-115 against *m. lesinensis* 46-47, 164, 193, 108). The differences, however, are small and we failed to recognise any large and consistent morphological distinction between *m. lesinensis* and typical *crassiceps* as well as between the latter and *parnon* (table 10, fig. 218). In this case the calling song only is the only reliable means for morphological identification.

Apart from the most distinct songs, the morphological differences between typical *crassiceps* and typical *moreanus* are discussed above under the latter (table 10, fig. 212) and those between *crassiceps* and *b. parnassicus* refer mainly to the absence of any enlargement of the head and the relatively longer stridulatory file in the latter (table 14).

Some populations of *crassiceps* resemble Uvarov's Anatolian *C. bozdaghi* but their affinity is still an open question (compare Mol *et al.*, 2003).

The difference between *crassiceps* (both typical and atypical forms) and the longer winged species *bornhalmi*, *b. euhedickei* and *v. dissimilis* is obvious, both in morphology and song.

Also the smaller sized and morphologically atypical short winged populations of *crassiceps* are easily separated from *willemsei* by the wide open tympanal apertures, the red hind tibia, different wing venation in the latter and, of course, the song.

Table 15. Biometric data to separate males of typical *Chorthippus pulloides* from typical *C. crassiceps* (fig. 219).

	pulloides (typical)	*crassiceps* (typical)
ratio length of pronotum / maximum width of head	1.03 (0.95-1.11)	0.95 (0.88-0.99)
length of fore wing (mm)	7.4 (6.2-8.4)	10.67 (9.6-11.5)
ratio distance stigma-tip / length of fore wing	0.13 (0.09-0.17) (stigma often absent)	0.31 (0.29-0.33)
ratio maximum / minimum diameter of tympanal opening	6.89 (4.0-13.1)	3.51 (2.87-4.17)
width of C area (mm)	0.48 (0.36-0.52)	0.56 (0.50-0.62)

The separation between typical *crassiceps* and *pulloides* is quite easy and refers to the short fore wings, the not inflated head and the narrower tympanal aperture of the latter (table 15, fig. 219). However, the distinction between strongly morphologically atypical short winged *crassiceps* and *pulloides* is another matter. The situation is even more complicated by the occurrence of relatively short winged atypical forms of *moreanus* and the transitional populations bridging *moreanus* and *pulloides* (compare table 19). It will be discussed below under *pulloides*. In most of these cases the song will be necessary for a closer identification.

Discussion.— The song of *crassiceps*, until recently unknown, is broadly similar to that of *mollis* (Ragge *et al.*, 1990). The resemblance in morphology and bioacoustics of the typical form of *crassiceps* with *mollis*, indicates a close relationship between these taxa. However, as pointed out above, the temporal pattern of the song appears different. We consider this difference important for mate recognition by the female and therefore decided to treat *crassiceps* as a distinct species.

Many of the song characters of *crassiceps* are also shared by *pulloides*. The importance of these characters may be underlined by the observation that although *crassiceps* occurs allopatric with *mollis*, *pulloides* indeed may live syntopic with *mollis*, at least in the mainland of Greece. Yet we failed to find clear distinctive characters between *crassiceps* and *pulloides*, neither morphologically nor bioacoustically, all being bridged by atypical transitonal forms (morphologically and bioacoustically) (table 19).

We believe that *crassiceps* and *pulloides* are closer related to each other than to *mollis*. For the time being, we propose to preserve a taxonomic distinction between *crassiceps* and *pulloides* because the typical forms of both are easily recognisable (table 15, fig. 219) but on the other hand to treat them as a closely related *pulloides-crassiceps* complex. Further analysis of behaviour and genetics would be most welcome.

Based on its slightly larger tympanal aperture, Storozhenko (2002) proposed to arrange *crassiceps* under *Chorthippus* instead of *Glyptobothrus* in which he arranged the closely related *m. mollis* and a number of subspecies of the latter. Apparently, the delimitation between *Chorthippus* and *Glyptobothrus* has not been settled yet, see the introduction.

As noted above under *moreanus* and *m. mollis*, most records of *crassiceps* in Willemse (1984) actually refer to *moreanus*, with exception of the island of Poros.

Distribution & ecology.— The range of *crassiceps*, until recently only known from the type locality (Harz, 1975), including atypical forms, covers the northeastern peninsula of the Peloponnese, extending west into Korinthia and southeast into northeastern Arkadhia (fig. 268). The exact boundaries of the western and southeastern extension is arbitrary, due to undefined taxonomic limits between *crassiceps*, *pulloides* and the parapatric transitional forms between *pulloides* and *moreanus* (see heading below under *C. pulloides* "Atypical and transitional populations").

Except for *bornhalmi*, syntopic occurrence with any other member of the angled pronotal group of *Chorthippus* has not been observed.

The habitat of topotypical *crassiceps* is open undergrowth with heath, *Cistus*, other low shrubs and few grasses in open coniferous forests. Other sites are dry rocky hills with sparse vegetation, sometimes cultivated or heavily grazed slopes with scattered *Quercus coccifera*, altitudes ranging from sea level up to 1000 m. The habitats are very dry and have a poor insect life. Maybe there is a relation between these habitats and the large head and mandibles. It is a late season species, adults appear usually not before August. The habitat of *crassiceps* differs from the mountainous habitats of nominate *mollis* in the southern mainland of Greece. It is an open question why the development of *crassiceps* in this arid and hot habitat is apparently later than *mollis* in the cooler and less dry mountain habitats in the mainland of Greece. *C. crassiceps* shares this habitat preference with *vagans dissimilis* as discussed under the latter.

Chorthippus parnon spec. nov.

(figs 58-59, 118-120, 169, 198, 213-214, 218, 245-247, tables 10, 16-18, 32-33, cd 23, 24, 25)

Chorthippus (*Glyptobothrus*) *crassiceps* [nec Ramme]: Willemse, 1984: 145, map 198 (partim, only the localities Kosmas and A. Vasilios in Mt. Parnon).

Material studied.— ♂ Holo-, ♀ allo-, 7 ♂ & 5 ♀ paratypes labelled: “Greece, Peloponnisos, Lakonia, 500 m S of Monemvasia, 8.x.1992, stony mountain slope, R. Kleukers” (CW).
Additional paratypes:
PELOPONNISOS: Arkadhia: A. Vasileos, 24.viii.1998, F. Mayer (1 ♂) (CvH) & Mt. Parnon, A. Vasileos, 1000-1200 m, 25.vii.1978 (2 ♂) (CW); above Prastos, SE of Astros, 27.viii.1990, O. von Helversen (3 ♂) (CvH); Lakonia: Karitsa, 11.vi.1995, von Helversen & F. Mayer (as subadult) (1 ♂) (CvH) & 23.viii.1998, F. Mayer (20 ♂, 10 ♀, alcohol)(CM); 4-10 km NW of Lambokambos (NE of Molai or Molotai), 850 m, 7.ix.1992, J. Smid & F. Smid-Elbers (3 ♀ in CT & 1♀ in CW) (not indicated in figs 268-269); 4 & 6 km W of Velanidhia (SE of Neapoli), 550 & 650 m, 8.ix.1992, J. Smid & F. Smid-Elbers (1♂, 3 ♀ in CT and 3 ♂, 3 ♀ in CT & 1 ♂, 1 ♀ in CW) (not indicated in figs 268-269); 3 km S of Monemvasia, 3.x.1992 (1 ♂, 1 ♀) & 5.x.1992 (7 ♂, 3 ♀, of which 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P)), R. Kleukers, stony mountain slope; 3 km W of Nomia, 4.x.1992, R. Kleukers, stony mountain slope (6 ♂, 1 ♀); 2 km W of Nomia, 4.x.1992, R. Kleukers, roadside (3 ♂, 1 ♀); 1 km W of Foutia, 6.x.1992, R. Kleukers, roadside (3 ♂, 1 ♀); 500 m E of Elliniko, 6.x.1992, R. Kleukers, roadside (1 ♂, 2 ♀); 2 km S of Elliniko, 550 m, 30.vii.1991, “phrygana” (1 ♀, 5 juveniles); 3 km S of Sikea, 30.vii.1991, “phrygana” (1 ♂); E of Molotai [= Molai], above village Metamorfosis, 600 m, stony slope & plateau, low shrubs, 30.vii.1991 & 24.vii.2001 (6 ♂, 2 ♀, 3 juv.).
Additional material: Kithira Isl.: near airport W of Diakofti near OTE station, 450 m, WGS84 N36°15’55.0” E023°03’00.1”, macchia, very dry (2 ♂, 4 ♀); near Milopotamos, 330 m, WGS84 N36°14’26.7” E 022°57’36.3”, roadside, under *Pinus* trees in cultivated land, dry (1 ♂, 3 juv); between Potamos & Kambos 310 m, WGS84 N36°17’12.1” E022°57’54.8”, *Pinus* forest, sparse undergrowth of shrubs and grasses, very dry (1 ♂, 2 juv.); W of Kato-Vouriadhes near Pitsanianika, 360 m, WGS84 N36°12’44.9” E022°57’26.4”, undergrowth of some *Pinus* trees (1 ♂, 2 juv.); 4.5-5.5 km S of A. Pelagia (to Potamos) 320 m, WGS84 N36°18’16.5-18.5” E 022°58’11.5-24.3”, road side, *Pinus* forest, dry, sparse grasses (18 ♂, 13 ♀, 4 juv., of which 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P); 3 km N of Potamos, 350 m, WGS84 N36°18’33.6” E022°57’02.3”, undergrowth of some *Pinus* trees (5 ♂, 1 ♀, 2 juv.) (all 24-27.vii.2001).
Material tentatively arranged under this species: Arkadhia: Kosmas & 10 km E of Kosmas, both 1000 m, 23.vii.1970 (5 ♂, 1 ♀). (unless otherwise stated all collected by the Willemse’s and in CW)

It came as a great surprise to find *Chorthippus* populations with specimens morphologically similar to typical *crassiceps* in extreme southeastern Arkadhia, southeastern Lakonia and its offshore island of Kithira but producing a different song.

Recognition.— General appearance (figs 58-59) as typical *crassiceps*. Head capsule remarkably inflated, in male greatest width ranging from 2.95-3.45 mm, commonly more than the length of the pronotum, average ratio pronotal length to maximum width of the head 0.96 (♂) and 0.94 (♀). Pronotal prozona often slightly longer than metazona, sulcus commonly located just behind the middle of pronotal length, average ratio of pro- to metazonal length 1.07 (♂) and 0.98 (♀) (fig. 169). Fore wings in both sexes extending just beyond tip of abdomen, reaching at least base of hind knee; average ratio length of fore wing to that of hind femur 1.08 (♂) and 1.09 (♀); shape relatively slender (as in *mollis*), stigma well indicated; Sc area relatively narrow, in male average 0.19 mm and ratio between maximum width of C to width of Sc area measured along same line mean 2.92 (figs 118-120). Tympanal aperture relatively wide, ratio between maximum and minimum distance of opening in male 3.12, in female 3.67 (fig. 198). Number of stridulatory pegs in male 97-138, mean 116 and spacing average 38 pegs per mm.

Measurements (mm): body ♂ 12.3-15.4, ♀ 18,9-23.0, pronotum ♂ 2.7-3.3, ♀ 3.7-4.3; elytron ♂ 9.7-11.1, ♀ 13.2-14.9; hind femur ♂ 9.0-10.3, ♀ 11.7-13.7. Biometric data for the male and female in tables 32-33.

Bioacoustics (figs 245-247, cd 23-25).— The calling song (fig. 245) is a buzzing echeme, lasting 1-3 s. Oscillographic analysis and analysis of the leg movement shows that the echeme consists of about 50-100 equal syllables, repeated at the rate of about 50/s. There is a small time lag between the movements of both legs. It appears from analysis of the song of one-legged specimens that within a syllable the upstroke and downstroke produce an equally loud sound. An aftersong as described below rarely follows the calling song.

In the courtship song (fig. 246) the same buzzing echemes may be heard, but they last 1-4 s and they may be grouped into echeme-sequences, lasting about 3-6 s. These echeme-sequences in their most pronounced form start very quietly and gradually increase in loudness. The first leg movements seem to produce no sound. All but the last echemes begin with a sharp "tick", presumably produced by a single downstroke and are followed by a series of echemes that closely resemble those of the calling song. The number of audible echemes in the sequence is between 3 and 15. The duration of first echemes is about 350 ms. The 1-3 concluding echemes lack ticks but are very pronounced, both in loudness and in duration, lasting up to 4 s. Echeme-sequences may lack "ticks" and may consist only of buzzing echemes of 1-2 s.

A quiet aftersong sometimes follows an echeme or echeme-sequence in the courtship song. This aftersong lasts about 2,5-4 s and consists of 5-7 quiet echemes that are produced with the hind legs in a relatively high position and with small amplitude of movement (fig. 246). The syllable repetition rate in the aftersong is about 40/s.

During rivalry (fig. 247) echeme-sequences can be heard with relatively short echemes preceded by sharp ticks.

At first glance the calling song of *parnon* does not show a clear affinity with the song of any other Greek species. However, the courtship song in its most explicit form resembles the song of the *mollis* group (*C. mollis mollis, m. ignifer, m. lesinensis, crassiceps*). The echeme-sequence of the courtship song can be described as a short version of the song of the *mollis* group with strong emphasis on the final tickless echemes. Hence, our conclusion is that the echeme of the calling song, too, has to be regarded as a tickless echeme of the *mollis* group but of extraordinary length.

Variation.— Variation among populations throughout the extreme southeastern Peloponnese and the island of Kithira is comparatively minor but morphology and bioacoustics of populations occurring along the border of this area (only a northern border exists) are badly known. They appear shorter winged, and thus resembling atypical forms both of *pulloides-crassiceps* and *moreanus*. Whether in this area of contact bioacoustically intermediate populations of *parnon* occur is uncertain. There is some evidence but more observations are needed (*e.g.* population of Anaryiri, locality 66 of figs 268-269).

Differential diagnosis.— *Chorthippus parnon* is defined by its morphological similarity with *crassiceps* in combination with its quite distinct male calling song, a buzzing echeme of 1-3 s (fig. 245) instead of the molloid echeme-sequence of *crassiceps* (figs 243-244).

Morphological distinction between *parnon* and the typical form of *crassiceps* from the Argolis area, far to the north, is arbitrary. Both share the inflated head, greatest width ranging from equal to slightly larger than the pronotal length. While the length of the forewings and the width of C area are similar, the combined C & Cs areas in *parnon* are sometimes slightly narrower, due to a comparatively narrower Sc area (figs 118-120 against 114-116 (117 atypical)). This difference, however, is subtle and of little practical use for individual identification (table 10, 16, fig. 218).

The recognition of *parnon* and its syntopic occurring species *willemsei*, *bornhalmi* and *v. dissimilis* (the latter to be expected) is very clear. A few obvious differences are summarised: *willemsei* without inflated head, much shorter fore wings, red coloured hind tibiae and much more open tympanal aperture; both *bornhalmi* and *v. dissimilis* without inflated head, much longer fore wings, pronotum with sulcus in front of the middle of pronotal length and in *v. dissimilis* also a much higher number of stridulatory pegs.

Chorthippus parnon is also easily to distinguish from *biroi*, *sangiorgii*, short-winged morphologically and/or bioacoustically atypical forms of *crassiceps*, *moreanus*, *pulloides* and transitional populations between the latter taxa because all of them are apparently shorter winged and, except in *crassiceps*, lack the strongly inflated head, particularly obvious in the female.

The differences between *parnon* and *m. mollis* from continental Greece are the same as between *crassiceps* and *mollis*, the latter characterised by the less inflated head and a slightly narrower tympanal aperture and relatively longer fore wings (table 16, figs *parnon* 58-59, 118-120 & 198 against figs *m. mollis* 50-53, 110-113 & 194-196 respectively).

Separation of *parnon* from typical *moreanus* has to be based upon the less inflated head and a slightly narrower tympanal aperture of the latter (fig. 198 against 192). Apart from that the Sc area of the male fore wing in *parnon* is narrower than in *moreanus* (table 17 & figs 213-214; figs fore wing *parnon* 118-120 against 103-106 in *moreanus*).

The distinction between *parnon* and *biguttulus euhedickei* and *b. parnassicus* is also clear. The latter is characterised by the absence of an inflated head, by a pronotal sulcus located more in front and in the male by the quite distinctly wider C & Sc areas, the longer stridulatory file and the more widely spaced stridulatory pegs (table 18, figs pronotum *parnon* 169 against 160-161 & 162 in *biguttulus* subspecies & fore wing *parnon* 118-120 against 93-102 in *biguttulus* subspecies).

Discussion.— Although populations of *parnon* from the southeastern Peloponnese appear morphologically similar to typical *crassiceps*, the calling song is quite characteristic and different from the latter (compare fig. 245 against 243-244) as well as from all other related species in Greece. Comparison of rivalry and courtship song indicates an alliance between *parnon* and *crassiceps*. Taking into account the importance of the song for mate recognition, we propose to separate *parnon* from *crassiceps* and treat it as a new species. However, further research on its taxonomic ranking is urgently needed, especially since the status of *crassiceps* itself is uncertain.

Table 16. Biometric data of males of *Chorthippus parnon*, Greek *C. mollis mollis* and typical *C. crassiceps*, showing the similarity between *C. parnon* and typical *C. crassiceps* and the weak distinction with nominate Greek *C. mollis* (fig. 218).

	parnon	*crassiceps* (typical)	*mollis mollis* (Greece)
length of fore wing (mm)	10.5 (9.7-11.1)	10.7 (9.6-11.5)	10.7 (8.7-12.7)
width of combined C & Sc area (mm)	0.73 (0.67-0.80)	0.81 (0.75-0.88)	0.80 (0.66-0.95)
width of C area (mm)	0.54 (0.47-0.62)	0.56 (0.50-0.62)	0.52 (0.44-0.60)
width of Sc area (mm)	0.19 (0.15-0.25)	0.23 (0.20-0.28)	0.28(0.22-0.35)
ratio width of C / Sc area	2.9 (2.0-4.0)	2.42 (1.91-3.0)	1.85 (1.53-2.22)
ratio length of pronotum / maximum width of head	0.96 (0.83-1.02)	0.95 (0.88-0.99)	1.12 (1.01-1.22)
ratio maximum / minimum diameter of tympanum	3.12 (2.5-3.83)	3.51 (2.87-4.17)	4.89 (3.38-7.33)
ratio length of fore wing / length of hind femur	1.08 (0.96-1.14)	1.07 (1.00-1.14)	1.19 (1.09-1.40)

On the basis of morphological similarity we arranged the specimens from Kosmas & 10 km E of Kosmas (as *crassiceps* in Willemse, 1984) under *parnon*, but confirmation based on the song is needed.

Distribution and ecology.— As far as known the range of *parnon* (fig. 268) covers all the extreme southeastern part of the Peloponnese (the Epidhavros Limira District of Lakonia), extending south into the offshore island of Kithira and north along the eastern slopes of Mt. Parnon, at least as far north as Prastos (= S of Astros in Kinouria District of Arkadhia). Apart from *bornhalmi* and *willemsei*, syntopic occurrence of *parnon* with congenerics with angled pronotal lateral keels has not been observed.

Table 17. Biometric data to separate males of *Chorthippus parnon* from typical *C. moreanus* and typical *C. pulloides* (figs 213, 214).

	parnon	*moreanus* (typical)	*pulloides* (typical)
ratio length of pronotum / maximum width of head	0.96 (0.83-1.02)	1.08 (0.96-1.14)	1.06 (0.95-1.16)
ratio maximum / minimum diameter of tympanum	3.12 (2.5-3.83)	4.95 (3.57-7.14)	6.34 (3.0-13.1)
length of fore wing (mm)	10.5 (9.7-11.1)	10.9 (10.3-11.7)	7.5 (6.2-8.8)
length of hind femur	9.73 (9.0-10.3)	10.0 (9.4-10.6)	9.1 (8.1-10.3)
ratio length of fore wing / length of hind femur	1.08 (0.96-1.14)	1.10 (1.0-1.23)	0.82 (0.71-0.99)
width of C area (mm)	0.54 (0.47-0.62)	0.58 (0.55-0.62)	0.49 (0.36-0.60)
width of Sc area (mm)	0.19 (0.15-0.25)	0.26 (0.22-0.32)	0.29 (0.20-0.37)
ratio width of C / Sc area	2.91 (2.0-4.0)	2.23 (1.69-2.67)	1.72 (1.26-2.5)
ratio width of combined costal areas × 100 / length of fore wing	6.97 (6.31-7.73)	7.69 (7.13-8.18)	10.33 (9.26-11.62)
distance stigma to tip of fore wing (mm)	3.26 (2.9-3.7)	2.9 (2.7-3.3)	0.93 (0.6-1.3)
ratio distance stigma to tip of fore wing / length of fore wing	0.31 (0.27-0.33)	0.26 (0.23-0.29)	0.12 (0.08-0.18)
number of stridulatory pegs	116.5 (97-138)	115.7 (100-136)	99.7 (71-141)
number of stridulatory pegs / mm	37.6 (31.3-43.1)	33.8 (29.4-36.3)	31.7 (25.5-40.9)

The habitat is rather arid. It ranges from open *Pinus* forest with low undergrowth of heath and other shrubs and grasses to open sites or stony slopes with sparse vegetation or abandoned cultivated land. The localities range from coastal areas up to slopes of middle altitudes. It is a late season species, most adults found from mid August to mid October. Habitat and seasonal characters are shared with *crassiceps*.

Etymology.— The name is a noun in apposition, after its occurrence in the Parnon range.

Chorthippus pulloides (Ramme, 1926)

(figs 15, 60-65, 121-130, 139-140, 171-173, 199-201, 215, 219-222, 248-251, 268, 269, tables 5, 15, 17, 19, 34, 35, cd 26, 27, 28, 29)

Stenobothrus bicolor var. *brunneri* Werner, 1902: 114 (syntypes from H. Vlasis, 800-1300 m; Chelmos 1500 m; Olonios & Taygetos, 2000 m, M. Holtz; NM/W); Harz, 1971: 336 (as synonym of *pulloides*; Werner's material "lost"); Willemse, 1984: 146. (Despite the fact that according to Harz (1971) the types of Werner's (1902) *Stenobothrus bicolor* var. *brunneri* could not be found in the musea of Vienna or Berlin, it is worthwhile to try again tracing this material. It is very likely that Werner's taxon is a senior synonym of Ramme's *pulloides*, Harz's *willemsei* or both which then will have to result in nomenclatural changes).

Stauroderus pulloides Ramme, 1926: 275, fig. 3 (description; ♂ holotype, Mt. Chelmos, 1500-2000 m, 15.viii.1901, Holtz leg.; MNHU/B).

Chorthippus (*Glyptobothrus*) *pulloides*: Harz, 1971: 336; 1975: 863, figs 3121, 3167, 3219-3225 (description; faunistics); Willemse, 1984: 146, map 199 (full references, faunistics, nec *sangiorgii*); Willemse, 1986: 75, figs 989-992 (identification).

Glyptobothrus pulloides: Storozhenko, 2002: 4 (comb. nov.) (taxonomic status).

Chorthippus pulloides (Ramme, 1926) was described from Mt. Chelmos (= Mt. Aroania), the Peloponnese. It is defined mainly by angled pronotal lateral keels, slit-like tympanal apertures, short fore wings with widely rounded apex, reduced hind wings and lack of any striking colour pattern (Harz, 1975; Willemse, 1984 & 1986). Such populations were known throughout large parts of the Peloponnesean peninsula (Willemse, 1984: map 199) and recently are also found locally in the western mainland of Greece.
Typologically the name *pulloides* applies to the population of its type locality, Mt. Chelmos, the Peloponnese. Also populations occurring in adjacent mountains agree fairly well with the topotypical one, both morphologically and in song. However, populations from more remote areas in the Peloponnese particularly from areas bridging the ranges of *pulloides-crassiceps* complex with that of *moreanus* present diverse variations. Analysis of the song revealed that some of these populations show molloid elements, typical of *pulloides-crassiceps* together with biguttuloid elements, typical of *moreanus*. The latter populations will be discussed below, see heading "Atypical and transitional populations". Among *pulloides* occurring in the mainland of continental Greece, populations with biguttuloid elements in the song have not been observed.

Table 18. Biometric data useful to separate males of *Chorthippus parnon* from *C. biguttulus parnassicus.*

	parnon	*biguttulus parnassicus*
ratio length of prozona / length of metazona	1.07 (0.93-1.23)	0.86 (0.81-0.95)
width of combined S & Sc areas (mm)	0.73 (0.67-0.80)	0.84 (0.76-0.97)
length of stridulatory file (mm)	3.09 (2.8-3.4)	3.51 (3.2-3.75)
number of stridulatory pegs / mm	37.6 (31.3-43.1)	30.7 (26.4-35.8)
ratio length of pronotum / maximum width of head	0.96 (0.83-1.02)	> 1.0

Fig. 220. Scatter diagram showing a plot of the ratio of the length of the fore wing (mm) against the maximum width of the C area (mm) in males of typical *Chorthippus moreanus* and typical *C. pulloides*.

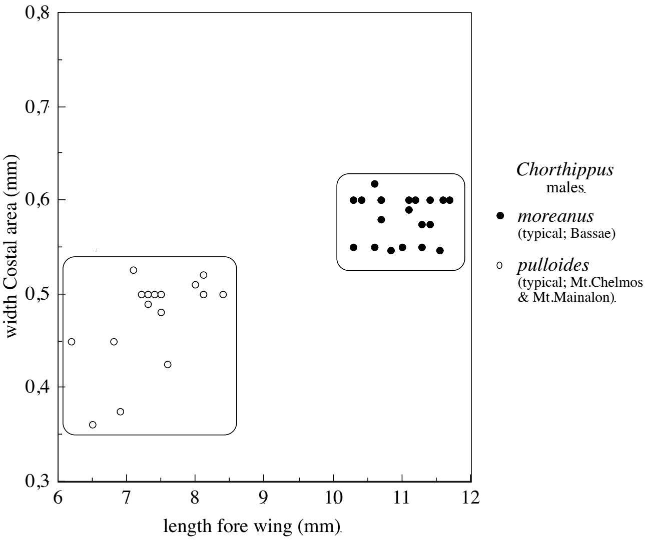
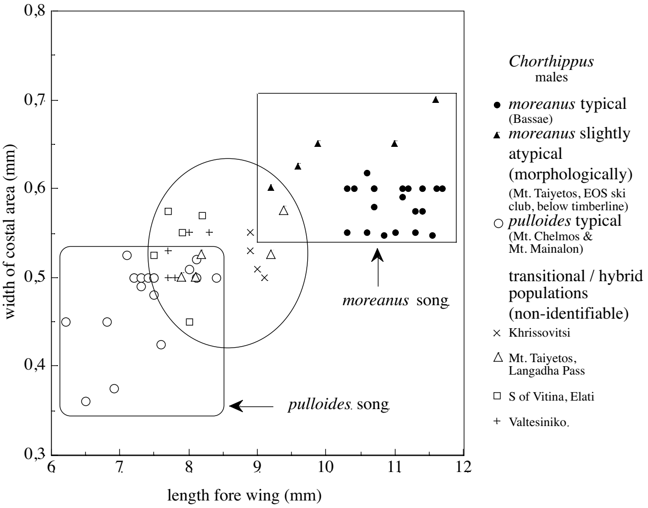


Fig. 221. Scatter diagram showing a plot of the ratio of the length of the fore wing (mm) against the maximum width of the C area (mm) in males of morphologically typical and slightly atypical *Chorthippus moreanus*, typical *C. pulloides* and a number of transitional populations.



Material studied (typical form).— Topotypes: Akhaia, Mt. Chelmos, Kato Lousoi, 1000 m & above Kato Lousoi, 1700-2000 m & plateau and slopes near ski centre, 1400 & 1520 & 1600-1800 m, 31.vii & 1.viii.1970 & 30.vii.1988 & 27.vii.1991 & [26.vii.2005, N38°01'51.3" E22°12'36.3"], pine forest, clearings, stony slopes above timberline (58 ♂, 34 ♀, in CW including 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P) & Kiefernwald, 1600-1800 m & alpiene Grasweiden, 2000-2100 m, 24-25.viii.1989, O. von Helversen (3 ♂) (CvH).

Additional material: PELOPONNESE Arkadhia, Mt. Mainalon above Kardhara 1500-1980 m, 27.vii.1975 & 20.vi.1986 & 2.viii.1988 (16 ♂, 6 ♀) & 1500-1600 m, 27.viii.1986, O. von Helversen (8 ♂, 3 ♀, alcohol vials 6/004 & 6/0042 & 6/0181) (CvH) & Mt. Mainalon, 20.viii.1990, O. von Helversen (2 ♂) (CvH); Arkadhia, Mt. Oliyirtos above Kandhila, 900-1200 m, 26.vii.1975 (23 ♂, 2 ♀); Korinthia, Mt.

Oliyirtos above Lavka, 1200-1500 m, 18.vii.1991 (1 ♂, 1 ♀) Mt. Oliyirtos, 15.viii.1998, F. Mayer (1 ♂, 1 ♀, alcohol) (CM); Mt. Killini above Trikala, 1700-2000 m, 6. viii.1970 (13 ♂, 19 ♀) & plateau near Lamos, 1500 m, 24.vii.2005, N37°56′54.9″ E22°25′44.3″ (1 ♂); CENTRAL GREECE: Aetolia-Akarnania, Mt. Akarnanika above Thirion, 800-1400 m, 18.vii.2000 (34 ♂, 21 ♀, of which 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P)) & 1000-1450 m, 9-10.vii.1986 & 800-1380 m, 27.vii.1987 (58 ♂, 33 ♀) & 970 m, 18-20. viii.1990, O. von Helversen (1 ♂, 1 ♀) (CvH) & 19.viii.1998 (10 ♀, alcohol) (CM); Mt. Tsakalakis, S of Ano Chora & Kendriki, 1200-1300 m & 1200-1560 m, 6-7.viii.2004 (28 ♂, 17 ♀, CW, except 1 ♂, 1 ♀ in BMNH/L) & near Eleftheriani, 900 m & 1060 m, 6.viii.2004 (8 ♂, 7 ♀); N of Ambelakiotasis, pass between Mt. Ardhinis & Tsekoura, 1260 m, 7.viii.2004 (1 ♂), IPIROS: Arta, Mt. Tzoumerka, 1200-1900 m, 4-6.viii.1978, von Helversen (4 ♂, 1 ♀ in CW) & 18.viii.1968 (2 ♂, 2 ♀) (CvH) & SW of Theodhoriana, 1400-1600 m, 25.vii.1987 & 17-18.viii.1988 & N of Vourgareli, 1400-1800 m, 18-19.viii.1988 (21 ♂, 11 ♀, of which 1 ♂, 1 ♀ in BMNH/L) & above Vourgareli, 1550 m, 28-29.vii.2003 (13 ♂, 6 ♀) & above Katarraktis, 1550 m, 10.viii.2005 (5 ♂, 5 ♀); Ioannina, Mt. Kakardhitsa above Matsouki (N of Pramandha), 1800-1850 m, below summit Kataracias (2280 m), 27.vii.2003 (8 ♂, 13 ♀); Mt. Lakmos above Kalarrites, 31.viii.2004, O. von Helversen (2 ♂, 4 ♀) (CvH). (unless otherwise stated collected by the Willemse's and in CW).

Recognition (typical form).— Small and relatively robust (figs 60-65). Head slightly but not remarkably inflated, about as wide as pronotal length. Fastigium verticis wide, interocular distance relatively large, in male 0.79-0.90, in female 1.1-1.4 mm. Pronotal length ♂ 2.6-3.7 mm, ♀ 3.7-4.7 mm, with prozona commonly just longer than metazona and thus the sulcus commonly just behind middle of pronotal length, ratio pro- to metazonal length ♂ from 0.93-1.16, ♀ 1.0-1.5 (figs 171-173). Tympanal aperture slit-like, minimum distance between margins ranging from about 1/3 to 1/20 of maximum distance, average in ♂ 6.3, in ♀ 11.4 (figs 199-201). Fore wings short and wide, length ♂ 6.2-8.8 mm, ♀ 6.4-8.0 mm; in male (figs 121-130, 139-140) just reaching tip of abdomen but commonly shorter, in female not far beyond middle of abdomen, in male about 0.71-0.99, in female 0.50-0.65 times the length of the hind femur; in male fore and hind edges over most of its length almost parallel, fore edge far distally increasingly convex, merging with widely rounded apex, stigma often lacking or if present approaching much the tip, distance to tip of fore wing in ♂ 0.6-1.3 mm, located at about 0.08-0.18 times total length of fore wing; Sc and R from slightly divergent to parallel to each other, C reaching fore edge just before the tip, R commonly simple without Rs and reaching middle of the tip of fore wing.; in ♂ C area relatively narrow, Sc area relatively wide, ratio maximum width of C to Sc area measured along same line 1.26-2.50. Hind wings reduced, slightly more than half to three-quarters of length of fore wing. Length of hind femur in ♂ 8.1-10.3 mm, ♀ 10.6-13.2 mm, relatively thick, length of stridulatory file of ♂ 2.5-4.3 mm, number of pegs 71-141, spacing about 26-40 pegs, average 32 per mm. Biometric data for the male and female in tables 34-35.

Bioacoustics (figs 15, 248-251, cd 26-29).— The calling song (fig. 248) is an echeme-sequence of about 3-8 s, with 10-30 echemes repeated at the rate of about 3-4/s. As pointed out under terminology (figs 15-16), the pattern of the leg movements is molloid (Em). Echemes last about 150-300 ms, showing clear more or less silent inter-echemic intervals of 80-130 ms. The first echemes are usually very weak and maximum intensity is reached near the end of the echeme-sequence. Echemes consist of about 6-10 more or less equally loud syllables, repeated at the rate of about 35-55/s. Usually, only the downward movement of the legs produces a strong sound. The two legs alternate in producing sound, so within every syllable two separate sounds can be recognised, separated

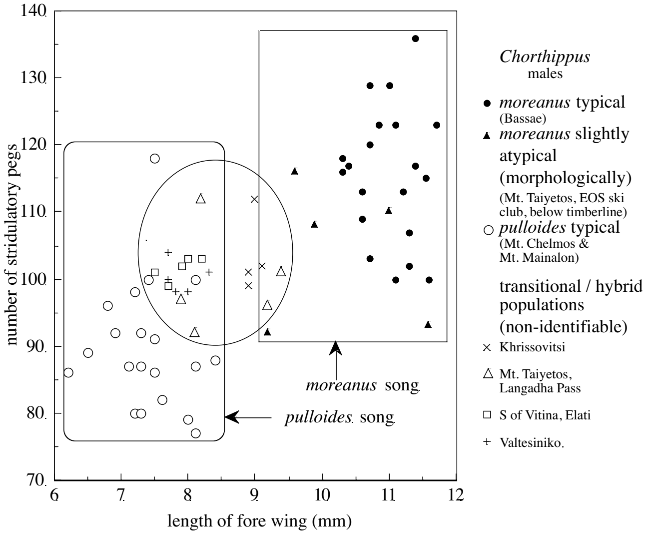


Fig. 222. Scatter diagram showing a plot of the ratio of the length of the fore wing (mm) against the number of stridulatory pegs in males of morphologically typical and slightly atypical *Chorthippus moreanus*, typical *C. pulloides* and a number of transitional populations.

by silent inter-syllabic intervals of about 5-10 ms. The first syllable of an echeme is usually more spaced from the others and may produce a tick sound like in *crassiceps* or *mollis*. An aftersong is absent in the calling and courtship song (exception see below). In the courtship song the echeme-sequence usually lasts longer.

The song shows some variation. Especially the songs from the populations from Mt. Akarnanika and Mt. Lakmos are different. Those from Mt. Akarnanika (fig. 249) show a slower syllable repetition rate of 35-40/s, the number of syllables per echeme is lower, 6-7/echeme and the inter-echemic intervals are relatively longer. Especially the song from the population from Mt. Lakmos (figs 250-251) is different from others. It shows, at least in the calling song (fig. 250), a strong first syllable in every echeme, coinciding with a pronounced leg movement. Also the echemes often show long silent intervals, up to about 500 ms. Apart from that, the courtship song from Mt. Lakmos (fig. 251), as an exception in this species, is followed by an aftersong of about 8 echemes, produced with the legs in a very high position. These aftersongs are quite similar to the calling song except for the silent inter-echemic intervals which are apparently longer.

Variation.— While the variation within populations is limited, it is considerable throughout the geographical range. Populations of central northern Peloponese covering the type locality and its adjacent mountains (Mt. Chelmos, Mt. Mainalon & Mt. Oliyirtos) are uniform and considered the typical form. Material from the Peloponnese outside this area differs slightly in morphology but also in some particulars of the song and are discussed below under the heading "Atypical and transitional populations".

The populations of the mainland of Greece commonly agree well morphologically with topotypical *pulloides* from the central northern Peloponese, except for that of Mt. Akarnanika. Here, individuals are smaller, shorter winged (table 34-35, figs 125, 140) and the male stridulatory file is shorter and spacing of the pegs wider: length of file 2.2-3.0 mm and number of pegs 52-67 in Mt. Akarnanika population against 2.5-4.3 mm and 71-141 (!) pegs in *pulloides* from elsewhere. Bioacoustical particulars of this

Table 19. Some morphological and bioacoustical data of males of typical *Chorthippus moreanus*, *C. pulloides* and *C. crassic*
refer to those of figs 268-269 (figs 212, 215, 219-222).

Morphological identification males	***moreanus*** typical	***moreanus*** typical	**"transitional"** very atypical
locality (number on map fig. 269) or area & altitude	from Bassae (80) throughout Messinia to SW Mt. Taiyetos (Ilia, Messinia & Lakonia) 100-1450 m	Petralona (32) (Ilia) & Nedhoussa (73) (Messinia) 900 & 1100 m	Karkalou (36) (Arkadhia) & Mt. Parnon-Vamvakou (68) (Lakonia) 1100 m & 1300 m
length of fore wing (mm)	11.0	9.7	7.5
ratio length of fore wing / length hind femur	1.10	0.96	0.87
distance from stigma to tip of fore wing (mm)	2.89	2.1	1.75
ratio distance of stigma to tip / length fore wing	0.26	0.21	0.23
ratio length of pronotum / max. width of head	1.07	1.02	1.10
ratio maximum / minim. diameter of tympanum	4.95	6.14	5.0
Bioacoustical identification	***moreanus*** typical	***moreanus*** atypical	non-identifiable very atypical
leg movements (see terminology)	biguttuloid	biguttuloid (molloid)	biguttuloid & molloid
structure of song	echeme sequence consisting of biguttuloid echemes, repeated at the rate of 9-11/s	echeme sequence consisting of biguttuloid echemes, repeated at the rate of 9-11/s, but grouped in molloid echemes with short intervals	echeme sequence consisting of an irregular mix of molloid and biguttuloid echemes
length of molloid echeme, if present	n/a	300-600 ms	200-300 ms
length of interval between molloid echemes, if present	n/a	50-80 ms	<100 ms
pre-echemic tick (molloid echemes)	absent	absent	absent
aftersong (courtship)	present	present	not observed
song figures	figs 237-238	figs 16, 256-257	figs 258-259
Final identification	*moreanus* **(typical)**	***moreanus*** **(atypical)**	**"transitional"**

population are described above. Nevertheless we arranged the Mt. Akarnanika population under this taxon. Many characters do agree with typical *pulloides*, like the habitus (figs 64-65: Mt. Akarnanika, figs 60-61: Mt. Chelmos), the wide fastigium verticis (fig. 173: Mt. Akarnanika, figs 171-172: Mt. Chelmos/Mainalon), the slit-like tympanal apertures (fig. 200: Mt. Akarnanika, fig. 199: Mt. Chelmos) and the song (fig. 249: Mt. Akarnanika, 248: Mt. Mainalon). Another example is presented by the northernmost known population occurring in the highest parts of the mountain range extending from Mt. Tsoumerka to Mt. Lakmos, south of Metsobon (district of Ioannina). Here the song (figs 250-251) differs slightly from the typical one (see variation).

It is remarkable that on the mainland of Greece (Mt. Akarnanika, Mt. Tsoumerka and Mt. Lakmos) the species occurs together with *m. mollis*, either syntopic or narrowly *eps* compared with atypical and transitional (hybrid) populations between these taxa. The numbers behind the localities

pulloides typical	***pulloides*** typical	***crassiceps*** atypical	***crassiceps*** typical
Mt.Panakhaikon (18) Mt. Erimanthos (25) (both Akhaia) & Mt.Lambia (26) (Ilia)	Mt. Chelmos (11-12) (Akhaia), Mt. Oliyrtos (41) & Mt. Mainalon (40) (both Atkadhia)	Arachnaio Mts., Limnes (6) (Argolis)	Poros Isl. (1) & opposite Argolis (Ana Fanari & Methana) (allArgolis)
600-1800 m	900-2000 m	600 m	10-120 m
8.1	7.4	7.5	10.6
0.89	0.82	0.81	1.07
0.90	0.96 (if present)	1.17	2.7
0.11	0.12	0.16	0.31
1.11	1.03	0.95	0.98
5.1	6.89	4.44	3.51
pulloides atypical	***pulloides*** typical	***crassiceps*** atypical	***crassiceps*** typical
molloid & biguttuloid	molloid	molloid	molloid
echeme sequence consisting of well separated molloid echemes. Molloid echemes consist of 5-10 biguttuloid echemes, repeated at the rate of 14-15/s	echeme sequence consisting of well separated molloid echemes. Molloid echemes consist of 6-8 molloid syllables	echeme sequence consisting of well separated molloid echemes. Molloid echemes consist of 9-10 molloid syllables	echeme sequence consisting of well separated molloid echemes. Molloid echemes consist of 10-15 molloid syllables
200-800 ms	180-200 ms	250 ms	350-425 ms
150-200 ms	80-100 ms	70-80 ms	50-70 ms
absent	indistinct	present	present
absent	absent	absent	rarely present
figs 15, 253	fig. 248	fig. 244	fig. 243
pulloides **(atypical)**	***pulloides*** **(typical)**	***crassiceps*** **(atypical)**	***crassiceps*** **(typical)**

parapatric. Evolutionary pressure might have resulted in song character displacement, resulting in a more explicit difference between these species, especially in *pulloides*. The differences in temporal pattern could be important for specific recognition, to wit the comparatively striking difference in length of the silent inter-echemic interval as well as the intra-echemic syllable repetition rate. The ratio between the length of the echeme and its silent interval is about 0.25 in *m. mollis* but 0.35-0.5, up to at least 1.0 in *pulloides*. The syllable repetition rate in *pulloides* is 35-55/s against 60-80/s in *m. mollis*.

Noteworthy is also a clinal variation of coloration of the hind tibia, particularly shown in the male. Brown coloured hind tibiae are found throughout the Peloponnese but the populations of Mt. Panakhaikon, extreme northwestern Peloponnese, have a reddish flush. This flush is also found in the populations of the opposite mainland of

Greece (Mt. Akarnanika & Mt. Tsakalakis in Aitolia-Akarnania) but increases farther north to the more northern populations of Mt. Tzoumerka (Arta) to red and even bright red (similar to that of *willemsei*) in the northernmost known population of Mt. Kakardhitsa and Mt. Lakmos (both Ioannina).

Differential diagnosis.— The short wings of *pulloides* are shared by *willemsei*, *biroi* and *sangiorgii*. Useful characters to separate *pulloides* from these taxa are the different habitus (robust or slender), width of fastigium verticis and interocular distance, tympanal aperture, location of the transverse sulcus of the pronotal disc, length and width of fore wing and width of Sc area in the male, general aspect of venation and membrane of the fore wings and the colour of the hind tibia. Both *biroi* and *sangiorgii* occur allopatric, but *willemsei* may occur syntopic with *pulloides*. The latter two are easily recognisable by the tympanal aperture being wide in *willemsei*: average ratio maximum/minimum diameter in male 2.6, female 2.35 in the latter against in male 6.34, female 11.4 in *pulloides* (or even more in the Mt. Akarnanika population of the latter) (figs 199-201 against 183-184). Another obvious distinction is found in the colour of the hind tibia: in *willemsei* bright red all over its range against yellowish brown in *pulloides* in the southern part of its range. However, as described above, the hind tibia of the populations of the northern part of the *pulloides* range may either be red, even as bright as in *willemsei*. The allopatric taxa *biroi* and *sangiorgii* differ from *pulloides* both in slender habitus with narrower fastigium verticis with an average interocular distance (mm) in male of 0.65, female 0.91 in *biroi* and 0.62 and 0.92 in *sangiorgii* respectively, apparently less than in *pulloides*, male 0.83 and female 1.23 (figs *pulloides* 171-173, *biroi* 154-155, *sangiorgii* 170). The morphological differentiation between *pulloides*, its small sized individuals of the population from Mt. Akarnanika and both from *willemsei*, *biroi* and *sangiorgii* is summarised in table 5.

However, to differentiate typical *pulloides* from other short winged forms, to wit the strongly morphologically atypical forms both of *crassiceps* and *moreanus* or, as will be shown below, of transitional populations between these taxa may be difficult and often arbitrary (table 19, figs 215, 219-222). The shape of the apex of the male fore wing is sometimes helpful: in typical *pulloides* commonly wide, obtusely and regularly rounded (figs 121-128) against narrower and slightly angularly rounded in atypical *crassiceps* (fig. 117), atypical *pulloides* (figs 129-130) and transitional populations (figs 133-138). However, morphological character states are commonly not well defined and the song may be more useful. Compare the non-identifiable populations under the heading "Atypical and transitional populations".

The short wings of *pulloides* are obviously different from the relatively longer winged species *bornhalmi*, *v. dissimilis*, *b. euhedickei*, *b. parnassicus*, *m. mollis*, *parnon*, including also typical *moreanus* (table 17, figs 215, 220-222) and typical *crassiceps* (table 15, fig. 219).

Discussion.— We restricted the diagnosis of typical *pulloides* to populations showing a set of morphological and especially song characters as pointed out above. We did not observe any important distinction between these typical *pulloides* of the Peloponnese and those of the Greek mainland where locally *pulloides* lives syntopic with *m. mollis*. The latter observation indicates that *pulloides* is reproductively isolated from *m. mollis* though the general structure of the song of both taxa shows some resemblance. As pointed above, the difference refers maybe to the temporal pattern of the syllables of the echemes, a character also shared by *crassiceps*. The main differences between *mollis* and *pulloides* lie in the syllabic structure of the echemes: *pulloides* showing a lower number of syllables, a lower syllable repetition rate, a longer interval between echemes and a less pronounced pre-echemic tick.

Due to transitional populations bridging typical *crassiceps* and *pulloides*, as pointed out under the former, we failed to find a reliable limitation between these taxa. Therefore we consider *pulloides* and *crassiceps* strongly related species, closer to each other than to *m. mollis*. Yet, the degree of their alliance (*e.g.* conspecifity) is an open question.

Similar questions arise on the relationship between some Peloponnesean populations arranged here under *pulloides* and discussed below under the heading of "Atypical and transitional populations".

Distribution and ecology.— Previously, the range of *C. pulloides* was badly known. Apart from the Peloponnese, *pulloides* as defined above also proved to be distributed in the western mainland of Greece and was found in the following districts: Ioannina (Mt. Lakmos & Mt. Kakardhitsa), Arta (Mt. Tzoumerka), Aetolia-Akarnania (Mt. Akarnanika &, pass between Mt. Ardhinis-Mt. Tsekoura, N of Ambelakiotasis & Mt. Tsakalakis). In the Peloponnese the range of the typical form covers the high parts of Mt. Mainalon, Mt. Chelmos and Mt. Oliyirtos in central northern Peloponnese (for atypical populations see below under "Atypical and transitional populations").

There is no doubt that *pulloides* is absent from most of the southeastern parts or in extreme northeastern parts where either *moreanus*, *parnon* or *crassiceps* occur. Exceptions are the isolated populations in the alpine zone of Mt. Taiyetos and Mt. Parnon (figs 267, 268).

The habitat ranges from sunny slopes, stony ground with grass, sparse low vegetation and scattered shrubs, to open forest, forest edges and clearings, commonly above 500 m and extending to far above the timberline. Adults occur from mid July, but are most abundant in August and September.

Congenerics found syntopic with *pulloides* are *willemsei*, *bornhalmi* and *v. dissimilis* in the Peloponnese and in the mainland of Greece with *m. mollis*, *b. euhedickei* and *apricarius*.

Chorthippus sangiorgii (Finot, 1902)

(figs 66-67, 131-132, 142, 170, 202-203, 252, 267, tables 5, 34-35, cd 30)

Stenobothrus sangiorgii Finot, 1902: 53, figs 1-4 (description; ♂ & ♀ syntypes from Cherasimi & Dhilinata in Ionian Is of Kefallinia [Gherasimoi et Dilinata, in insula Cephalonia, tempore autumnali], MNHN/P)

Stenobothrus (*Stauroderus*) *sangiorgii*: Werner, 1927: 149 (Kefallonia).

Stauroderus sangiorgii: Ramme, 1926: 275 (distinction with *pulloides*).

Chorthippus (*Glyptobothrus*) *sangiorgii*: Harz, 1975: 863, figs 3120, 4176, 3214-3218 (description; Kefallinia); Willemse, 1977: 55 (Lefkas, Komilion); 1984: 146, map 199 (references, faunistics); 1986: 75, figs 985-988 (identification).

Chorthippus pulloides [nec Philippi]: Szijj, 1992: 51 (diagnosis?, Louros Delta).

Glyptobothrus sangiorgii: Storozhenko, 2002: 4 (comb. nov.) (taxonomic status).

Chorthippus sangiorgii: Papapavlou & Katsouni, 2008: 35 (Kefallonia; Ithaki).

Material examined.— Topotypes (s.l.): Ionian I., Kefallinia, Mt. Ainos, 1000-1300 m, (7 ♂, 4 ♀) & surr. Neokhorion, 400 m (2 ♂) & Dhilinata, 350 m (2 ♂) (topotypes s.s.) & 1 km SE Platiai, 100 m (1 ♂), all 2-6. vii.1986.

Additional material: IONIAN IS: Levkas, Komilion, 500 m, 15.vii.1976, (2 ♂); Levkas, Vassiliki, x.1996, J. Schul (CvH). (unless otherwise stated collected by the Willemse's and in CW)

This taxon has been described from Cherasimi & Dhilinata, the Ionian island of Kefallinia (Finot, 1902) and recorded since from the nearby island of Levkas (Willemse, 1977; 1984) and Itaki (Papapavlou *et al.,* 2008). The song was unknown and is described below, based on topotypical specimens and of a male from the island of Lefkas, the latter in combination with registration of hind leg movements.

Recognition.— Resembles *pulloides* but differs as follows: habitus more slender (figs 66-67); fastigium verticis narrower, interocular distance smaller, in male 0.54-0.69, in female 0.80-1.01 mm (in *pulloides* male 0.79-0.90, female 1.1-1.40 mm respectively) (fig. 170); tympanal aperture relatively wider, average ratio maximum/minimum diameter in male 4.7, in female 5.4 (against in *pulloides* male 6.3, female 11.4) (figs 199-200); slightly shorter fore wings, in male 5.6-7.1, female 4.9-7.1 mm (in *pulloides* male 6.2-8.8, female 6.5-8.0 mm) (figs 131-132, 142). Biometric data for the male and female in tables 34-35.

Bioacoustics (fig. 252, cd 30).— The calling song can be described as an echeme-sequence of 2,5-11 s, consisting of 5-16 echemes that are repeated at the rate of about 1.4-2/s. Echemes last 400-500 ms, inter-echemic intervals 200-300 ms. Each echeme consists of 5-8 loud sounds, the loudest ones at the end of the echeme, repetition rate 14-16/s. In the only available registration with leg movements both legs produce continuously to-and-fro movements, during the echemes with high amplitude but also, though with low amplitude, during the inter-echemic intervals. Syllable repetition rate during the echemes is about 24/s, during the intervals about 20/s. The loud sounds of the echemes are not clearly linked to either of the upward or downward movements of the hind legs. The calling song is consistent in both Levkas and Kefallinia, although the echeme-sequences in Kefallonia are shorter, up to about 5 s.

A recording in the presence of a female shows a short song with about the same structure as the calling song, only starting with very short echemes.

As the leg movement continues throughout the echeme-sequence it can be argued to describe the calling song as an echeme with variation in the amplitude of the movement, thus resulting in a variation in loudness. Yet, we prefer to use sound units as pointed out under the terminology and describe the song as an echeme-sequence.

Differential diagnosis.— This species resembles *pulloides,* particularly the short winged population of the latter from Mt. Akarnanika. The distinction between both taxa is pointed out above under the diagnosis of *sangiorgii* (table 5). The slender habitus and the narrow interocular distance of *sangiorgii* also differentiate it clearly from the *pulloides* population of the adjacent Mt. Akarnanika. Interestingly the number (about 93) and spacing of stridulatory pegs (about 34 per mm) in *sangiorgii* equals that of *pulloides* (number about 100, spacing about 32 per mm), but in the *pulloides* population of Mt. Akarnanika the number is about 60 and spacing about 23 per mm.

The differences between *sangiorgii* and *biroi* and *willemsei* refer mainly to the more robust habitus, wider fastigium and interocular distance and red colour of hind tibia in *willemsei* (figs 31-32), the more open tympanal aperture and the location of the third pronotal sulcus, slightly more behind the middle of pronotal length both in *willemsei* and *biroi* (figs 152-153 against 160, figs 183-184 against 185-187), and in the obviously narrower Sc area of the male fore wing in *biroi* (figs 85-87). A summary is given in table 5.

All other congeneric members of *Chorthippus* are well distinct by their longer wings.

Discussion.— Ramme (1926) used the difference in width of the fore wing to separate *pulloides* from Finot's *sangiorgii*. Indeed, the fore wings of *sangiorgii* compared with those of *pulloides* are as a rule slightly narrower than, but when taking larger series of specimens of the latter into account, the difference disappears (tables 34-35).

The relationship of *sangiorgii* is uncertain. Though morphologically close to *pulloides* and thus to *mollis*, the song is distinctly different and shares some characteristics with the song of *vagans* and its relatives, although it has distinctive leg movements.

The clearly visible to and fro leg movements during the silent inter-echemic intervals have not been observed in any other example of Greek congenerics.

Distribution and ecology.— Known only from the Ionian islands of Kefallinia, Ithaki and Levkas from which no other member of *Chorthippus* with angled lateral pronotal keels is known (although *bornhalmi* at least may be expected) (fig. 267, Ithaki record not on map).

J. Szijj observed two females in a dry rocky hill of the Louros delta (Arta, Louros delta, Solaora Gulf, Mavrovouni hill, 1989, J. Szijj, pers. comm. J. Szijj). The specimens (CS) have not been studied properly; the male song is unknown and its diagnosis uncertain.

This taxon has been found from the lowlands up to the highest part of these islands, Mt. Ainos in Kefallinia, 1300 m. The habitat is arid and has stony ground with poor vegetation. Adults have been found in July and may be expected also in August and September.

Atypical and transitional populations

Chorthippus (*Glyptobothrus*) *crassiceps* [nec Ramme]: Willemse, 1984: 145, map 198 (partim).
Chorthippus (*Glyptobothrus*) *pulloides*: Willemse, 1984: 146, map 199 (partim).

The morphology and bioacoustics of most taxa described in this paper show little if any variation across populations throughout their range in Greece. Because of the consistence in morphology and bioacoustics, individual specimens from most populations in Greece can easily be assigned to a particular taxon. However the morphology and bioacoustics in populations belonging to the C. *pulloides* complex (*pulloides*, *crassiceps* & possibly *parnon*) and *C. moreanus* clearly are not consistent throughout their range. Because of their bioacoustics we consider this group of species to be related to *C. mollis*, the latter to *C. biguttulus*. With the exception of *C. pulloides*, which also occurs in the Greek mainland, *C. parnon*, *C. crassiceps* and *C. moreanus* are limited to the Peloponnese where they occur (para-)allopatric, their distribution areas not overlapping (fig. 268). Within the relatively small distribution range of these taxa, morphological and bioacoustical characteristics show distinct geographically inclined variation. For instance, comparison of the figs 43-46, 58-59, 50-53, 32-36 and the location of the site within the range of the corresponding taxon (figs 267-268, locality nrs 1, 4, 6, 65, 11, 40, 33, 64, 78, 80) clearly shows that the variation in *e.g.* the length of the fore wing is clinal, i.e. shortening towards the periphery of the range both in *C. crassiceps* and *C. moreanus* or the reverse in the *C. pulloides* population of Mt. Taiyetos (note that the latter in Mt. Akarnanika, mainland Greece, also may show a shortening of fore wings as variation).

In some populations the variation (as compared to the nominate population) is predominantly obvious in morphological characteristics, the bioacoustics not differing at all or only showing a subtle variation so as to be still well recognisable. As we rate bioacoustical characteristics in this group of Orthoptera as being more reliable for identification, we arranged these populations as atypical ones of the taxon concerned. Such populations are presented by *C. crassiceps*, *C. moreanus* and *C. pulloides*

At the boundaries of the distribution areas of two taxa the deviation, both in morphology but especially in bioacoustics, from the nominate populations may be even so great that it is impossible to identify such populations with any certainty. Such an area was found in the Peloponnese in between the distribution areas of *C. moreanus* and *C. pulloides*. Populations from this comparatively extensive area could not be identified because the songs consist of *pulloides*-like elements (molloid) as well as *moreanus*-like elements (biguttuloid) without any prevalence of either of the two. These populations are treated below as non-identifiable, transitional ones, bridging *C. moreanus* with the *C. pulloides* complex.

Atypical populations of *C. pulloides*

(figs 15, 128, 221-222, 253-255, 268-269, table 19, cd 32, 33)

Material studied (all the Peloponnese).— Northwestern Peloponnese: Akhaia, Megaspilion, 700 m, 28.vii.1988 (1 ♂) & 1000 m, 24.viii.1989, O. von Helversen (2 ♂) (registration leg movements "Y") & Mega Moni Spileon, N of Kalavrita, 900-1000 m, 28.viii.1986, O. von Helversen (2 ♂, 2 ♀, alcohol vial 6/0049) (CvH); Akhaia, Aroania village, 1000-1100 m, 2.viii.1970 & 29.vii.1988 (29 ♂, 6 ♀); Drymos, East of Aroania [west of Klitoria], 1100 m, 25.viii.1989, O. von Helversen (2 ♂, 1 ♀) (CvH) (registration leg movements "34"); Akhaia, Mt. Panakhaikon, 900 & 1350 m, 21/22.viii.1986, O. von Helversen (8 ♂, alcohol vial 6/0173 & 6/0057) (CvH) (registration leg movements "AG") & above Katafigio, 1600-1700 m, 29.vii.2005, N38°12′29.2″ E21°51′39.7″ (5 ♂, 2 ♀) & above Romanou, 1000 m & above Zastova, 1000-1800 m & Zastova-Psarthri, 1000-1650 m, 16.vii.1974 & 30.vii.1975 (12 ♂, 8 ♀) & oberhalb Souli, 1500 m, alpiene Matten, stark beweidet, 21.viii.1986, O. von Helversen (1 ♂, 2 ♀) (CvH); Akhaia, Mt. Panakhaikon, southern hills, pass SE above Mirali, 1250 m, 8.viii.2003, N38°07′23.9″ E21°50′46.9″ (4 ♂, 4 ♀); Akhaia, Mt. Klokos, between Fteri & A. Mavriki, 1250 m, 28.vii.2002, N38°08′05.6″ E22°02′59.2″ (4 ♂, 6 ♀) & 1300-1500 m, 28.vii.2005, N38°08′25.7″ E22°02′16.1″ (4 ♂, 4 ♀); Akhaia, Kalentzi, 1000 m & Mt. Erimanthos above Kalentzi, 900-1100 & 1700-2000 m & above Mika 1250 m, 3.viii.1970 & 16.vii.1987 (31 ♂, 17 ♀, of which 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P) & Mt. Erimanthos below Kriovrissi, 13.vi.1992, O. von Helversen (1 ♂) (CvH) (registration leg movements "3"); Akhaia, Kalavrita-Egeo, surr. Petsaki, 850 m, 28.vii.2005, N38°06′32.3″ E22°02′07.0″(1 ♂); Akhaia, 4 km N of Skepasto, 1160 m, 26.vii.2005, N38°04′19.8″ E22° 04′03.8″ (1 ♀); Akhaia, Vlasia (W of Kalavrita), 500 m, 3.viii.1970 (4 ♂); Akhaia, Kalanos (40 km W of Kalavrita), 1.viii.1988 (1 ♂, 1 ♀); Ilia, Ilia, W of Ayia Panopoulou, 500 m, 6.ix.1989 (1 ♂, 1 ♀); Ilia, 6 km E of Triadha (W of Mt. Lambia), 600 m, 14.vii.1991, *Quercus* forest (1 ♂, 4 ♀) (song recorded); Ilia, Lambia (= Lampeia), 800 m, 26.viii.1989, O. von Helversen (4 ♂, 1 ♀) (CvH) (registration of leg movements "AK", "AJ"); Ilia, Agias Kyriaki (W of Lambia), 700 m, 28.vii.1975 (5 ♂, 3 ♀); Ilia, Marmara (Erimanthos river), 600 m, 30.vii.1970 (30 ♂, 21 ♀). (unless otherwise stated, collected by the Willemse's and in CW) Southeastern Peloponnese: Lakonia, Mt. Taiyetos above Anoyeia and refuge EOS, 1600-1700 m & below Profitis Ailias summit, 1700-2200 m & summit 2404 m, 23.vii.1971 & 1.viii.1991, stony slopes above timberline (40 ♂, 18 ♀, of which 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P) (6 oscillograms of 5 different males CW) & 9.viii.1998, F. Mayer (4 ♂, 7 ♀, alcohol, CM) (registration leg movements "20"); Lakonia, Mt. Parnon, Gipfelregion, 1600-1700 m, 26.viii.1986, O. von Helversen (14 ♂, alcohol vial 6/0166) (CvH) & above Vamvakou, 1500 -1935 m, 28.vii.1978 (7 ♂, 2 ♀) & above Kastanitsa, 1500-1800 m, 25.vii.1978 (5 ♂, 3 ♀). (unless otherwise stated, collected by the Willemse's and in CW).

The typical form of *pulloides* occurs in the high altitude parts of Mts. Chelmos, Oliyirtos and Mainalon in central northern Peloponnese. Morphologically similar populations cover also the lower altitudes of these mountains, extending slightly south and considerably west throughout all of the northwestern part of the Peloponnese, including the high altitude parts of the Mts. Panakhaikon, Erimanthos and Lambia. Furthermore there are a few scattered and isolated *pulloides*-like populations in the southeastern part of the Peloponnese covering the alpine summits of the Taiyetos and Parnon ranges (figs 268-269). An example both of the northwestern and southeastern Peloponnese are illustrated below.

Northwestern Peloponese.— Comparison of populations from the northwestern Peloponnese with typical *pulloides* reveals that the morphological distinction is subtle and neglectably small (compare *e.g.* fig. 128 with 121-124**)**. The song however, shows atypical characters. Examples of such atypical songs are given for populations from Mt. Lambia (fig. 253, locality 26 of fig. 269) and Mt. Erimanthos (fig. 15: locality 25 of fig. 269).

The calling song consists of a sequence of echemes (E) with a repetition rate of about 2-4/s, typical for *pulloides* (as well as for *m. mollis*, *m. lesinensis* and *crassiceps*). The intervals between the echemes are relatively long (100-200 ms against 80-130 ms in typical *pulloides*). However, these echemes consist of grouped syllables with a typical biguttuloid pattern (Eb) resembling strongly *moreanus*. These leg movements consist of a strong syllable (S1) being followed by 2-3 or more weak syllables (S2). The number of these biguttuloid echemes per echeme varies from 5-10, exceptionally more during the end of the song. While in *moreanus* the repetition rate of these biguttuloid echemes (Eb) commonly is 10/s (7-12/s), the rate in these atypical populations is faster, commonly 15/s (12-18/s) and sometimes almost twice as fast. It is completely unknown whether this difference in temporal pattern affects the ability of the female to discriminate between *moreanus* and *pulloides*. One could suppose that a series of biguttuloid echemes produced by fast leg movements are recognised as a molloid echeme produced by slow leg movements.

Southeastern Peloponnese.— A good example is the isolated population occurring in the alpine zone (above 1600 m) of the highest summit of Mt. Taiyetos, Prof. Ilias (2404 m) (figs 254-255, locality 65 of fig. 269). Morphologically males of this population differ only slightly from typical *pulloides* by the apex of the fore wing being more attenuate (figs 129-130) than in typical *pulloides* (figs 121-124) and thus somewhat resembling that of short winged forms of *moreanus* (fig. 107). Its song differs slightly from that of typical *pulloides*. The leg movements of the first syllables of the echemes are not simply molloid but irregular and sometimes resemble biguttuloid movements as shown above for the atypical forms from the northwestern Peloponnese.

Discussion.— Populations occurring near typical *pulloides*, including those living at altitudes lower than the typical ones, are almost identical to this form. The populations from more remote sites in the northwestern Peloponnese agree quite well morphologically (fig. 128) with the typical form, but differ in their song. The structure of these songs (figs 15, 253) is somewhat irregular and the leg movements during the first parts of the echemes show a complicated syllable structure typical for *moreanus* (with biguttuloid characters). In the southeastern Peloponnese the same structure can be recognised in the song of the isolated *pulloides*-like population from Mt. Taiyetos (figs 254-255). In this case there is a, slight but consistent additional morphological distinction with typical *pulloides*: while the male fore wing of typical *pulloides* has parallel margins and a widely rounded apex, the male fore wing in the Taiyetos males commonly shows a less reduced apical part, the apex being angulately rounded (figs 121-124: typical Peloponnesean *pulloides* against figs 129-130: Taiyetos population). Moreover the situation in Mt. Taiyetos is quite interesting. On this mountain *moreanus* occurs from the lowlands of the southern and western side of the mountain (Kardhamili, Kambos, Areopolis, Mani peninsula) throughout the forested part of this mountain up to the timberline at 1500-1600 m while *pulloides*-like populations are completely absent here. *Pulloides*-like populations are found only above the timberline up to the summit at 2404 m, where *moreanus* is completely absent in this alpine zone. Along the narrow parapatric zone at 1500-1600 m altitude we found neither syntopic occurrence nor hybridization. Also the gap of morphology and general structure of the song between these local *moreanus* and *pulloides* populations is obvious. Apparently a morphologically slightly atypical *pulloides*-like population producing an atypical song (atypical because it is mixed with biguttuloid hind leg movements) is reproductively isolated from *moreanus*. We assume that the structure of the song divided in echemes with distinct inter-echemic intervals, irrespective of the intra-echemic biguttuloid leg movements, corresponds with the innate releasing mechanism of *pulloides* females. Therefore we feel confident about this population being conspecific with the latter. With reference to this case, we assigned many of the widely distributed *pulloides*-like populations from the northwestern Peloponnese to atypical *pulloides*. Yet, further research may yield other conclusions concerning the phylogenetic and taxonomic status of these populations.

Atypical populations of *C. moreanus*
(figs 16, 221-222, 256-257, 268-269, table 19, cd 34, 35)

Material studied (all the Peloponnese).— Ilia, Petralona, W of Bassai, 23.viii.1986, O. von Helversen (10 ♂, 4 ♀, alcohol vial 6/0060 & 6/0097) (CvH) (registration leg movements "33"); tentatively arranged here: N of Andritsaina, Sekoula, 27.viii.1989, O. von Helversen (1 ♂, 1 ♀) (CvH).
Messinia, Westhang Taiyetos-Gebirge, Nedhoussa, 1100-1200 m, 25.viii.1986, O. von Helversen (1 ♂, alcohol vial 6/0038 in CvH) (registration leg movements "P") & Schlucht neben der Strasse Kalamata-Sparta, Abfahrt "Nedhoussa", 24/25.viii.1986, O. von Helversen (1 ♀ in alcohol vial 6/0177) (CvH).

As pointed out under *moreanus*, remarkable clinal variation both in morphology and song was observed among populations occurring at the periphery of the range of this species (figs 268-269). Here we give two examples of populations showing some differences with typical *moreanus*, both located at the periphery of the range of the typical form. One is from the westernmost (Petralona) and one from the easternmost (Nedhoussa) part of its range.

The specimens from Petralona (fig. 269: locality 32) morphologically agree with the typical form, showing well developed fore wings. Also, the syllabic structure of the song (figs 16, 256) is clearly biguttuloid and identical to that of *moreanus*. However, the song tends to be split into echemes lasting about 300 ms in the beginning to 700 ms at the end of the song. The song lacks the relatively long and regularly produced inter-echemic intervals of *pulloides*.

Nedhoussa (fig. 269: locality 73) is relatively far from the type locality. The fore wing of the male almost reaches the supra-anal plate and is thus slightly shorter than in typical *moreanus* but the overall agreement with *moreanus* is obvious. The syllabic structure of the song (fig. 257) is like that of *moreanus*. However, the more or less regular *moreanus* (read biguttuloid) pattern is irregularly interrupted by unusually long lasting syllables with a leg movement, that shows affinity with the leg movement during and just after the long inter-echemic intervals in *pulloides*.

Discussion.— Similar to the example provided for atypical *pulloides*, these *moreanus*-like populations agree roughly with the typical form of the latter although the song contains elements that are reminiscent of *pulloides*. In this paper these populations have been arranged under *moreanus* albeit as atypical forms.

Non-identifiable populations

(figs 16, 68-71, 133-138, 221-222, 258-259, 268-269, table 19, cd 36, 37)

Material studied (all the Peloponnese).— Arkadhia: Karkalou-Langadhia, ostl. Olympia (& W of Vitina), 1100 m, 28.viii.1989, O. von Helversen (2 ♂) (CvH) (registration leg movements "AL"); Khrisovitsi, 4 km W, 1100 m, 28.vii.1978, L. Willemse & J. Tilmans (1 ♀) & 11.5 km W, 1100 m, stony plateau, cultivated & shrubby areas, 9.ix.1989 (12 ♂, 10 ♀) & 10 km W, 1200 m, along *Abies* forest, (4 ♂, 3 ♀) & 8 km W, 1150 m, forest clearing, (1 ♀) & 6 km W, 1200 m, large clearing in forest, (3 ♂) & 3 km W, 1200 m, forest clearing, (6 ♂, 5 ♀), all 11.ix.1989, F. Willemse) (CW) (song recordings of 6 males); N & S of Valtesiniko (N of Vitina), 1300 m, 18.ix.1989, F. Willemse (13 ♂, 8 ♀) (CW) (song recordings of 5 males); S of Vitina, 4 km S of Elati, 1200 m, forest clearing, 11.ix.1989, F. Willemse (20 ♂, 7 ♀) (CW) (song recordings of 13 males); Tripolis, 5 km W, 28.vii.1978, L. Willemse & J. Tilmans (1 ♂) (CW); SE Tripolis, Karies-A. Petros, 800 m (6 ♂, 2 ♀) & 4-6 km E of A. Petros, 850-900 m (15 ♂, 2 ♀), 2.viii.1991, various habitats (song recordings of 4 males); A. Ioannis-O. Meligou (S of Astros), 700 m, 2.viii.1991, extreme dry habitat, few shrubs, grasses almost lacking, F. & L. Willemse (2 ♂, CW) (song recording of 1 male). S of Alepochori, 30 km N of Sparti, 500 m, 4.viii.1988, cultivated area, shade of scattered trees, F. Willemse (5 ♂, 3 ♀) (CW); Lakonia:15 km N of Sparti, 26/27.viii.1986, riverside, wet place, O. von Helversen (2 ♂, 1 ♀, alcohol vial 6/0059 in CvH); Mt. Taiyetos, Longanikos, 1 km S, 720 m, 28.vii.1991, F. & L. Willemse, near bridge, bushes and shrubs (1 ♂, 1 ♀) (CW) (song recording of 1 male); Mt. Taiyetos, Yeoryitsi, 1450 m, 28.vii.1991, F. & L. Willemse, forest clearing above the village along road turning to Langadha Pass, F. & L. Willemse (11 ♂, 3 ♀) (CW) (song recording of 1 male); Sparti-Kalamata, 1000 & 1100 & 1200 & 1300 m, 24.vii.1970, Willemse & Scherpbier (16 ♂, 10 ♀ in CW) & Langadha Pass, just W of Pass, wayside of forest road, 1500 m, 3.viii.1988, F. Willemse (15 ♂, 12 ♀, of which 1 ♂, 1 ♀ in BMNH/L & 1 ♂, 1 ♀ in ZI/P)(CW) (song recording of 8 males) & Sparti-Kalamata, Passhoehe, 4.ix.1980, Dr. Zilch (6 ♂, 4 ♀) (CvH) & Taigetos Osthang zwisschen Kalamata und Sparta, 1300 m, Kiefernwald (registration leg movements "Q") & NO-Hang, 1300 m, 25.viii.1986, O. von Helversen (5 ♂, 2 ♀, alcohol vial 6/0066 & 6/0178 in CvH); 12 km W of Sparti, 1000-1300 m, 1.x.1962, Ent. Exc. Zool. Mus. Amsterdam (2 ♂, 2 ♀) (CW); Polidrosos (or Tzitzina) (NE of Sparti), near bridge & forest clearings 2 & 3 & 5 km W, 950-1000 m, 31.vii.1991, F.& L. Willemse (27 ♂, 14 ♀) (CW) (song recording of 7 males); Parnon Gebirge, *Abies* Wald oberhalb Vamvakou, 1300 m, 26.viii.1986, O. von Helversen (12 ♂, 1 ♀, alcohol vial 6/0051 & 6/0165) (CvH) (registration leg movements "AI"); A. Anaryiroi (3 km S) (SE Sparta), 300 m, 30.vii.1991, F. & L. Willemse (1♂, 1 ♀) (CW) (song recording of 2 males).

Based on morphology and song the populations listed here could not properly be identified. Habitus (figs 68-71) and biometrics do not agree with any of the typical forms of either *pulloides*, *moreanus*, *crassiceps* or *parnon* but are intermediate (figs 221-222, table 19). The fore wings are shortened, not as much as in *pulloides* but shorter than in typical forms of the other three taxa. The apical part of the male fore wing (figs 133-138) is strongly reduced but not as much as in *pulloides* that has the apical margin evenly and broadly rounded. The song does not agree with either one of these four taxa. Populations with such transitional morphological and bioacoustical characteristics are found across a wide area connecting the range of *moreanus* with that of the *pulloides* complex (localities indicated as X in fig. 268). While a few refer to intermediate forms between *pulloides* and *crassiceps* and/or *parnon* (localities 44-45, 66 in fig. 269), the majority shows a *pulloides*-like structure (molloid) in combination with *moreanus*-like elements (biguttuloid). Among the large number of the latter observations illustrating this situation in various degrees, two examples are presented, one from the northwestern and one from the southeastern part of the Peloponnese (figs 258-259, localities 36 & 68 in fig. 269 respectively).

Apart from the intermediate morphology, the song in both populations shows a mixture of biguttuloid and molloid elements. There is a tendency to produce echemes at the rate of 2-4/s but these echemes consist both of biguttuloid and molloid leg movements without clear prevalence of either of the two. Also inter-echemic intervals throughout the song tend to be irregular, intermediate or almost absent, neither agreeing with *pulloides* nor *moreanus*.

Discussion.— There is no doubt that a comparatively large area of the Peloponnese adjacent to the ranges of *moreanus* and the *pulloides-crassiceps* complex (fig. 268: localities indicated with X) is inhabited by populations that morphologically are intermediate between these species (figs 221-222, table 19) producing songs which lack a well recognisable structure. Such songs both contain the biguttuloid elements of *moreanus* with short inter-echemic intervals and the molloid elements of *pulloides* and *crassiceps* with longer inter-echemic intervals. For us they constitute non-identifiable intermediate forms and are considered transitional populations bridging two different taxa.

It should be noticed that we are dealing with natural populations, not with incidental individual variability, to say most if not all individuals of such populations presenting intermediate characters, though in various degrees. It would be most interesting to test and compare the preference of females of such transitional populations as well as that of the females of populations of typical *moreanus* and *pulloides* for the male songs of both of these intermediate populations as well as the songs of typical *moreanus* and *pulloides*.

Conclusions

Gomphocerinae in general and *Chorthippus* in particular are a group of grasshopper species that morphologically resemble each other closely. Their taxonomy has always been considered difficult, resulting into much instability of nomenclature. Among this group of insects the song is known to be the most important means of mate recognition and reproductive isolation. This paper is a fine example how traditional classification based on morphology, has benefitted enormously from the inclusion of non-morphological characters. Bioacoustic data proved to be a very reliable guide for identification.

Historical review

Some two decades ago, based on traditional morphology, ten taxa of *Chorthippus* with angled lateral pronotal keels were recognized from Greece (Willemse, 1984). Since then the situation has changed dramatically, as in this publication only 4 out of the 10 names have remained unchanged. For convenience of the reader, the previously used names (Willemse, 1984; partly 1985 & 1986) are presented here with reference to their current names (this publication).

brunneus: absent in Greece, replaced by *bornhalmi*;

biguttulus hedickei: absent in Greece, replaced by *biguttulus euhedickei*;

mollis mollis: all Peloponnesean records refer to *vagans dissimilis* subspec.nov.;

lesinensis: now classified as *mollis lesinensis* stat.nov. and restricted to the typical form from Dalmatia; Greek records of this taxon have been arranged under nominate *mollis* and partly under *biguttulus parnassicus* subspec. nov.;

sp. affine *lesinensis* refers probably partly to *vagans dissimilis* and *bornhalmi*;

crassiceps: now treated partly as *pulloides-crassiceps* (*parnon* spec. nov.) complex and *moreanus* spec. nov., including transitional forms between these taxa;

pulloides: now treated as *pulloides-crassiceps* complex including both typical and atypical forms of both taxa;

willemsei, *biroi*, *sangiorgii* and *apricarius* remained unchanged.

Actual review

A preliminary classification is proposed for *Chorthippus* members with angled pronotal lateral keels occurring in Greece. Thirteen taxa are recognized, the ranking of some still being uncertain. Data on song, morphology, ecology and distribution are given.

Most species are more or less well defined, both morphologically and by their songs.

Chorthippus brunneus has not yet been recorded for Greece but is replaced by *bornhalmi*, the most common species, occurring throughout the whole of Greece, from sea level up to far above the timberline.

The occurrence of *vagans* in Greece has been confirmed. The species occurs scattered all over Greece but in a morphological atypical form described in this paper as *vagans dissimilis* (figs 224-225), lacking the key characters of nominate *vagans* and liable to be mistaken for other species, particularly *mollis* and *bornhalmi*. The song of the endemic taxon *C. cypriotus* is described here for the first time (fig. 223) and resembles that of *vagans*. As its morphology also resembles *vagans dissimilis*, the taxon has been arranged as another subspecies of *vagans*, *vagans cypriotus* stat. nov. Based on morphological and previously unknown bioacoustic data (figs 227-231) *willemsei* and *biroi* are considered to be closely related to *vagans*. The alliance of *sangiorgii* remains uncertain (fig. 232).

In the *biguttulus*-group, *biguttulus hedickei* is replaced by *b. euhedickei*. Apart from the latter subspecies, a not yet recognized form occurs in the alpine zone of Mt. Parnassos (and possibly other high mountains). Morphologically this form is much like *mollis* rather than *b. euhedickei*. It is described as *biguttulus parnassicus*. Its song (fig. 236) differs from *b. euhedickei* and agrees broadly with that of nominate *biguttulus*. However, its morphology is distinct from both of them. At Mt. Parnassos *b. euhedickei* and *b. parnassicus* occur parapatric along a narrow zone of contact without evidence of interbreeding. The observation that both forms are closely related to *biguttulus biguttulus* and occur parapatric without obvious interbreeding, is peculiar. We gave this unknown form tentatively the state of subspecies but leave its ranking open because further research is needed to assess its relational status and degree of reproductive isolation. Another not yet described relative of *biguttulus* was detected in the district of Messinia, southern Peloponnese and is given the name of *moreanus*. Further remarks on the latter see below.

The situation around *mollis* and its closest relatives is more complicated. The song of *C. lesinensis* was unknown (figs 241-242) and proved to be very similar to that of *mollis*, particularly of *m. ignifer*. However, morphologically *lesinensis* is distinct from both nominate *mollis* and *m. ignifer* by its large and inflated head. Therefore we propose the new combination *mollis lesinensis* stat. nov., pointing out that its range is confined to the Adriatic part of Dalmatia where the specimens uniformly show their widely inflated head. The taxon *mollis pechevi*, described by Karaman from Bulgaria, has been studied and a lectotype has been selected. Its song is unknown but based on its morphology most probably resembles nominate *mollis*. The *mollis* specimens from Greece have no or an only slightly inflated head, differing in that respect from *m. lesinensis* and are no longer identified as such. Although *mollis* populations in Greece vary a bit from slender forms in the northern lowlands to a smaller more thickset form inhabiting mountain habitats, all of them are arranged under nominate *mollis*. Furthermore it has become evident that *m. mollis* does occur across mainland Greece but is definitely absent from the Peloponnese. Typical *pulloides*, another *mollis* relative, in the past only known from the Peloponnese, also inhabits the Greek mainland where it may live syntopic with *m. mollis*.

While the classification of this group of grasshoppers in the mainland of Greece and most of its islands has become more or less clear, the situation in the Peloponnese is rather complicated. Apart from the well recognisable species *bornhalmi*, *vagans dissimilis* and *willemsei*, four additional taxa occur in this part of Greece, the two already known *crassiceps* and *pulloides* but also two as yet undescribed species *parnon* and *moreanus*. The typical forms of these four taxa in the Peloponnese have comparatively small ranges that do not overlap each other. Syntopical occurrence has not been observed (fig. 268). The typical forms are well distinct from each other, either by morphology, song or both. While the bioacoustics of *crassiceps*, *parnon* and *pulloides* (figs 243-251) indicate a close relation to *mollis*, *moreanus* is related to *biguttulus*, shown by its typical leg movements during song production (figs 237-238).

Song and morphology of typical *crassiceps* resemble that of *m. mollis*, particularly of *m. lesinensis*, but *crassiceps* and *m. lesinensis* appear not identical (see discussions under the respective taxa). While the typical form of *crassiceps* occurs in the extreme northeastern Peloponnese, in the extreme southeastern Peloponnese another group of populations was found (described here as *parnon*), morphologically similar to *crassiceps* but with the males producing a distinct calling song. The song of typical *crassiceps* consists of an echeme-sequence, with each echeme preceded by a "tick" as in *mollis* (figs 243-244) resembling the general structure of *mollis* but with a slower syllable repetition rate. The calling song of *parnon*, however, is a single, long echeme, sometimes interrupted but never presenting a regular echeme series as in *crassiceps* (fig. 245). Both species are closely related to each other not only because of the arbitrary morphological distinction between both taxa but also and more so because the courtship and rivalry song of *parnon* show similarities with the song of *crassiceps* (figs 246-247).

Typical *pulloides* is quite distinct from typical *crassiceps* and *parnon* because of its short wings. Its song (figs 248-251) normally consists of a short echeme-sequence, with echemes commonly not preceded by a "tick". The syllables are typically molloid, the hind legs simply moving to-and-fro, strongly reminiscent of *mollis*, *crassiceps* and *parnon*. The syllable repetition rate is similar to or slower than in *crassiceps* and *parnon* and much slower than in *mollis*.

Typical *moreanus* has relatively well developed fore wings as in typical *crassiceps* and *parnon*, but produces a completely different song (figs 237-238) in which the hind legs produce a regularly and continuously repeated pattern of a small group of syllables, commonly 3-4 of which 2-3 are of a much lower amplitude than the first main syllable. Its syllables are therefore not the result of simple to-and-fro movements as in *mollis* and its relatives but are more complicated and typically biguttuloid.

These four typical forms (*pulloides*, *crassiceps*, *parnon* and *moreanus*) are quite distinct from each other, while at the same time being separated from each other geographically. Typical *moreanus* occurs mainly in Messinia, the central part of the southern Peloponnese, typical *pulloides* in the central part of the northern Peloponnese, *crassiceps* in the extreme northeastern part and *parnon* in the extreme southeastern part of the Peloponnese (figs 268-269).

It was a great surprise to find that populations occurring throughout the remaining parts of this peninsula clinally bridge the differences between these typical forms, for instance between *crassiceps* and *pulloides*, both closely related to each other but remarkably also between *pulloides* and *moreanus*. These species are much less related to each other, comparable with the differences between *mollis* and *biguttulus*.

The typical form of *crassiceps* (figs 54-55, 114-115) is known from the island of Poros and the opposite part of extreme eastern Argolis. The *crassiceps* sing-alikes occurring in central and northern Argolis have increasingly shorter wings (fig. 117) and those in adjacent northern Korinthia and extreme western Argolis even more so (figs 56-57, 118) approaching the wing length of typical *pulloides* which occurs more west (figs 60-61, 121-124). Likewise the bioacoustics of populations from northern Korinthia and extreme western Argolis do not exactly match the bioacoustics from populations from Poros and the extreme eastern Argolis, for instance the pre-echemic ticks are less well produced, all in all, wiping out the delimitation between typical *crassiceps* (figs 242-243) and *pulloides* (fig. 248). Therefore both taxa are treated here as the *pulloides-crassiceps* complex.

Whether the same happens between the typical forms of *crassiceps* and *parnon* in southern Arkadhia and eastern Lakonia is, though probable, not yet sufficiently known. Further observations are needed.

The bridging between *pulloides* and *moreanus* is even more conspicuous (table 19). The last species, with its typical song (figs 237-238), shows a remarkable clinal variation along the periphery of its range, sometimes mainly in morphology, sometimes mainly in bioacoustics or sometimes in both. For instance the song of a morphologically typical *moreanus* population (Petralona, not far to the west of the type-locality) differs from a typical *moreanus* song in being hesitating and tending to be split into an echeme-sequence, a key character of *pulloides* (fig. 256). On the other hand, the morphology of many populations changes gradually from typical *moreanus* to *pulloides* by becoming smaller in size but particularly by a shortening of the fore wings (figs 105-107). These atypical populations occur all around the northern and eastern borders of the *moreanus* range and produce songs with a less well-organized pattern, sometimes showing a tendency to be split into echeme-sequences of longer echemes, like in *pulloides-crassiceps* (figs 256-257).

Among *pulloides* populations similar observations were made. All populations throughout the northwestern Peloponnese present a song broadly similar to that of typical *pulloides* but registration of the leg movements show clearly that these partly are not molloid but biguttuloid as in *moreanus* (figs 16, 253). An interesting case was observed in the southeastern part of the Peloponnese, in the southern part of Mt. Taiyetos with its highest summit, named Prof. Ilias (2404 m). In this area both *moreanus* and *pulloides* occur. While the first (*moreanus*) is found from the lowlands across the forested slopes up to the timberline (up to 1600 m), the *pulloides*-like population lives exclusively above the timberline up to the summit (1600-2404 m). This *pulloides*-like population agrees morphologically more or less with typical *pulloides*, though the apex of the fore wing is not so broadly rounded as in the typical form (figs 121-124) but slightly attenuate (figs 129-130). The song of this population (figs 254-255) is also slightly different, presenting some biguttuloid elements of *moreanus*, similar to those of the northwestern Peloponnese. Based on the overall agreement with the typical *pulloides*, we classified this population under *pulloides*, as we also did with the populations from the northwestern Peloponnese but all of them as atypical forms. At the timberline of Mt. Taiyetos *moreanus* and *pulloides* live along a narrow parapatric zone where syntopic occurrence or hybridisation were not observed. Apparently both taxa behave at this locality as reproductively isolated species.

While most of the atypical forms of either *pulloides* or *moreanus* confidently could be arranged by their overall agreement with one of them, there are a number of populations in which this is not possible. Neither their morphology, which is intermediate (figs 68-71, 133-138), nor their song, without a clearly reproduced pattern (figs 258-259) allows recognition of either species. This type of populations has been observed in relatively large areas, located all along the zones of contact between the various taxa. The largest area covers the northern and eastern slopes of Mt. Taiyetos extending through the valley of the Evrotas River to the east into the western slopes of the range of Mt. Parnon (figs 268-269).

Having compared the song and morphology of our material with publications on hybrids specifically in the *biguttulus*-group (*e.g.* D. & O. von Helversen, 1975; Ragge, 1984; Ingrisch 1995), we are of the opinion that these transitional populations belong to natural so-called hybrid populations. Such populations occur in the contact zone (hybrid zone) of the ranges of their nominate parental forms and result from genetic introgression of genetically distinct but reproductively not yet completely isolated forms. In this case we are apparently dealing with two different alliances: a close one inside the molloid complex of *pulloides* and referring to the gradual transition of *crassiceps* (and possibly *parnon*) to *pulloides* and secondly and more remarkably, an alliance between less closely related taxa, *pulloides* and *moreanus* (read molloid against biguttuloid ancestry).

In connection with these observations, the question arises as to the taxonomic ranking of the *mollis* related taxa *pulloides*, *crassiceps*, *parnon* and the *biguttulus* related taxon *moreanus*. Because *pulloides* in mainland Greece occurs syntopic with *m. mollis* its specific ranking appears justified. Though the treatment of *crassiceps* and *parnon* as separate species appears justified, their taxonomic status against *pulloides*, is to be considered provisional. However, the large difference between the *biguttulus* related taxon *moreanus* and the *mollis* related taxa of the *pulloides* complex may justify the specific status of the former, regardless of the presence of hybrid populations in a relatively wide hybrid zone. This concept is also underlined by the observation in Mt. Taiyetos where both taxa live narrowly parapatric without evidence of widely distributed hybridization.

The data presented in this paper are intended to start a more comprehensive research including a.o. further behavioural and molecular analysis, to disentangle the degree of divergence and speciation for a better understanding of this taxonomic and evolutionary puzzle in Greece, particularly in the Peloponnese. It is noticed that the present day distribution of some other taxa including mainland Greece, appears quite interesting from a biogeographic point of view (a.o. *biguttulus* complex).

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Appendix 1. Songs

Figs 223-259, 223-241, 243-254, 256-259. Synchronous registrations of the movements of left and right hind leg (both upper tracks) and the oscillogram (lower track) of males of *Chorthippus* species. Numbers indicate the time scale (seconds), lower parts are details of upper tracks but faster. Figs 242 and 255 oscillograms without registration of leg movements.

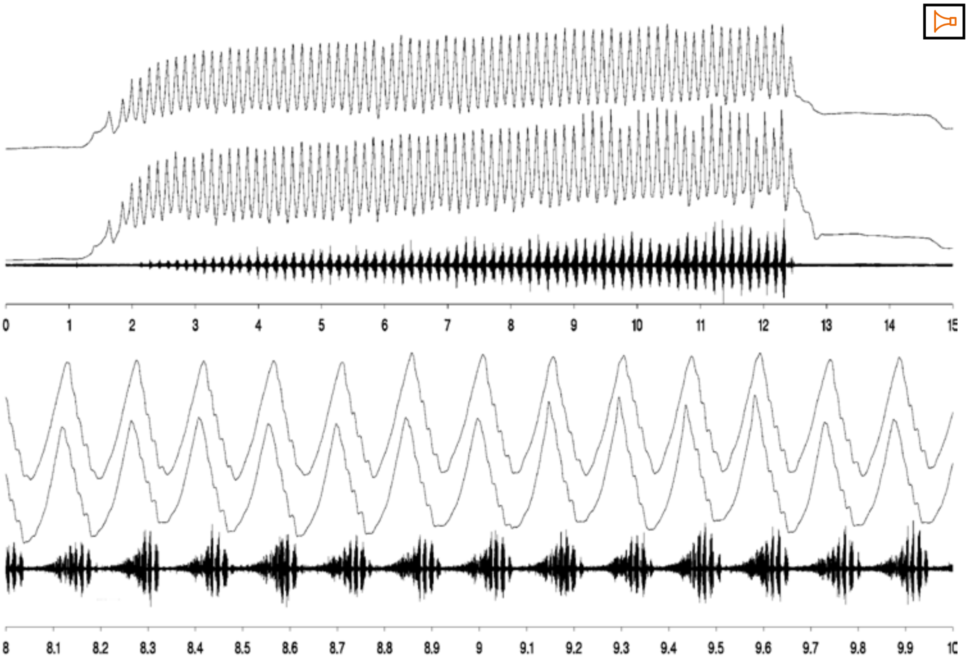

Fig. 223. *Chorthippus vagans africanus,* Tunesia, Teboursouk, ix.1997, leg. D. Dachlauer, 31°C; calling song (registration L), CD1.

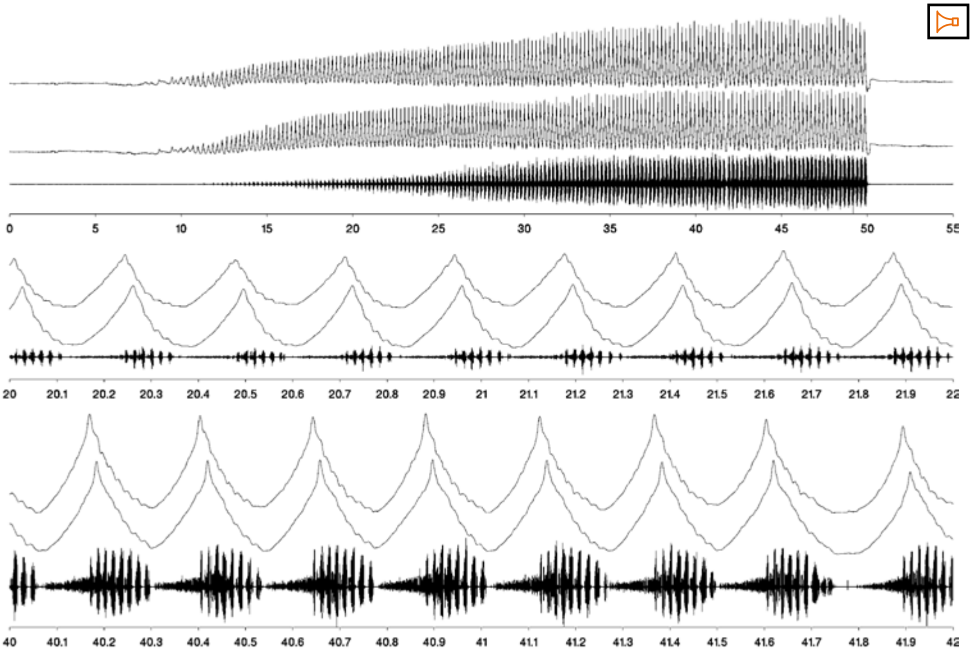

Fig. 224. *Chorthippus vagans dissimilis*, Greece, Akhaia, Megaspilea, viii.1986, leg. O. von Helversen, 31°C; calling song (registration K), CD2.

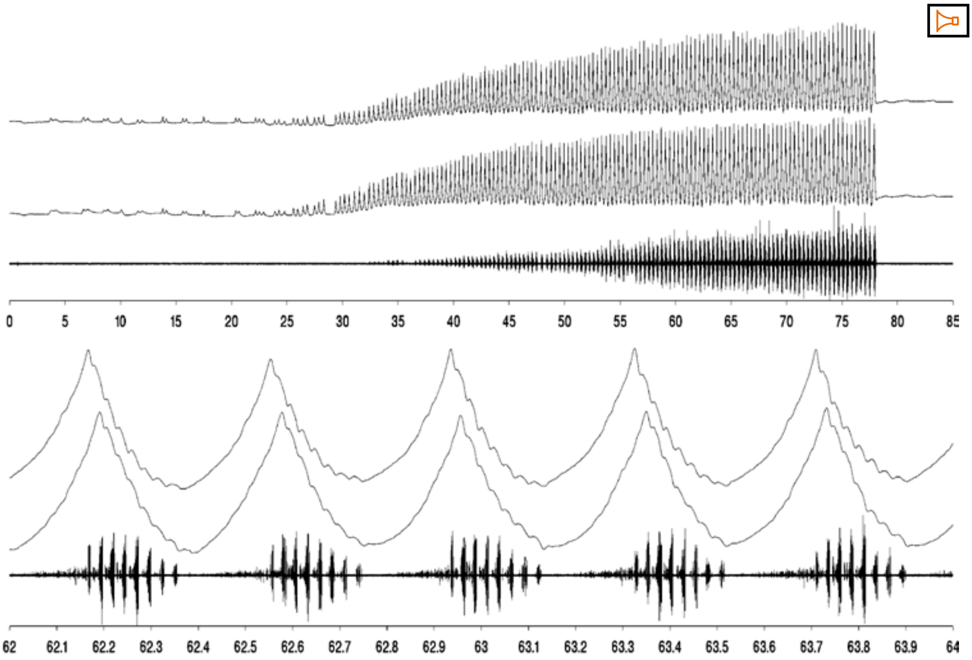

Fig. 225. *Chorthippus vagans dissimilis*, Greece, Thrakian Is., Samothraki, 1982, leg. Zilch, 25°C, courtship song (registration 18), CD3.

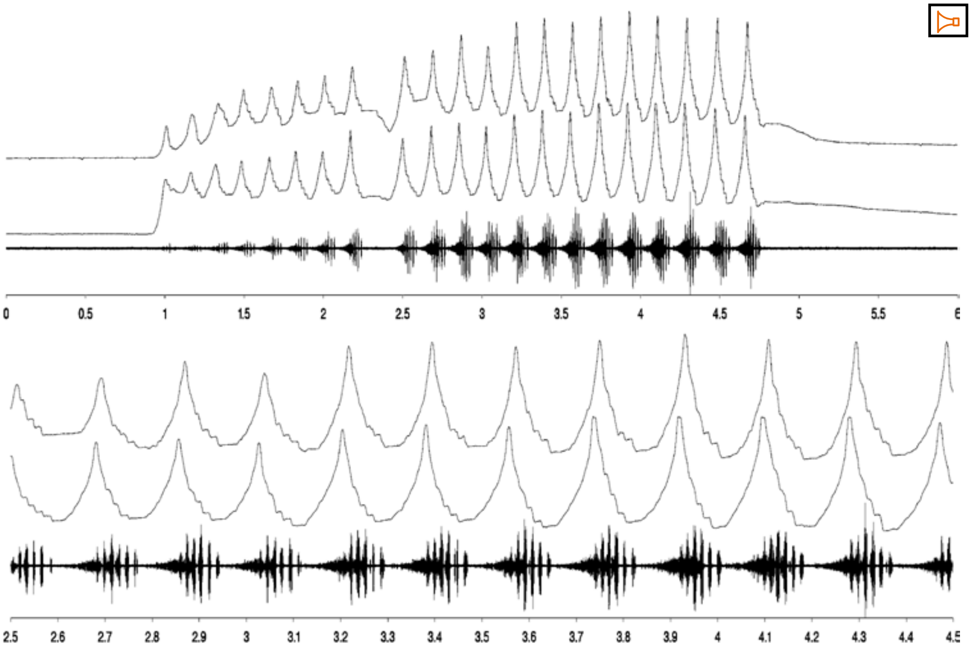

Fig. 226. *Chorthippus vagans cypriotus* (topotype), Cyprus, Troodos, Mt. Olimbos above 1600 m, 21. viii.1996, leg. H. Kriegbaum, 31°C, calling song (registration M), CD4.

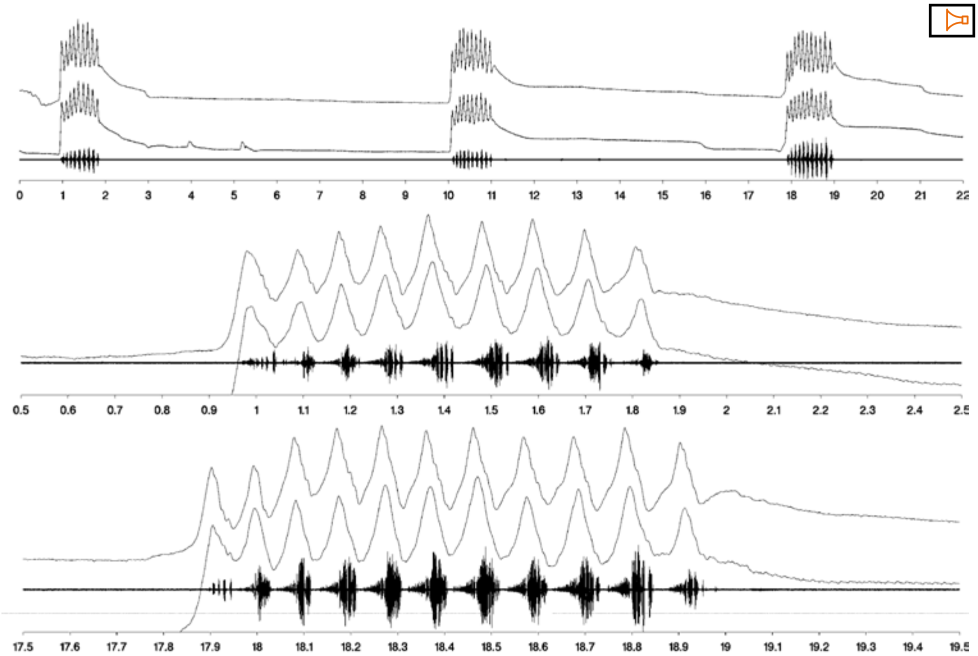

Fig. 227. *Chorthippus willemsei*, Greece, Fthiotis, Mt. Oiti, 18.viii.1981, leg. O. von Helversen, 28-30°C, calling song (registration G), CD5.

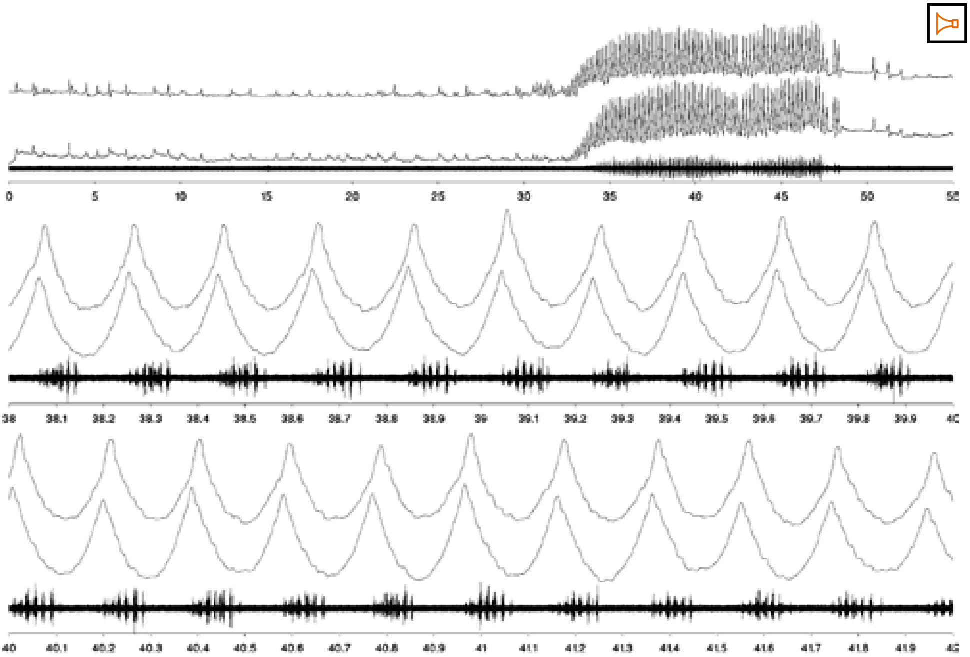

Fig. 228. *Chorthippus willemsei,* Greece, Fthiotis, Mt. Oiti, 18.viii,1981, leg. O. von Helversen, 28-30°C, courtship song (registration I), CD6.

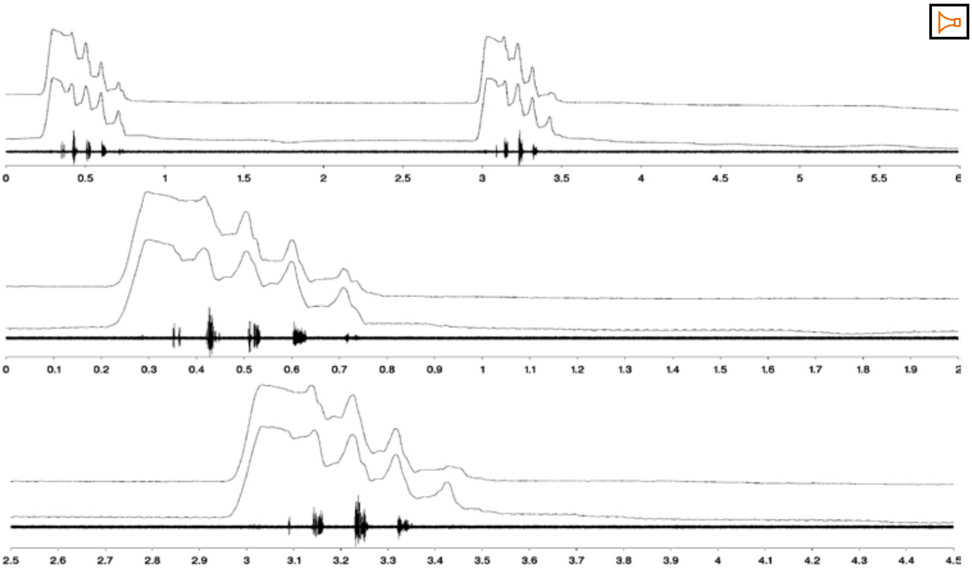

Fig. 229. *Chorthippus willemsei*, Greece, Fthiotis, Mt. Oiti, 18.viii.1981, leg. O. von Helversen, 28-30°C, rivalry song (registration J), CD7.

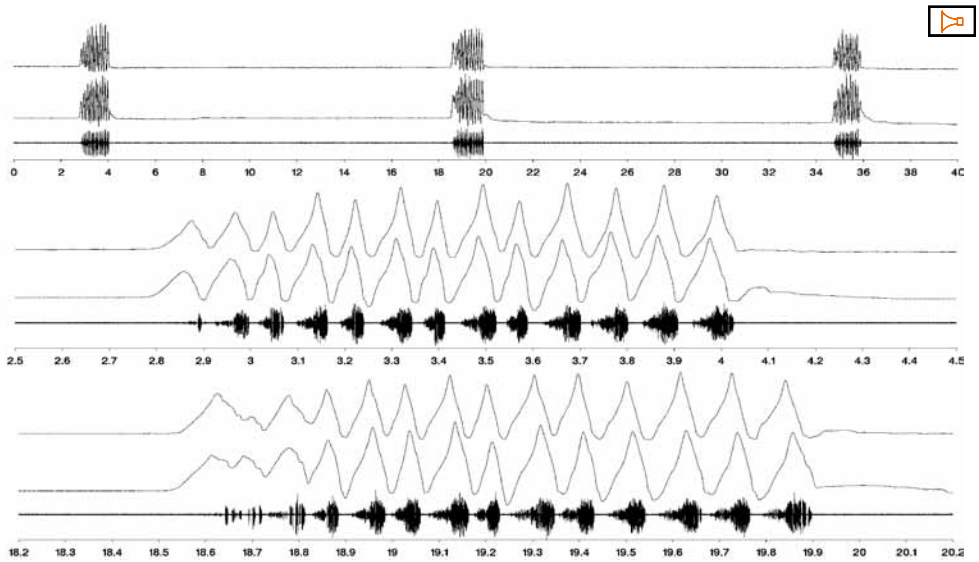

Fig. 230. *Chorthippus biroi*, Greece, Kriti, Rethimni, Mt. Idi, Zominthos, 12.ix.1999, leg. O. von Helversen, 31°C, just after removing female, calling song (registration 47), CD8.

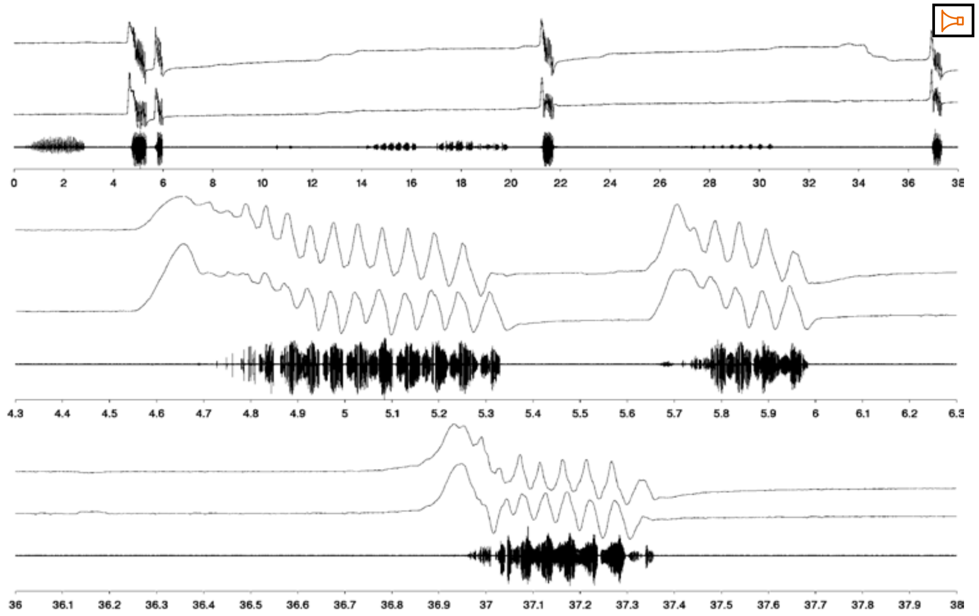

Fig. 231. *Chorthippus biroi* (topotype), Greece, Kriti, Chania, Omalos, viii.1989, leg. R. von Helversen, 33°C, rivalry song (registration 48), CD9.

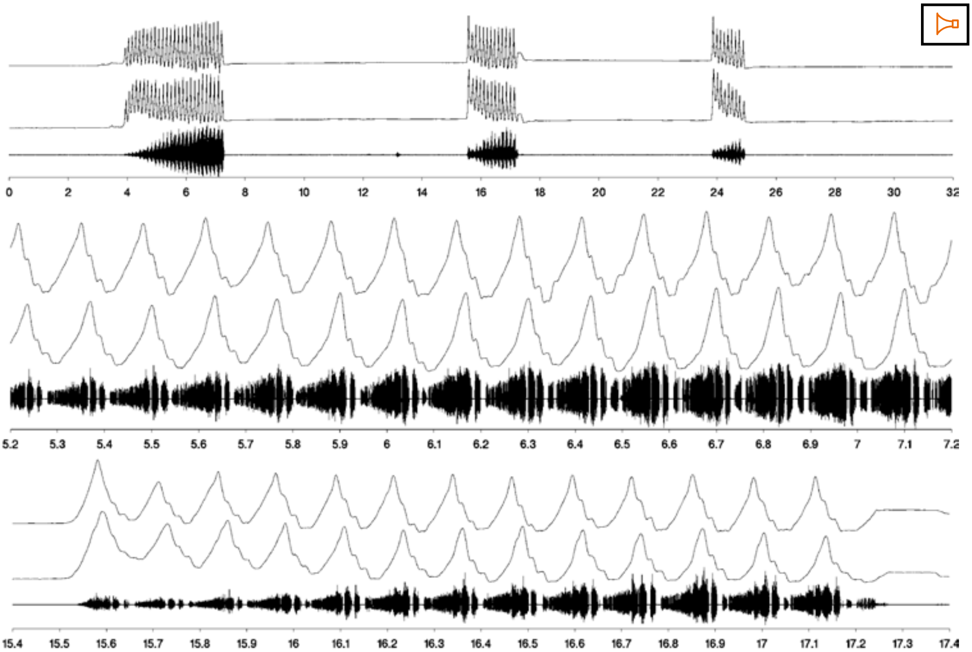

Fig. 232. *Chorthippus bornhalmi*, Greece, Vracha, North of Karpenision, 15.vi.1981, leg. O. von Helversen, temp. unknown, calling song (registration A), CD10.

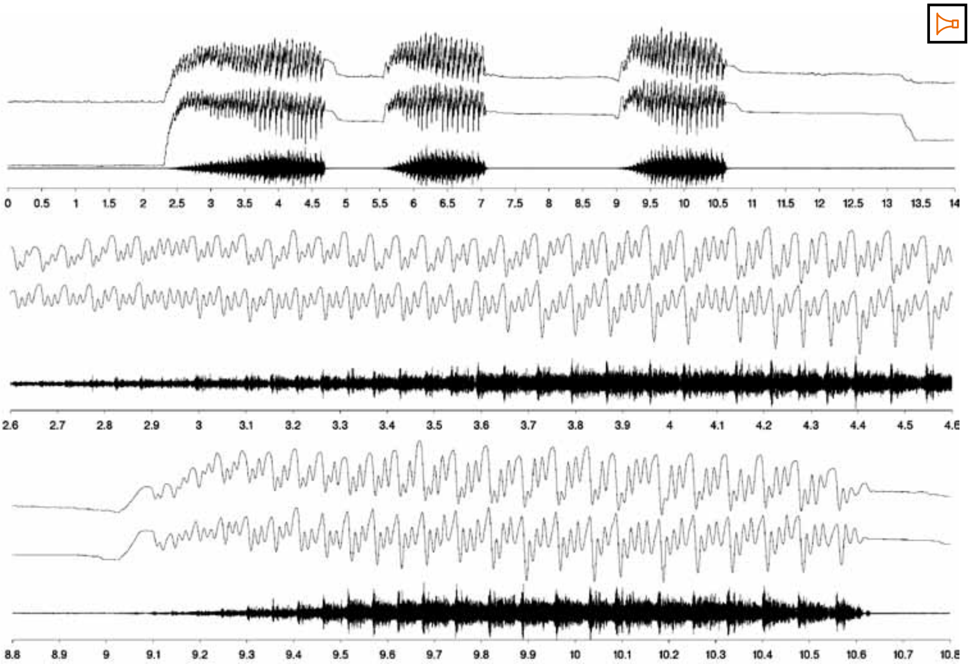

Fig. 233. *Chorthippus biguttulus biguttulus*, Germany, Seewiesen, 12.vi.2002, leg. B. Gottsberger, 30°C, calling song (registration AM), CD11.

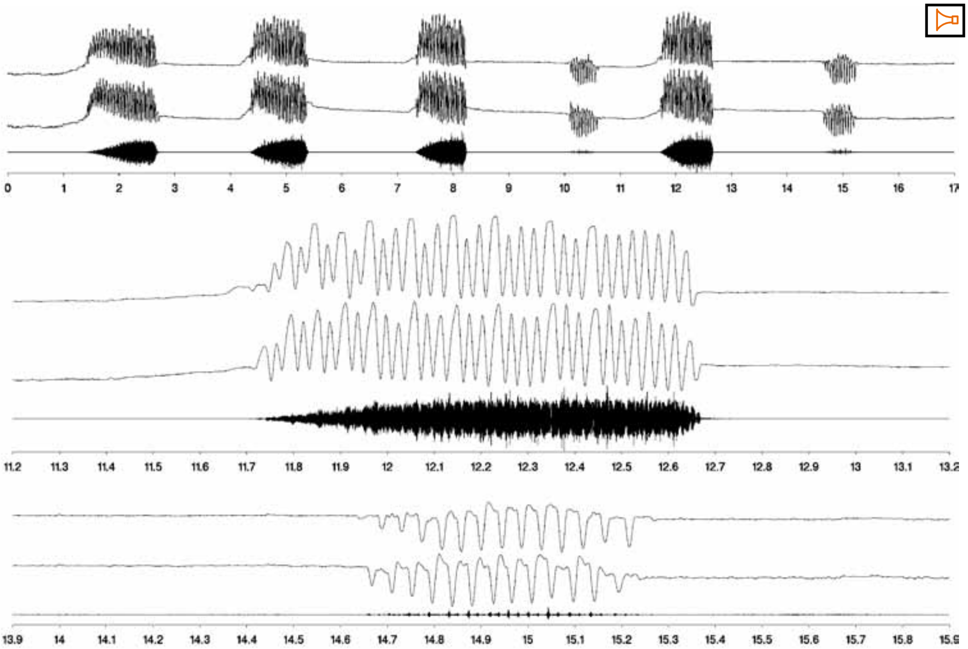

Fig. 234. *Chorthippus biguttulus euhedickei* (topotype), Greece, Drama, Mt. Pangaion, 1700 m, 9.ix.2001, leg. O. von Helversen, 32°C, courtship song (registration AN), CD12.

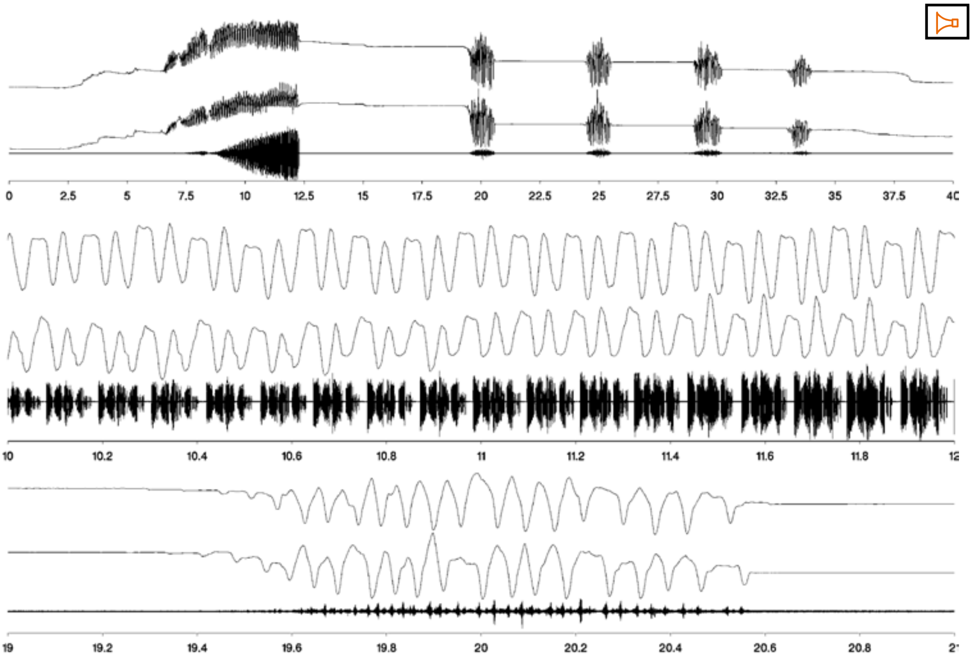

Fig. 235. *Chorthippus biguttulus euhedickei*, Greece, Drama, Mt. Falakron, 29.viii.1997, leg. O. von Helversen, 29°C, calling song (one fore wing removed) (registration 8), CD13.

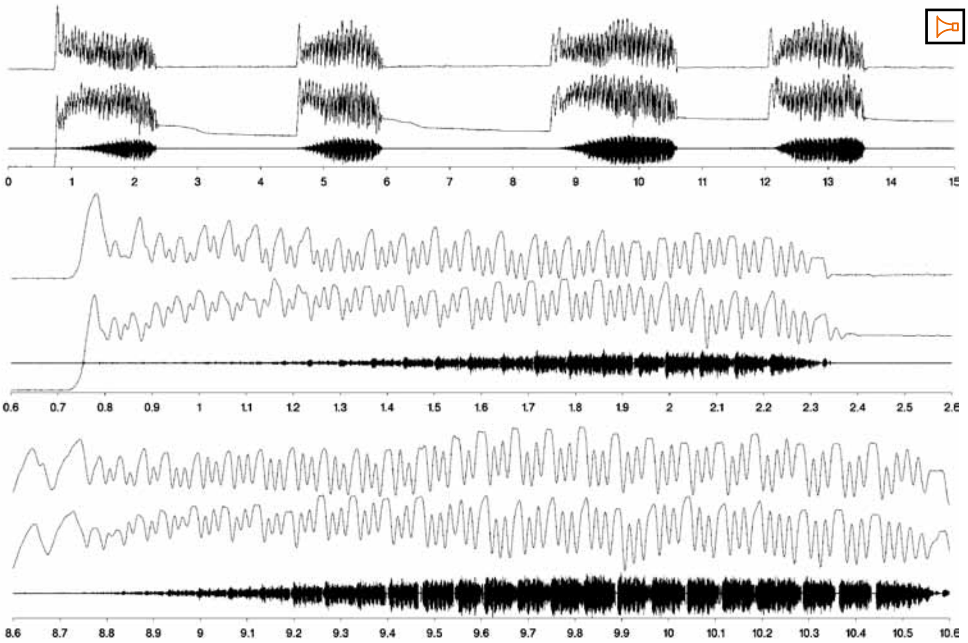

Fig. 236. *Chorthippus biguttulus parnassicus* (topoparatype), Greece, Voiotia, Mt. Parnassos, 1700-1750 m, 9-10.viii.1988, leg. F. Willemse, 35°C, calling song (registration D), CD14.

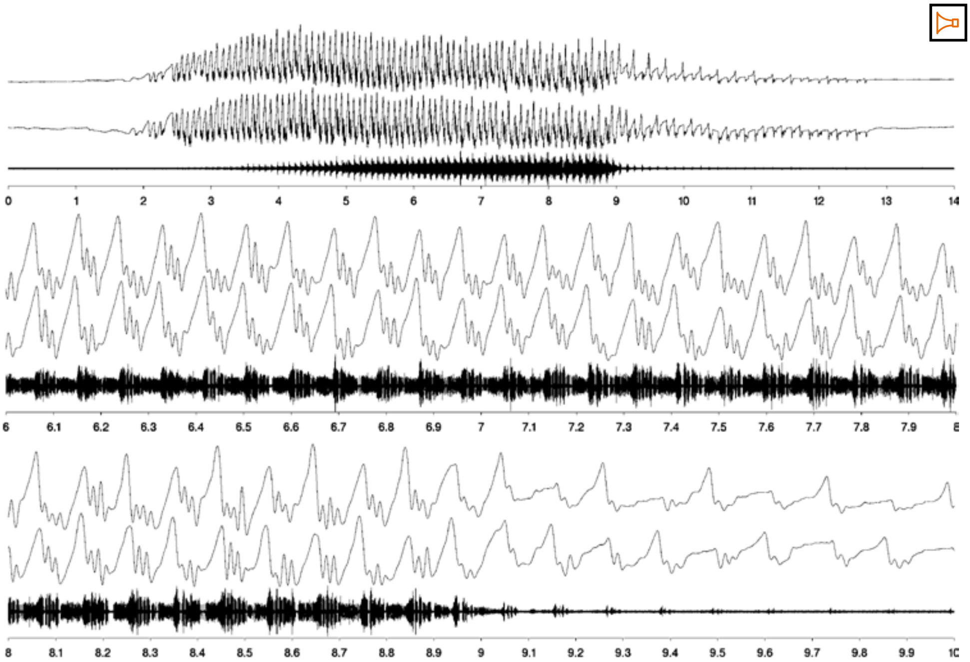

Fig. 237. *Chorthippus moreanus* (topoparatype), Greece, Peloponnisos, Ilia, Bassae, 1995, leg. O. von Helversen, temp. unknown, calling song (registration 1), CD15.

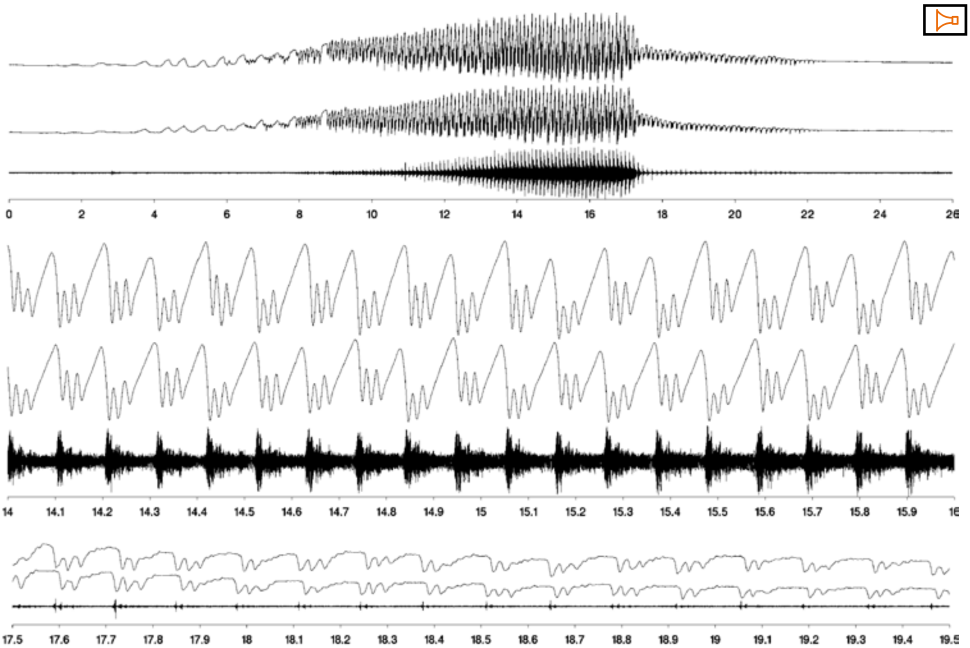

Fig. 238. *Chorthippus moreanus* (topoparatype), Greece, Peloponnisos, Ilia, Bassae, viii.1986, leg. O. von Helversen, 30°C, courtship song (registration N), CD16.

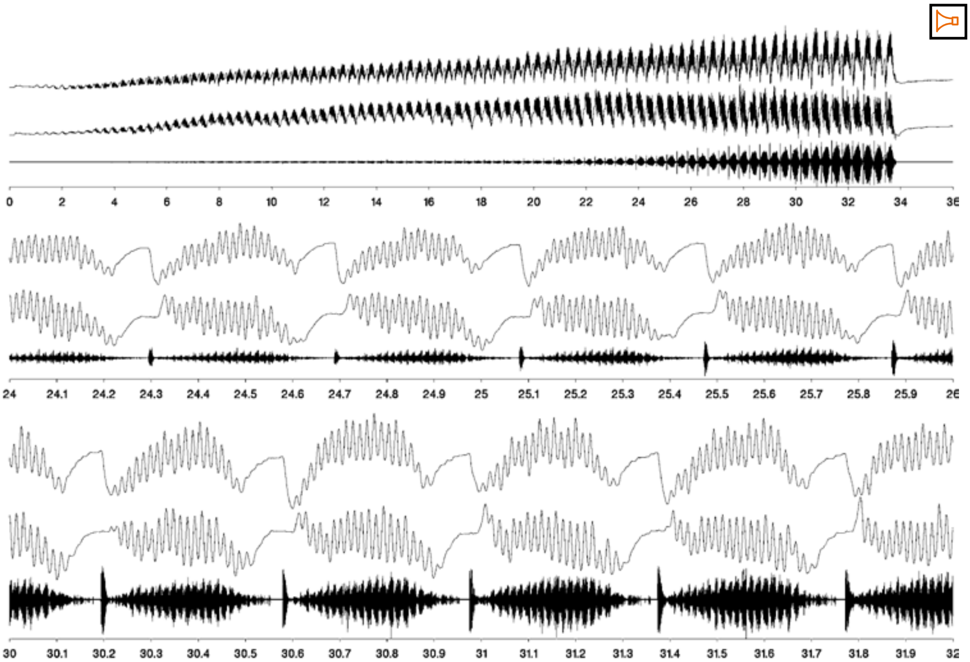

Fig. 239. *Chorthippus mollis mollis*, Greece, Ioannina, Lakmos, above Kalarrites, 31.viii.2004, leg. O. von Helversen, 32°C, calling song (registration 30), CD17.

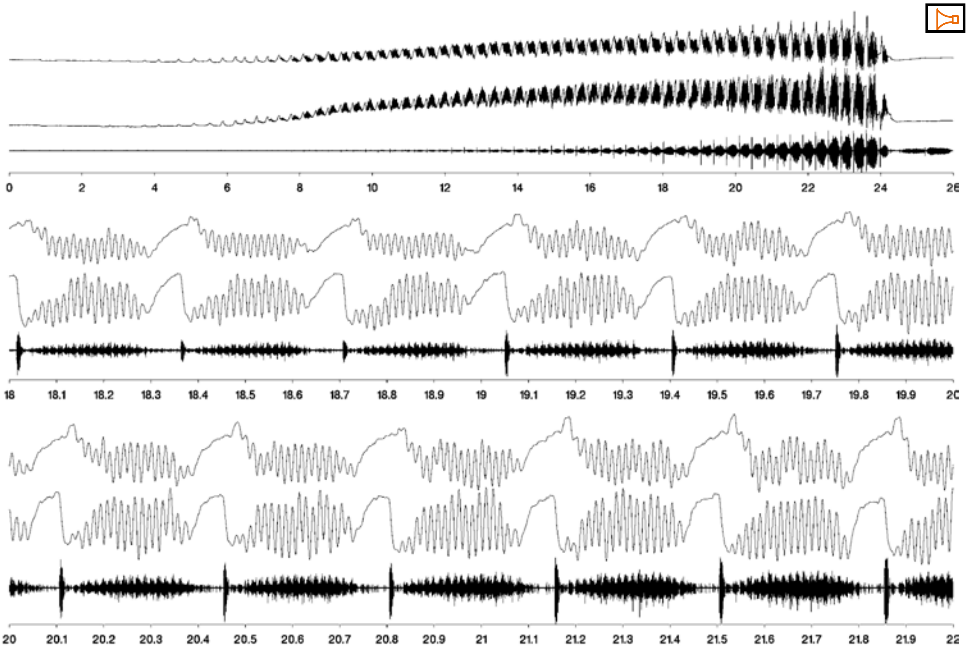

Fig. 240. *Chorthippus mollis mollis*, Greece, Aitolia-Akarnania, Mt. Akarnanika, 970 m, 18.viii.1990, leg. O. von Helversen, 31°C, calling song (registration F), CD18.

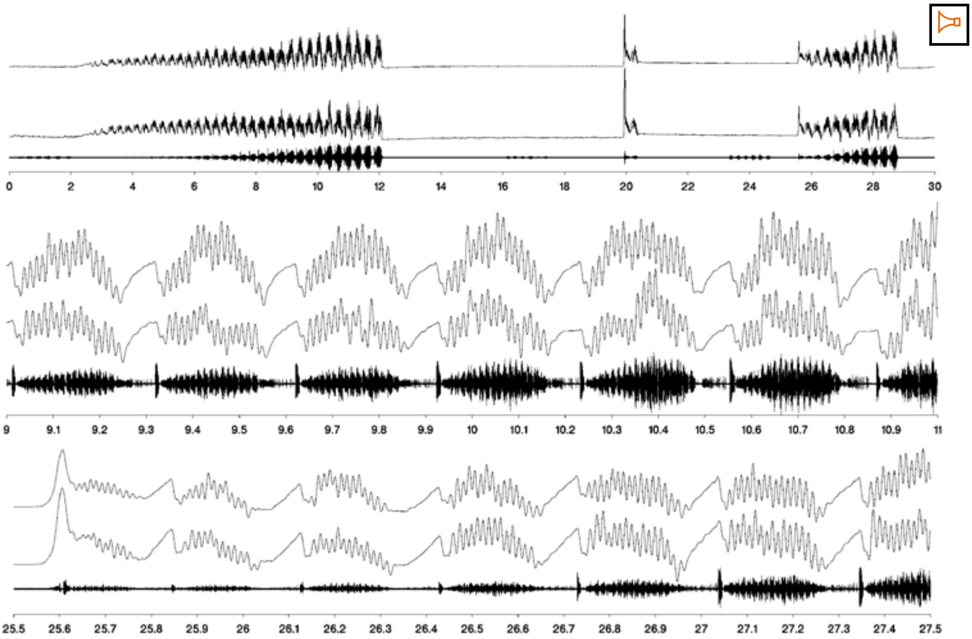

Fig. 241. *Chorthippus mollis lesinensis*, Montenegro, Insel Lovcen, 1999, leg. unknown, 37°C, calling song (left part of upper & middle track) and rivalry song (right part of upper and lower track) (registration 6), CD19.

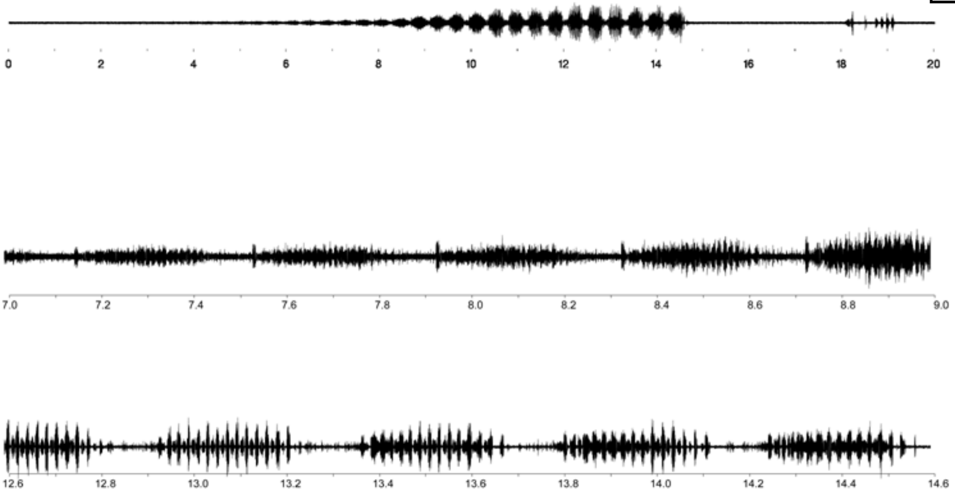

Fig. 242. *Chorthippus mollis lesinensis* (topotype), Croatia, Hvar I., Pitve, 13.viii.1996, leg. and rec. R. Kleukers, 26°C, courtship song without registration of leg movement (oscillograms of DCC recording (DCC 1996-4b: 80.58-89.32), CD20.

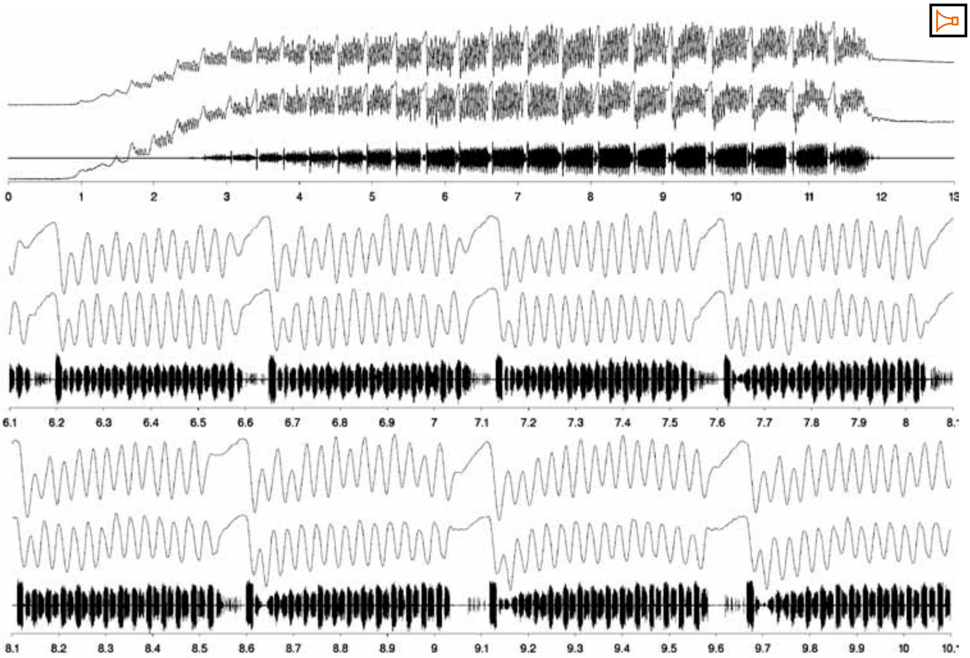

Fig. 243. *Chorthippus crassiceps* (topotype), Greece, Argolis, Poros, 9.viii.1979, leg. W. Elegast, temp. unknown, calling song (one fore wing removed) (registration U), CD21.

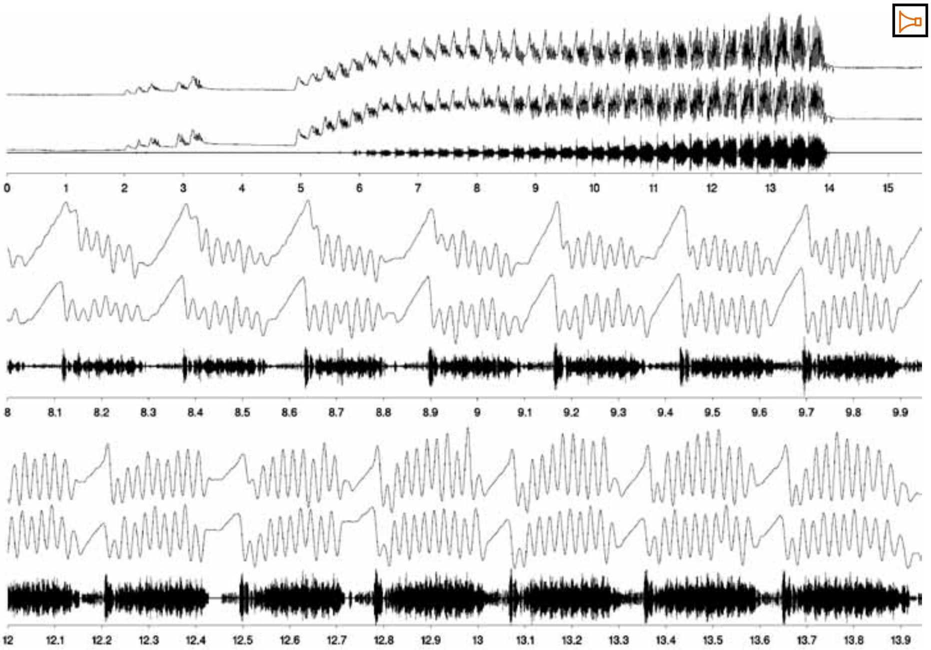

Fig. 244. *Chorthippus crassiceps*, morphologically atypical, Greece, Argolis, Arachneio Mts., Limnes-Ayionori, 600 m, 2.viii.1991, leg. F. Willemse, 32°C, calling song (registration W), CD22.

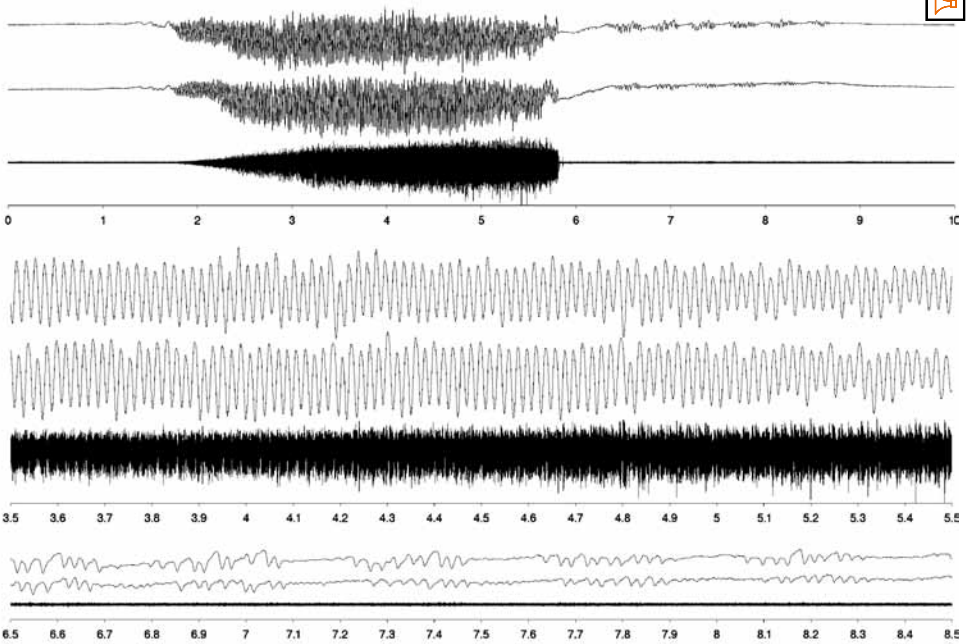

Fig. 245. *Chorthippus parnon*, Greece, Arkadhia, Prastos, 22.viii.1990, leg. O. von Helversen, 31°C, calling song (registration S), CD23.

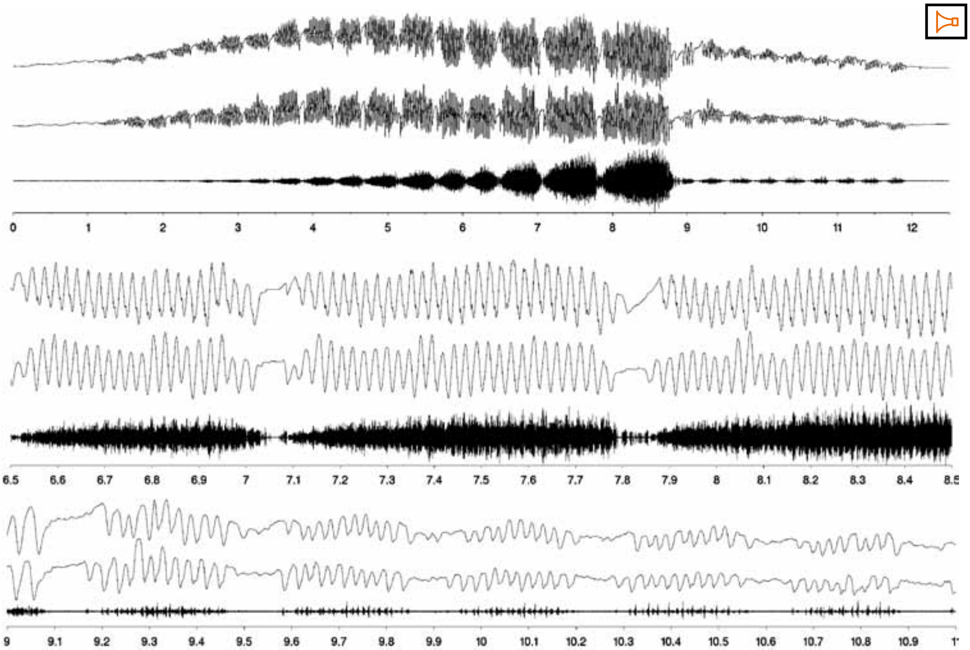

Fig. 246. *Chorthippus parnon*, Greece, Arkadhia, Mt. Parnon, A.Vassilios, 24.viii.1998, leg. F. Mayer, 34°C, courtship song (registration 25), CD24.

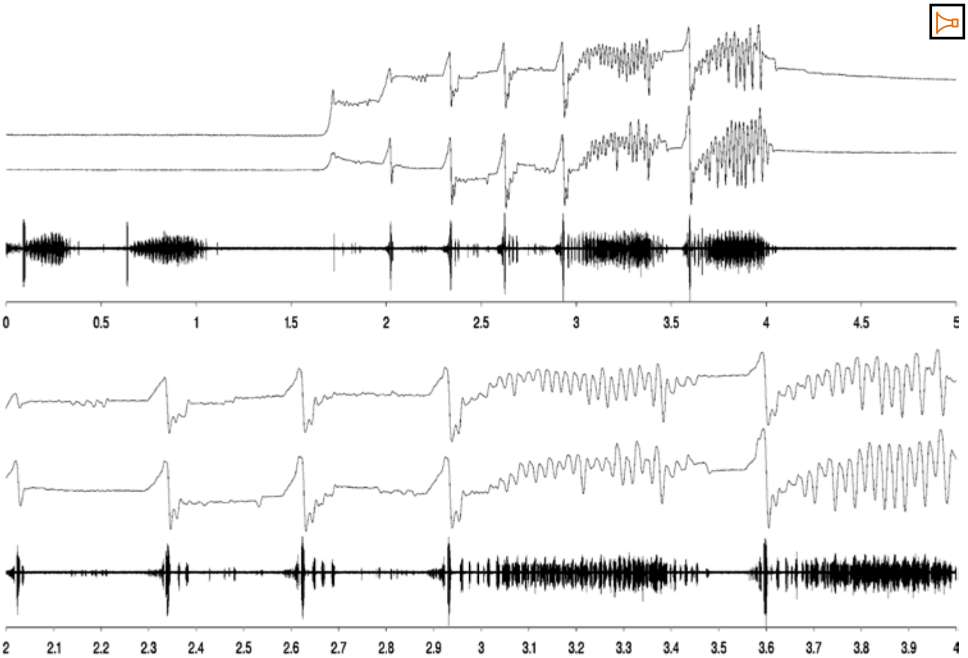

Fig. 247. *Chorthippus parnon*, Greece, Arkadhia, Prastos, 22.viii.1990, leg. O. von Helversen, 31.5°C, rivalry song (registration R), CD25.

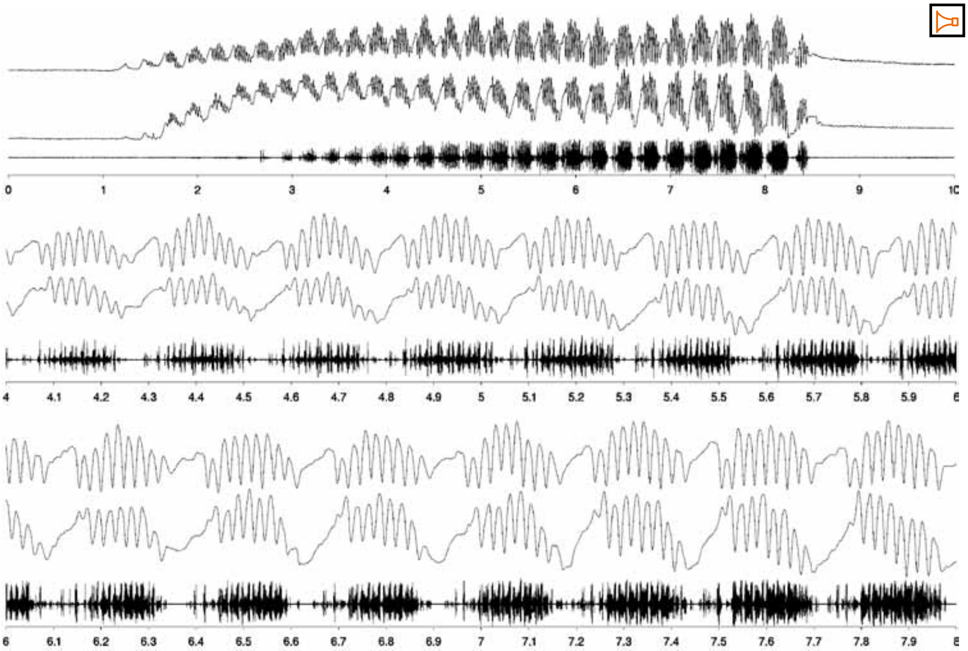

Fig. 248. *Chorthippus pulloides*, Greece, Arkadhia, Mt. Mainalon, 20.viii.1990, leg. O. von Helversen, 36°C, calling song (registration AC), CD26.

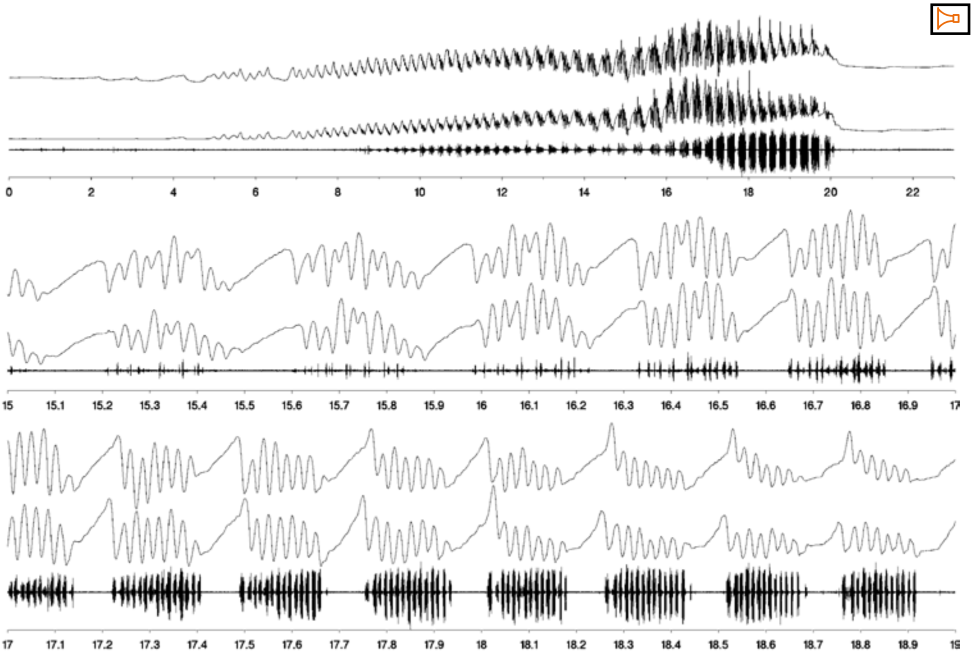

Fig. 249. *Chorthippus pulloides*, morphologically atypical, Greece, Aitolia-Akarnania, Mt.Akarnanika, 970 m, 18.viii.1990, leg. O. von Helversen, 31°C, calling song (registration AF), CD27.

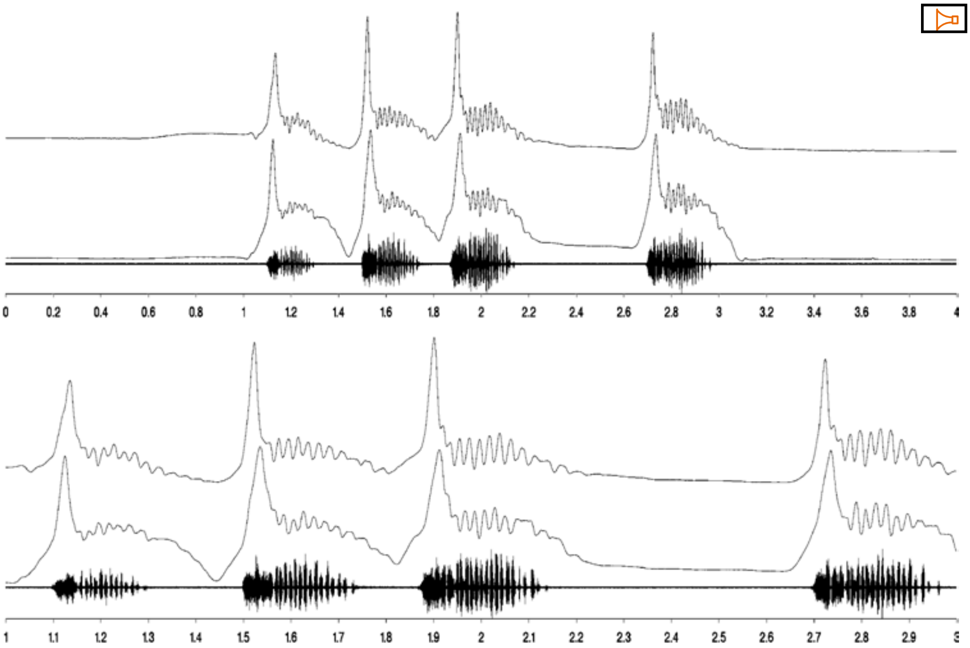

Fig. 250. *Chorthippus pulloides*, Greece, Ioannina, Mt. Lakmos above Kalarrites, 31.viii.2004, leg. O. von Helversen, 33°C, just after removing female, calling song (registration 40), CD28.

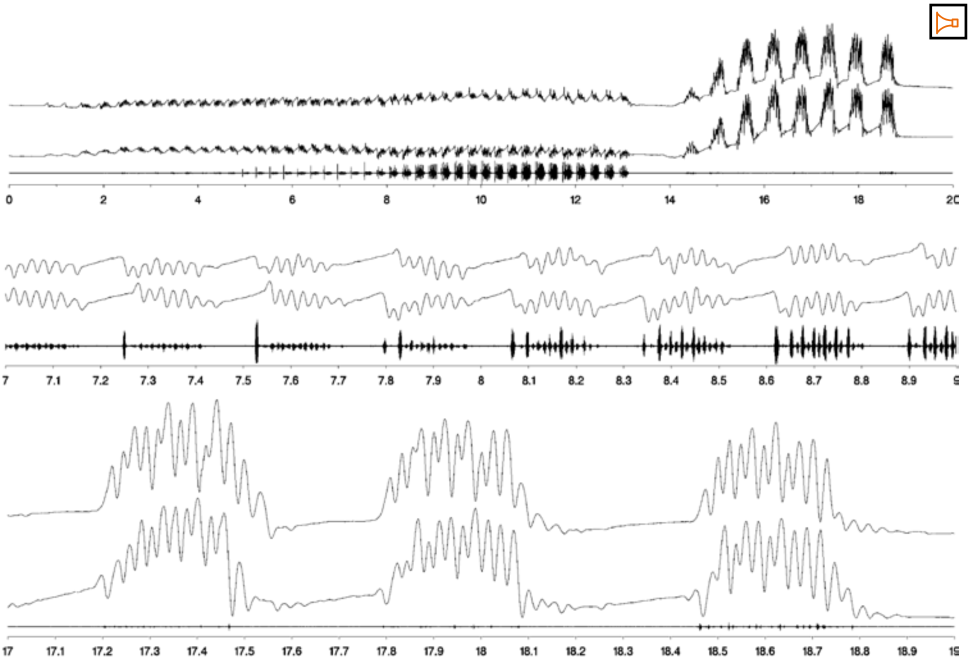

Fig. 251. *Chorthippus pulloides*, Greece, Ioannina, Mt. Lakmos, above Kalarrites, 31.viii.2004, leg. O. von Helversen, 33°C, courtship song (registration 43), CD29.

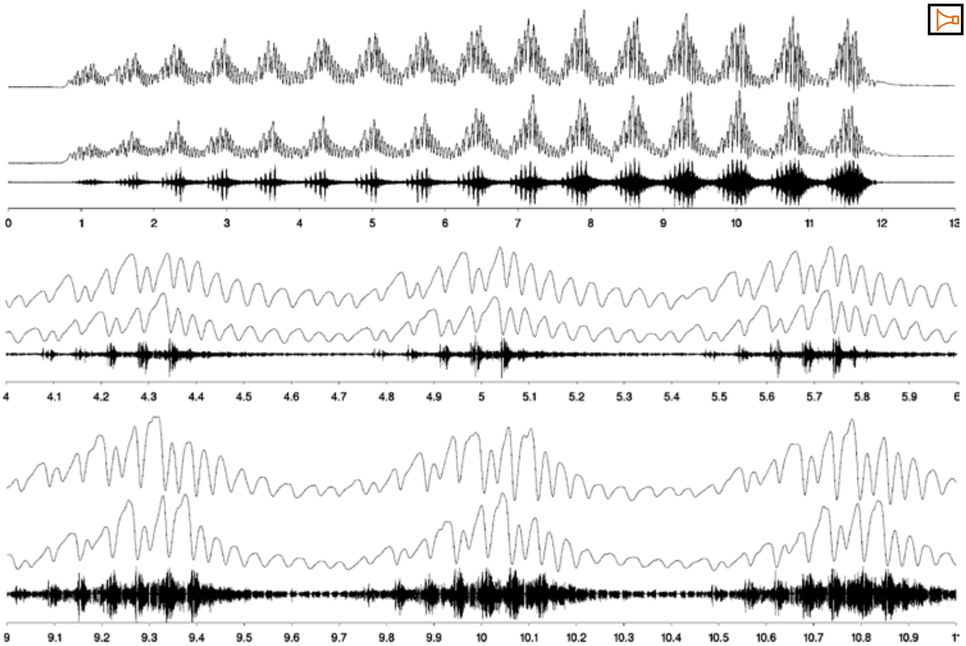

Fig. 252. *Chorthippus sangiorgii*, Greece, Ionian Is, Levkas, Vassiliki, x.1996, leg. J. Schul, 30°C, calling song (registration X), CD30.

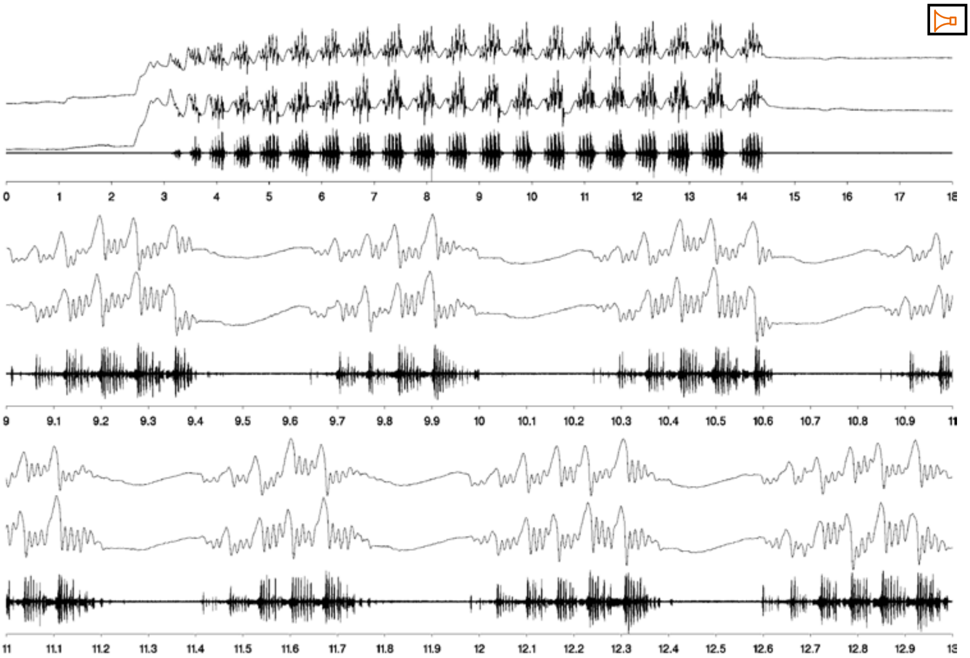

Fig. 253. *Chorthippus pulloides*, bioacoustically atypical, Greece, Ilia, Mt. Lampeia [= Lambia], 26.viii.1989, leg. O. von Helversen, 36°C, calling song (registration AK), CD31.

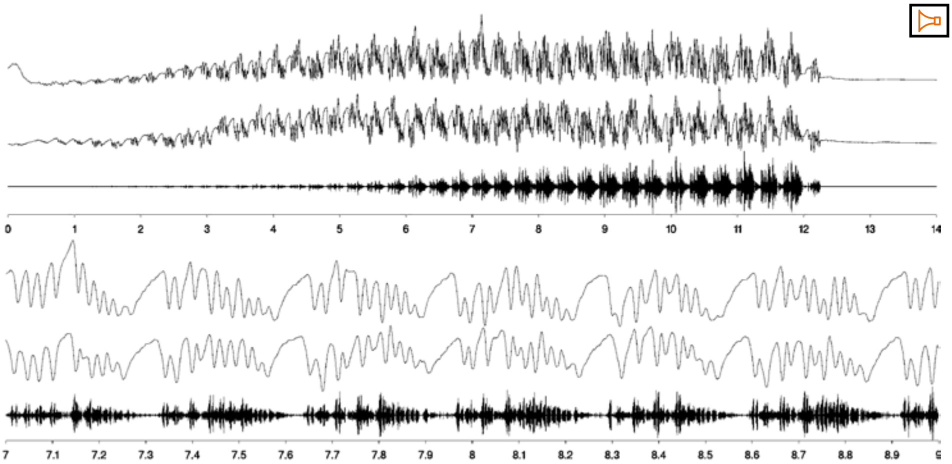

Fig. 254. *Chorthippus pulloides*, bioacoustically & morphologically atypical, Greece, Lakonia, Mt. Taiyetos summit, 9.viii.1998, leg. F. Mayer, 33°C, courtship song (registration 20), CD32.

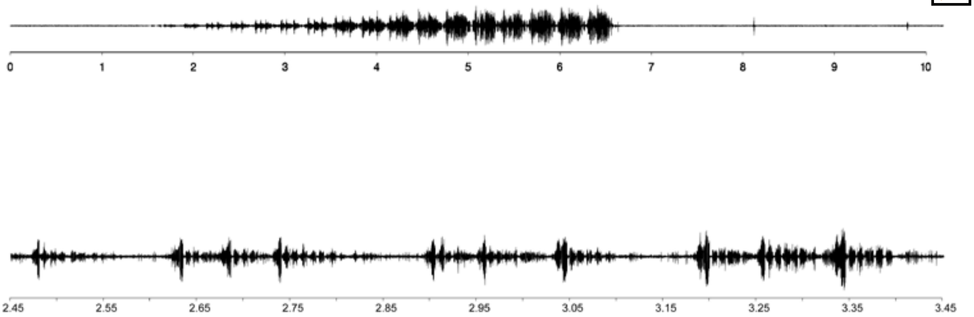

Fig. 255. *Chorthippus pulloides*, bioacoustically & morphologically atypical, Greece, Lakonia, Mt. Taiyetos above Eos club, 1600-1700 m, 1.viii.1991, leg. and rec. F. Willemse, 24°C, one-legged courtship song without registration of leg movement (oscillogram of recording 1991 copy 2 rood 085-121), CD33.

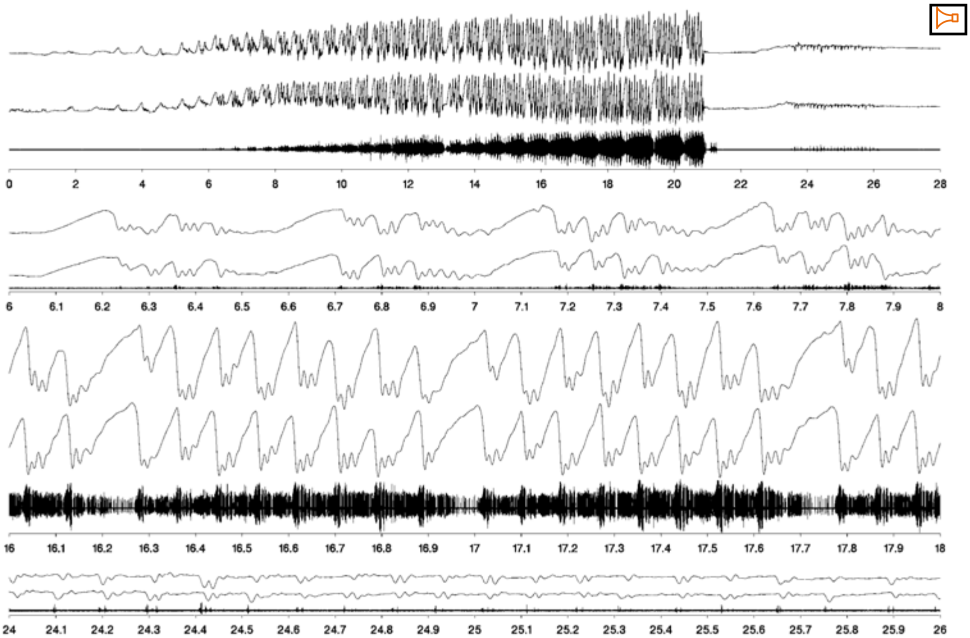

Fig. 256. *Chorthippus moreanus*, bioacoustically atypical, Greece, Peloponnisos, Ilia, Petralona, 23. viii.1986, leg. O. von Helversen, 30°C, courtship song (registration 33), CD34.

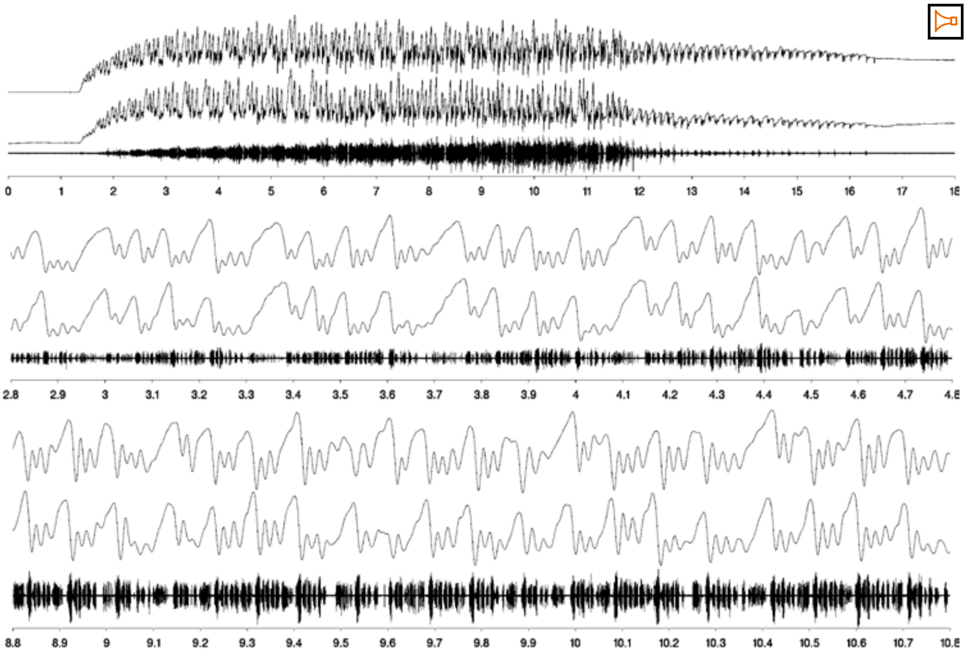

Fig. 257. *Chorthippus moreanus*, bioacoustically atypical, Greece, Messinia, W-side Mt. Taiyetos, Nedhoussa, 1200 m, 25.viii.1986, leg. O. von Helversen, 29°C, calling song (registration P), CD35.

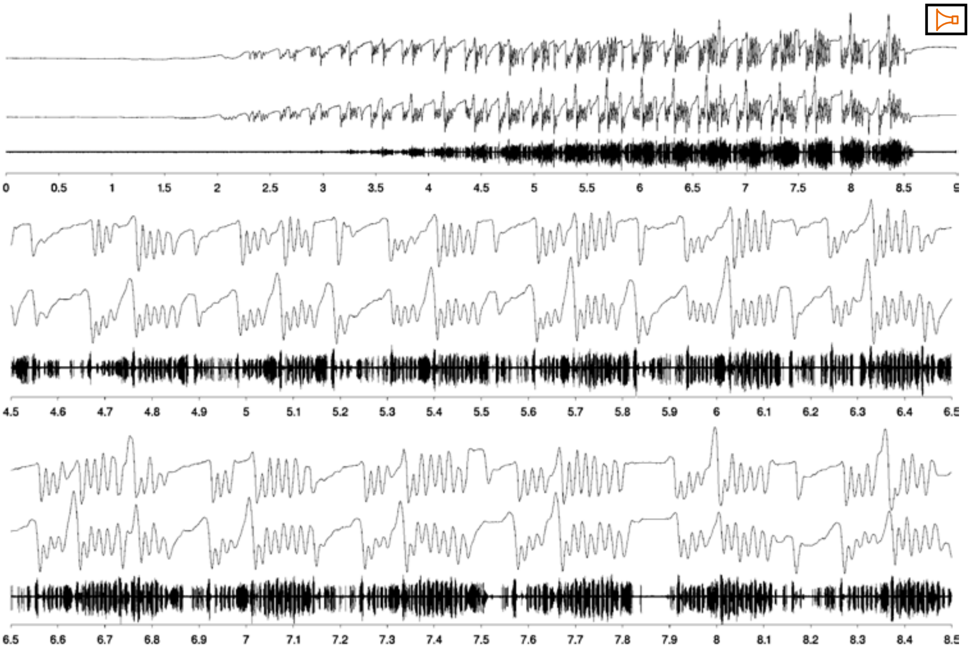

Fig. 258. *Chorthippus moreanus* × *pulloides-crassiceps*, transitional population, Greece, Arkadhia, Karkalou-Langadhia, 28.viii.1989, leg. O. von Helversen, 33-35°C, calling song (registration AL), CD36.

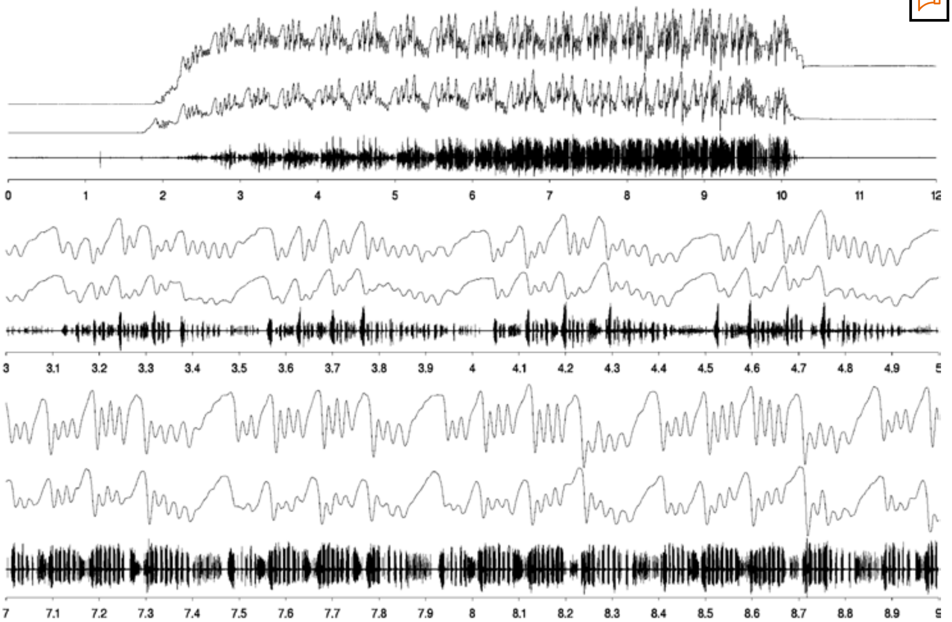

Fig. 259. *Chorthippus moreanus* × *pulloides-crassiceps*, transitional population, Greece, Lakonia, Mt. Parnon, *Abies* Wald oberhalb Vamvakou, 1300 m, 26.viii.1986, leg. O. von Helversen, 31°C, calling song (registration AI), CD37.

Appendix 2. Distribution maps

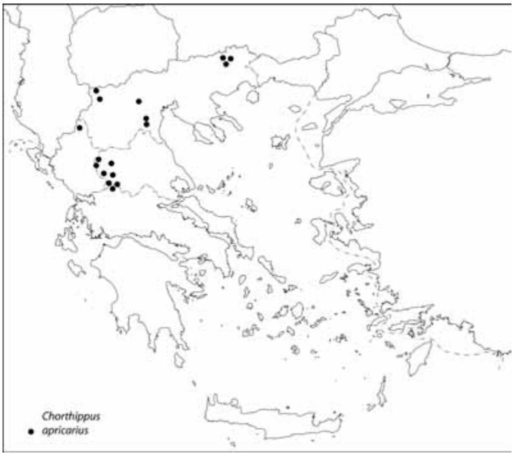

Fig. 260. Distribution of *Chorthippus apricarius* in Greece.

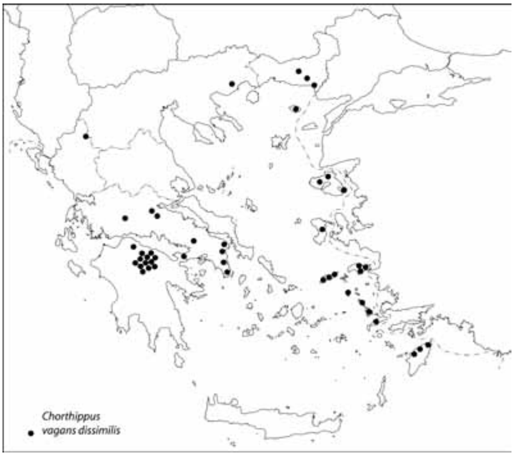

Fig. 261. Distribution of *Chorthippus vagans dissimilis* in Greece.

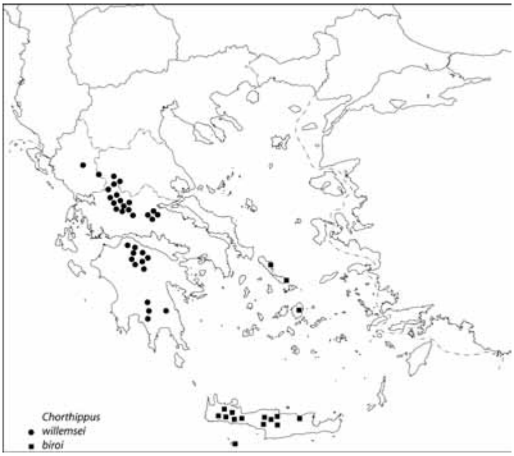

Fig. 262. Distribution of *Chorthippus willemsei* and *biroi*, both endemic to Greece.

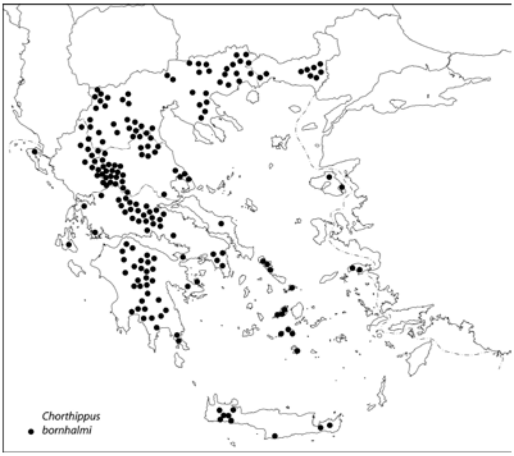

Fig. 263. Distribution of *Chorthippus bornhalmi* in Greece, based on material examined by the authors, excluding previous records.

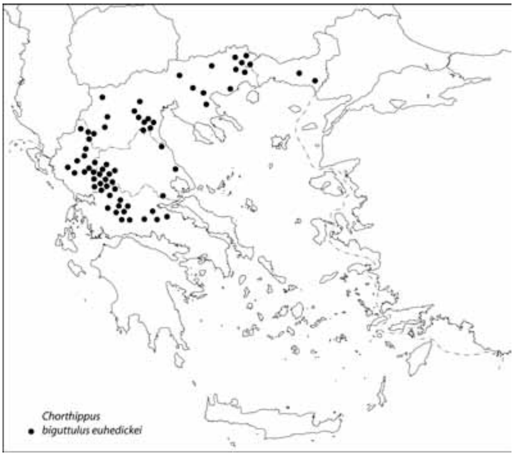

Fig. 264. Distribution of *Chorthippus biguttulus euhedickei* in Greece.

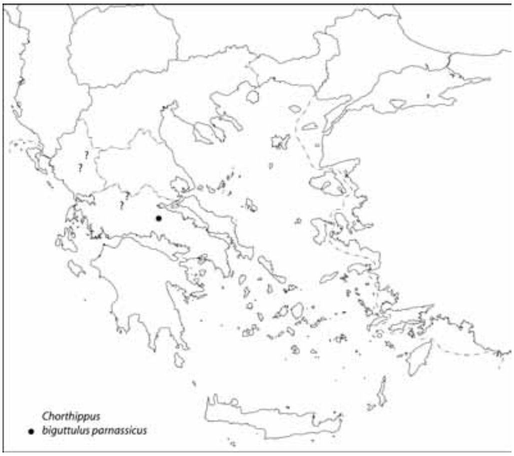

Fig. 265. Distribution of *Chorthippus biguttulus parnassicus*. Sites indicated with a question mark are discussed in the text.

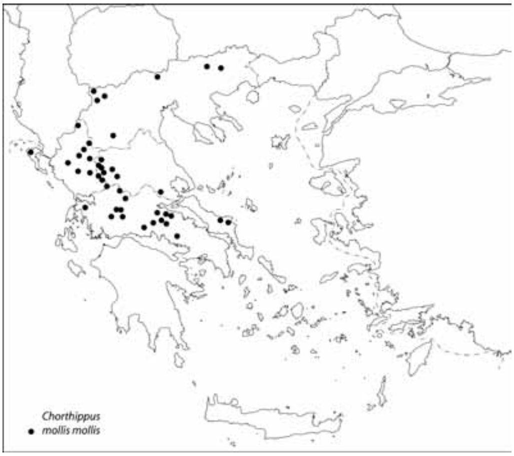

Fig. 266. Distribution of *Chorthippus mollis mollis* in Greece.

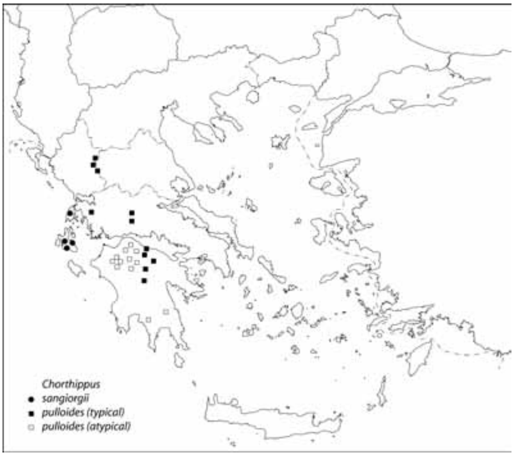

Fig. 267. Distribution of *Chorthippus pulloides* (typical and atypical populations) and *C. sangiorgii* (both endemic to Greece).

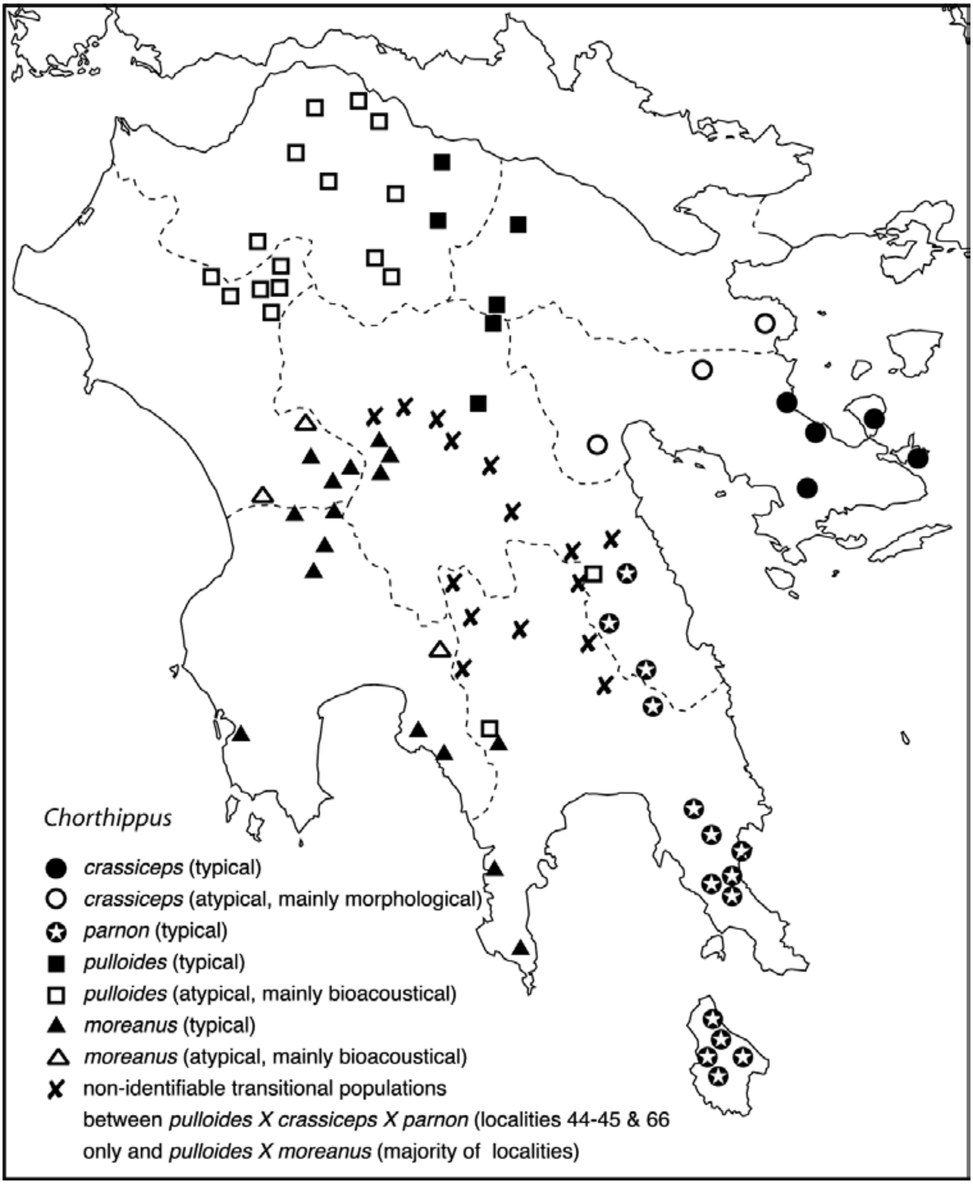

Fig. 268. Distribution of typical, atypical and transitional populations of *Chorthippus crassiceps*, *C. parnon*, *C. pulloides* and *C. moreanus* (except for *pulloides* all endemic to the Peloponnese)

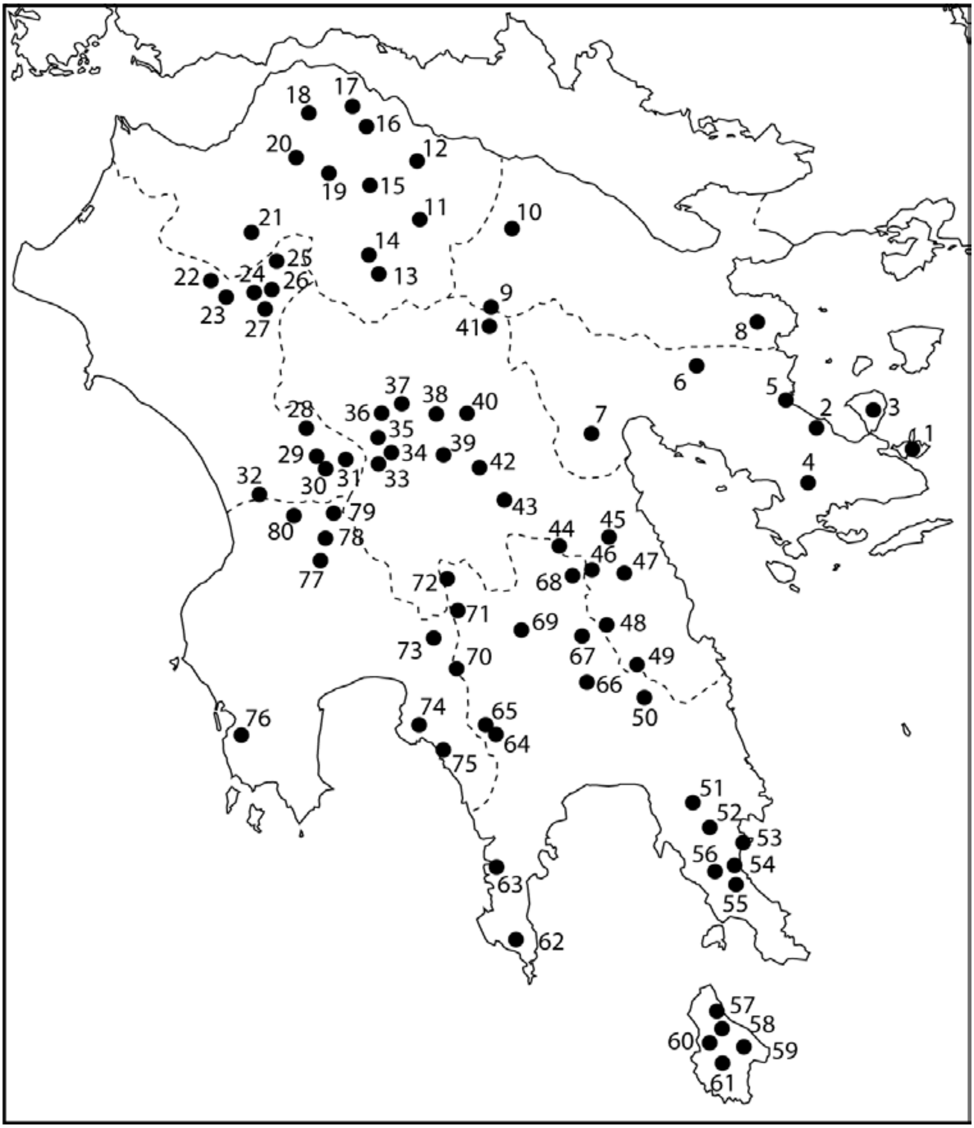

Fig. 269. Localities of studied material from the Peloponnese belonging to typical, atypical and transitional populations of *Chorthippus pulloides*, *C. crassiceps*, *C. parnon* and *C. moreanus* and summarised under regional headings of the nomi (districts) of Argolis (1-7), Korinthia (8-10), Akhaia (11-21), Ilia (22-32), Arkadhia (33-49), Lakonia (50-72) and Messinia (76-80). Particulars of the sites may be found throughout the text dealing with these taxa including whether bioacoustical data are available of the site treated under atypical and transitional populations.

ARGOLIS

1. Poros Island, 50-200 m
2. Ano Fanari, 120 m
3. Methana peninsula, above Kounoupitsa, 100 m
4. Mt.Dhidhimoi near summit, 1050 m
5. Palaio Epidhavros, 150 m
6. Arachnaion Mts, Limnes-Ayionori, 600 m
7. Zonga (Mt. Ktenias, SW of Argos)

KORINTHIA

8. N & S of Sofikon, 200 m
9. Mt. Oliyirtos, above Lavka, 1200-1500 m

10. Mt. Killini above Trikala, 1700-2000 m & plateau near Lamos, 1500 m

AKHAIA

11. Mt. Chelmos, Kato Lousoi, 1000 m & above Kato Lousoi, 1700-2000 m & near ski centre, 1400 &1600 m
12. Monast. Mega Spilaion, 900-1000 m
13. Aroania village,1000-1100 m
14. Drimos (W of Klitoria), 1100 m
15. Skepasto (4 km N), 1160 m
16. Kalavrita-Aiyion, surroundings Petsaki, 850 m
17. Mt. Klokos between Fteri & Ano Mavriki, 1250 m & 1300-1500 m
18. Mt. Panakhaikon above Souli, 900 m & 1350 m & 1500 m & above Katafiyio, 1600-1700 m & above Romanou, 1000 m & above Zastova, 1000-1800 m & Zastova-Psarthri, 1000-1650 m & southern hills, pass SE above Mirali, 1250 m
19. Vlasia (W of Kalavrita), 500 m
20. Kalanos (40 km W of Kalavrita)
21. Mt.Erimanthos, Kalentzi, 1000 m & above Kalentzi, 900-1100 m & 1700-2000 m & above Mika, 1250 m

ILIA

22. Ay. Triadha (6 km E), southern Mt. Erimanthos, 600 m
23. W of Panopoulou, 500 m
24. Ay. Kiriaki (W of Lambia), 700 m
25. Mt. Erimanthos, below Kriovrisi
26. Lambia, 800 m
27. Marmara (Erimanthos river), 600 m
28. Sekoulas (Alfios river) (N of Andritsaina)
29. Sikies (3 km N of Andritsaina), 1000 m
30. Andritsaina, 1000 m
31. W & E of Thisoa (E of Andritsaina), 500 m & 600 m
32. Petralona (W of Bassae)

ARKADHIA

33. Elliniko (N of Karitaina), 1050-1100 m
34. Ziyovitsi (N of Dhimitsana), 1100 m
35. Ipsous (Dhimitsana), 800 m
36. Karkalou (Karkalou-Langadhia), 1100 m
37. N & S of Valtesiniko (N of Vitina), 1300 m
38. S of Vitina, 4 km S of Elati, 1200 m
39. Khrissovitsi (NW of Tripolis) (3-11.5 km W), 1000-1200 m
40. Mt. Mainalon above Kardhara, 1500-1980 m
41. Mt. Oliyirtos above Kandhila, 900-1200 m
42. Tripolis (5 km W)
43. S of Alepokhori, (30 km N of Sparti), 500 m
44. Karies-Ay. Petros 800 m & 4-6 km E of A. Petros, 850-900 m
45. Ay. Ioannis-Orini Meliyou (SW of Astros), 700 m
46. Mt. Parnon above Kastanitsa 1500-1800 m & above Vamvakou, 1500-1934 m
47. Prastos (SW of Ay. Andreas)
48. Mt. Parnon, Ay. Vasilios (22.5 km N of Kosmas), 1000-1200 m
49. Kosmas & 10 km E of Kosmas, both 1000 m

LAKONIA

50. Karitsa (E of Yeraki)
51. Metamorfosis (E of Molaoi), 600 m
52. 3 km S of Sikea
53. Monemvasia (0.5 & 3 km S)
54. Nomia (2-3 km W)
55. Foutia (1 km W)
56. Elliniko (0.5 km E)
57. Kythira Island, 4.5-5.5 km S of A. Pelagia (to Potamos), 320 m
58. Kythira Island, between Potamos & Kambos, 310 m
59. Kythira Island, near airport W of Dhiakofti near OTE station, 450 m
60. Kythira Island, near Milopotamos, 330 m
61. Kythira Island, W of Karvounadhes, near Pitsanianika, 360 m
62. Mani Peninsula, between Tsikkali & Lagia, 380 m
63. 3 km E of Areopolis, 300 m
64. Mt. Taiyetos (W of Anoyeia & Palaiopanayia), forest road from Toritza to refuge of Alpine Club EOS, 1200-1550 m
65. Mt. Taiyetos, eastern slopes from 1550-2404 m, below summit Prof. Ilias (2404 m)
66. Ay. Anaryiri (3 km S) (SE of Sparti), 300 m
67. Polidrosos (NE of Sparti) near bridge, 1000 m & 2 & 3 & 5 km W, 950-1000 m
68. Mt. Parnon, Vamvakou, 1300 m
69. 15 km N of Sparti, riverside, wet place
70. pass between Sparti and Kalamata, above Tripi, 1000 & 1100 & 1200 & 1300 & 1500 m
71. Mt. Taiyetos, Yeoryitsi, 1250 m
72. Mt. Taiyetos, 1 km S of Longanikos, 720 m

MESSINIA

73. Mt. Taiyetos, E of Kalamata, turnoff to Nedhousa, 1100-1200 m
74. Kambos (S of Kalamata), 400-700 m
75. Kardhamili, 100 m
76. Palaioneri-Varakes (S of Pilos), 140 m
77. Aryirovouni, 600 m
78. Petra-Kakaletri, 600 m
79. Nedha (3-5 km N), 900-1100 m & Nedha, 800 m
80. Archeological site of Bassae [= Vasses] & surroundings (S of Andritsaina), 1100 m

Appendix 3. Biometric data

Table 20. Biometric data for males of *Chorthippus vagans vagans*, *C. vagans africanus*, *C. vagans dissimilis* and *C. vagans cypriotus*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of nominate *C. vagans* were taken from specimens from eastern, central and western Europe, of *C. vagans africanus* from paratypes, of *C. vagans dissimilis* from the type series and of *C. vagans cypriotus* from topotypes.

males	*vagans vagans*	*vagans africanus*	*vagans dissimilis*	*vagans cypriotus*
length of prozona	1.15-1.75 1.43 ± 0.16 n = 30	1.30-1.40 1.32 ± 0.04 n = 5	1.20-1.65 1.44 ± 0.11 n = 30	1.27-1.45 1.34 ± 0.07 n = 5
length of metazona	1.15-1.75 1.40 ± 0.16125 n = 30	1.40-1.65 1.55 ± 0.12 n = 5	1.55-2.15 1.74 ± 0.14 n = 30	1.40-1.65 1.51 ± 0.09 n = 5
ratio length of prozona / length of metazona	0.92-1.12 1.02 ± 0.05 n = 30	0.79-0.93 0.85 ±.06 n = 5	0.73-0.91 0.83 ± 0.05 n = 30	0.86-0.93 0.89 ± 0.03 n = 5
minimum width of pronotal disc	0.80-1.15 0.94 ± 09 n = 30	0.80-1.05 0.93 ± 0.10 n = 5	0.80-1.10 0.95 ± 0.0 n = 30	0.85-0.95 0.89 ± 0.04 n = 5
maximum width of pronotal disc	1.50-2.25 1.85 ± 0.19 n = 30	1.70-1.95 1.86 ± 0.10 n = 5	1.90-2.70 2.21 ± 0.17 n = 30	1.90-2.20 2.06 ± 0.11 n = 5
ratio maximum / minimum width of pronotal disc	1.72-2.21 1.98 ± 0.10 n = 30	1.86-2.31 2.01 ± 0.18 n = 5	2.10-2.65 2.33 ± 0.14 n = 30	2.11-2.47 2.31 ± 0.13 n = 5
minimum diameter of tympanal opening	0.45-0.66 0.55 ± 0.06 n = 30	0.425-0.50 0.45 ± 0.04 n = 5	0.30-0.45 0.36 ± 0.05 n = 30	0.26-0.41 0.31 ± 0.06 n = 5
maximum diameter of tympanal opening	1.00-1.37 1.13 ± 0.10 n = 30	1.01-1.25 1.13 ± 0.10 n = 5	1.07-1.37 1.24 ± 0.08 n = 30	1.1-1.25 1.18 ± 0.06 n = 5
ratio maximum/ minimum diameter of tympanal opening	1.74-2.39 2.07 ± 0.16 n = 30	2.38-2.65 2.50 ± 0.10 n = 5	2.67-4.25 3.51 ± 0.40 n = 30	3.05-4.23 3.83 ± 0.45 n = 5
length of fore wing	9.7-14.1 11.44 ± 1.01 n = 30	11.1-12.8 11.96 ± 0.7 n = 5	12.2-16.5 13.83 ± 0.9 n = 30	10.5-11.9 11.26 ± 0.5 n = 5
distance from stigma to tip of fore wing	3.2-5.2 3.85 ± 0.48 n = 30	4.0-5.0 4.4 ± 0.37 n = 5	4.6-6.3 5.17 ± 0.36 n = 30	3.6-4.4 4.07 ± 0.36 n = 4
ratio distance from stigma to tip / length of fore wing	0.31-0.38 0.34 ± 0.02 n = 30	0.35-0.39 0.37 ± 0.02 n = 5	0.35-0.40 0.37 ± 0.01 n = 30	0.32-0.38 0.37 ± 0.01 n = 5
width of C area	0.40-0.575 0.49 ± 0.04 n = 30	0.45-0.60 0.50 ◎± ◎0.06 n = 5	0.55-0.75 0.62 ± 0.04 n = 30	0.55-0.61 0.59 ± 0.02 n = 5
width of Sc area	0.23-0.35 0.28 ± 0.03 n = 30	0.15-0.25 0.20 ± 0.04 n = 5	0.20-0.35 0.27 ± 0.03 n = 30	0.2-0.3 0.25 ± 0.04 n = 5

males	*vagans vagans*	*vagans africanus*	*vagans dissimilis*	*vagans cypriotus*
maximum width of Sc area	0.25-0.38 0.31 ± 0.04 n = 30	0.20-0.28 0.23 ± 0.03 n = 5	0.25-0.40 0.32 ± 0.03 n = 26	0.27-0.31 n = 2
ratio width of C / width of Sc area	1.43-2.30 1.79 ± 0.20 n = 30	2.22-3.00 2.57 ± 0.3 n = 5	1.77-3.26 2.32 ± 0.31 n = 30	2.0-2.76 2.44 ± 0.34 n = 5
width of combined C & Sc areas	0.63-0.88 0.77 ± 0.07 n = 30	0.60-0.85 0.71 ± 0.09 n = 5	0.75-1.00 0.89 ± 0.06 n = 30	0.79-0.89 0.85 ± 0.04 n = 5
ratio width of combined C & Sc areas x 100 / length of fore wing	5.93-7.73 6.72 ± 0.49 n = 30	5.26-6.64 5.80 ± 0.50 n = 5	5.89-7.42 6.45 ± 0.36 n = 30	7.05-8.38 7.59 ± 0.55 n = 5
ratio length of fore wing / width of Sc area measured along same line as C area	32.0-51.27 41.90 ± 4.66 n = 30	51.2-76.0 61.3 ± 9.7 n = 5	40.62-62.67 51.09 ± 5.29 n = 30	37-56 46.9 ± 8.3 n = 5
ratio length of fore wing / maximum width of Sc area	30.0-51.2 37.2 ± 4.9 n = 30	46.5-57.0 52.5 ± 4.7 n = 5	36.6-51.7 44.3 ± 3.7 n = 26	38.4-42.9 n = 2
ratio length of fore wing / width of C area	19.30-26.11 23.41 ± 1.69 n = 30	21.03-25.30 23.80◎ ± ◎1.56 n = 5	17.60-26.40 22.36 ± 1.57 n = 30	17.5-20.4 19.17 ± 1.17 n = 5
ratio length of fore wing / width of combined C & Sc area	12.94-16.88 14.95 ± 1.07 n = 30	15.06-19.00 17.10 ± 1.44 n = 5	13.47-16.97 15.54 ± 0.85 n = 30	11.93-14.17 13.21 ± 0.94 n = 5
length of hind femur	7.9-11.0 9.32 ± 0.84 n = 30	8.8-10.0 9.44 ± 0.59 n = 5	8.9-11.7 10.08 ± 0.63 n = 30	8.2-9.1 8.66 ± 0.35 n = 5
ratio length of fore wing / length of hind femur	1.01-1.40 1.23 ± 0.08 n = 30	1.22-1.30 1.27 ± 0.03 n = 5	1.23-1.49 1.37 ± 0.06 n = 30	1.19-1.35 1.30 ± 0.06 n = 5
length of stridulatory file	2.8-4.25 3.60 ± 0.37 n = 30	3.65-4.0 3.87 ± 0.16 n = 5	3.7-4.7 4.13 ± 0.29 n = 30	2.9-3.50 3.13 ± 0.23 n = 5
distance from end of file to tip of knee	3.35-5.10 4.12 ± 0.45 n = 30	3.75-4.30 4.06 ± 0.23 n = 5	3.60-4.85 4.10 ± 0.31 n = 30	3.4-4.2 3.8 ± 0.31 n = 5
ratio length of file / distance from end of file to tip of knee	0.76-1.08 0.88 ± 0.07 n = 30	0.93-1.00 0.95 ± 0.03 n = 5	0.82-1.18 1.01 ± 0.09 n = 30	0.77-0.91 0.83 ± 0.05 n = 5
number of stridulatory pegs	115-169 141.5 ± 12.8 n = 30	129-165 149 ± 14.4 n = 5	135-189 163.3 ± 14.3 n = 30	115-119 117 ± 1.6 n = 5
number of stridulatory pegs per mm	27.06-49.06 39.68 ± 4.96 n = 30	34.4-41.77 38.51 ± 3.66 n = 5	30.0-45.19 39.64 ± 3.08 n = 30	34.0-40.68 37.52 ± 2.45 n = 5
length of tip of subgenital plate	0.25-0.60 0.41 ± 0.09 n = 30	0.40-0.60 0.48 ± 0.09 n = 5	0.20-0.50 0.37 ± 0.08 n = 28	0.45-0.57 0.5 ± 0.04 n = 5

Table 21. Biometric data for females of *Chorthippus vagans vagans*, *C. vagans africanus*, *C. vagans dissimilis* and *C. vagans cypriotus*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of nominate *C. vagans* were taken from specimens from eastern, central and western Europe, of *C. vagans africanus* from a few paratypes, of *C. vagans dissimilis* from the type series and of *C. vagans cypriotus* from topotypes.

females	*vagans vagans*	*vagans africanus*	*vagans dissimilis*	*vagans cypriotus*
length of prozona	1.6-2.1	1.6-1.8	1.6-2.0	1.5-1.8
	1.89 ± 0.18	1.72 ± 0.1	1.79 ± 0.17	
	n = 20	n = 4	n = 27	n = 2
length of metazona	1.6-2.2	1.8-2.2	1.9-2.7	2.0-2.0
	1.92 ± 0.18	2.0 ± 0.17	2.24 ± 0.22	
	n = 20	n = 4	n = 27	n = 2
ratio length of prozona / length of metazona	0.94-1.05	0.82-0.90	0.68-0.88	0.75-0.9
	0.98 ± 0.06	0.86 ± 0.12	0.79 ± 0.05	
	n = 20	n = 4	n = 27	n = 2
minimum width of pronotal disc	0.9-1.4	1.1-1.1	1.0-1.3	1.0-1.2
	1.2 ± 0.15	1.1 ± 0.00	1.17 ± 0.09	
	n = 20	n = 4	n = 20	n = 2
maximum width of pronotal disc	2.2-2.9	2.4-2.6	2.5-3.3	2.6-2.6
	2.6 ± 0.2	2.5 ± 0.4	2.91 ± 0.1	
	n = 20	n = 4	n = 20	n = 2
ratio maximum / minimum width of pronotal disc	1.93-2.44	2.18-2.36	2.31-2.80	2.16-2.6
	2.22 ± 0.17	2.27 ± 0.14	2.49 ± 0.14	
	n = 20	n = 4	n = 20	n = 2
maximum diameter of tympanal opening	1.3-1.65	1.3-1.6	1.3-1.55	1.32-1.55
	1.43 ± 0.09	1.4 ± 0.05	1.42 ± 0.08	
	n = 20	n = 4	n = 20	n = 2
minimum diameter of tympanal opening	0.5-0.85	0.45-0.6	0.25-0.5	0.31-0.46
	0.65 ± 0.06	0.55 ± 0.03	0.35 ± 0.09	
	n = 20	n = 4	n = 20	n = 2
ratio maximum / minimum diameter of tympanal opening	1.76-2.7	2.167-3.55	2.85-5.45	3.36-4.25
	2.22 ± 0.18	2.62 ± 0.37	4.18 ± 0.42	
	n = 20	n = 4	n = 20	n = 2
length of fore wing	12.5-16.8	13.7-15.4	14.8-17.6	14.7-14.9
	14.6 ± 0.9	14.8 ± 0.7	15.95 ± 0.8	
	n = 20	n = 4	n = 20	n = 2
distance stigma to tip of fore wing	4.1-5.6	5.2-6.0	5.6-7.2	5.3-5.8
	5.11 ± 0.6	5.65 ± 0.34	6.6 ± 0.45	
	n = 10	n = 4	n = 15	n = 2
distance stigma to tip / length of fore wing	0.33-0.39	0.38-0.41	0.33-0.42	0.35-0.39
	0.36 ± 0.02	0.39 ± 0.01	0.39 ± 0.02	
	n = 10	n = 5	n = 15	n = 2
length of hind femur	11.0-13.4	11.4-12.9	11.1-13.4	11.3-12.0
	12.4 ± 0.8	12.2 ± 0.5	12.24 ± 0.65	
	n = 20	n = 4	n = 20	n = 2
ratio length of fore wing / length of hind femur	1.08-1.26	1.19-1.26	1.17-1.44	1.24-1.30
	1.18 ± 0.06	1.22 ± 0.03	1.31 ± 0.075	
	n = 20	n = 4	n = 20	n = 2
length of sridulatory file	4.5-5.2	4.5-5.1	4.5-5.0	4.1-4.4
	4.9 ± 0.28	4.87 ± 0.2	4.82 ± 0.22	
	n = 9	n = 4	n = 15	n = 2

females	*vagans vagans*	*vagans africanus*	*vagans dissimilis*	*vagans cypriotus*
distance from end of file to tip of knee	4.6-5.8 5.01 ± 0.43 n = 9	5.05-5.12 5.26 ± 0.22 n = 4	5.1-5.7 5.31 ± 0.31 n = 9	4.7-4.9 n = 2
ratio length of file / distance from end of file to tip of knee	0.89-1.09 0.94 ± 0.06 n = 9	0.95-1.18 1.10 ± 0.01 n = 4	0.82-1.00 0.93 ± 0.08 n = 9	0.87-0.89 n = 2
number of stridulatory pegs	121-157 139 ± 17 n = 9	131-154 141 ± 9 n = 4	122-176 148 ± 16 n = 15	107-117 n = 2
number of stridulatory pegs per mm	27.0-39.1 29.6 ± 3.1 n = 9	26.1-36.2 29.3 ± 4.2 n = 4	26.7-37.4 30.8 ± 3.5 n = 9	24.3-28.5 n = 2

Table 22. Biometric data for males of *Chorthippus willemsei* and *C. biroi*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) were taken from specimens throughout their range.

males	*willemsei*	*biroi*
length of pronotum	2.8-3.7 3.29 ± 0.24 n = 14	2.6-3.0 2.79 ± 0.1 n = 14
length of prozona	1.5-2.0 1.79 ± 0.15 n = 14	1.4-1.6 1.49 ± 0.07 n = 14
length of metazona	1.3-1.7 1.47 ± 0.13 n = 14	1.2-1.4 1.29 ± 0.04 n = 14
ratio length of prozona / length of metazona	1.11-1.38 1.21 ± 0.08 n = 14	1.07-1.25 1.16 ± 0.06 n = 14
minimum width of pronotal disc	1.0-1.1 1.08 ± 0.04 n = 5	0.8-1.1 0.93 ± 0.09 n = 6
maximum width of pronotal disc	2.1-2.3 2.24 ± 0.08 n= 5	1.6-2.0 1.9 ± 0.13 n = 6
ratio maximum / minimum width pronotal disc	1.91-2.2 2.07 ± 0.02 n = 5	1.80-2.22 2.05 ± 0.13 n = 6
minimum diameter of tympanal opening	0.44-0.55 0.47 ± 0.03 n = 14	0.3-0.5 0.41 ± 0.06 n = 14
maximum diameter of tympanal opening	1.1-1.4 1.21 ± 0.07 n = 14	1.0-1.6 1.21 ± 0.1 n = 14
ratio maximum /minimum diameter of tympanal opening	2.3-2.6 2.59 ± 0.10 n = 14	1.9-5.5 3.04 ± 0.9 n = 14
length of fore wing	5.9-7.4 6.5 ± 0.39 n = 14	4.4.-6.1 5.28 ± 0.5 n = 14

males	*willemsei*	*biroi*
maximum width of fore wing	1.7-2.3	1.5-1.9
	2.05 ± 0.14	1.74 ± 0.12
	n = 14	n = 14
ratio length / width fore wing	2-3.5	2.6-3.9
	3.17 ± 0.17	3.03 ± 0.33
	n = 14	n = 14
width of C area	0.4-0.5	0.34-0.51
	0.46 ± 0.03	0.41 ± 0.04
	n = 5	n = 14
width of Sc area	0.17-0.25	0.09-0.16
	0.21 ± 0.02	0.13 ± 0.02
	n = 5	n = 14
ratio width of C / width of Sc area	1.6-2.7	2.27-4.53
	2.22 ± 0.4	3.36 ± 0.8
	n = 5	n = 14
length of hind femur	8.7-10.4	7.7.-8.9
	9.3 ± 0.46	8.38 ± 0.57
	n = 13	n = 6
ratio length of fore wing / length of hind femur	0.57-0.83	0.56-0.79
	0.69 ± 0.06	0.64 ± 0.09
	n = 13	n = 6
length of stridulatory file	2.7-3.4	2.0-2.9
	2.86 ± 0.22	2.65 ± 0.26
	n = 13	n = 14
distance from end of file to tip of knee	4.5-5.0	3.5-4.3
	4.8 ± 0.18	3.81 ± 0.34
	n = 5	n = 6
ratio length of file / distance from end of file to tip of knee	0.55-0.62	0.60-0.82
	0.58 ± 0.02	0.72 ± 0.09
	n = 5	n = 6
number of stridulatory pegs	81-111	43-84
	93.5 ± 11	73 ± 10
	n = 11	n = 14
number of stridulatory pegs per mm	30-35	21-37
	33.2 ± 2.2	27.6 ± 3.9
	n = 5	n = 14
minimum distance between eyes	0.8-1.0	0.6-0.7
	0.9 ± 0.05	0.65 ± 0.04
	n = 10	n = 6
maximum diameter eye	1.6-1.9	1.6-1.8
	1.77 ± 0.1	1.73 ± 0.07
	n = 10	n = 6
ratio interocular distance / diameter eye	0.47-0.61	0.33-0.41
	0.51 ± 0.04	0.37 ± 0.02
	n = 10	n = 6

Table 23. Biometric data for females of *Chorthippus willemsei* and *C. biroi*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) were taken from specimens throughout their range.

females	*willemsei*	*biroi*
length of pronotum	3.9-4.6	3.35-4.0
	4.29 ± 0.2	3.65 ± 0.21
	n = 17	n = 11
length of prozona	2.2-2.9	1.8-2.2
	2.40 ± 0.15	1.96 ± 0.13
	n = 17	n = 11
length of metazona	1.7-2.1	1.55-1.8
	1.94 ± 0.12	1.68 ± 0.1
	n = 17	n = 11
ratio length of prozona / length of metazona	1.14-1.61	1.05-1.25
	1.24 ± 0.11	1.16 ± 0.05
	n = 17	n = 11
minimum width of pronotal disc	1.1-1.5	1.1-1.5
	1.2 ± 0.14	1.19 ± 0.12
	n = 7	n = 5
maximum width of pronotal disc	2.6-3.2	2.4-2.7
	2.92 ± 0.18	2.5 ± 0.14
	n = 7	n = 5
ratio maximum / minimum width of pronotal disc	2.06-2.54	1.85-2.45
	2.25 ± 0.18	2.11± 0.22
	n = 7	n = 5
minimum diameter of tympanal opening	0.5-0.7	0.36-0.65
	0.59 ± 0.06	0.44 ± 0.07
	n = 14	n = 11
maximum diameter of tympanal opening	1.1-1.5	1.1-1.33
	1.38 ± 0.05	1.22 ± 0.08
	n = 14	n = 11
ratio maximum / minimum diameter of tympanal opening	2.0-2.6	2.0-3.2
	2.35 ± 0.19	2.6 ± 0.36
	n = 14	n = 11
length of fore wing	4.4-5.7	4.4-6.1
	4.95 ± 0.45	5.2 ± 0.51
	n = 7	n = 11
maximum width of fore wing	2.1-2.7	2.0-2.4
	2.48 ± 0.14	2.1 ± 0.17
	n = 7	n = 11
ratio length / width fore wing	1.66-2.28	2.16-2.8
	2.00 ± 0.21	2.47 ± 0.23
	n = 7	n = 11
length of hind femur	10.9-12.6	9.6-10.8
	11.83 ± 0.5	10.24 ± 0.4
	n = 17	n = 11
ratio length of fore wing / length of hind femur	0.36-0.47	0.44-0.56
	1.01 ± 0.04	0.50 ± 0.03
	n = 7	n = 11
minimum distance between eyes	1.1-1.3	0.8-1.0
	1.23 ± 0.06	0.90 ± 0.06
	n = 12	n = 11

females	*willemsei*	*biroi*
maximum diameter eye	1.96-2.2 2.07 ± 0.07 n = 12	1.8-2.25 2.03 ± 0.12 n = 11
ratio interocular distance / diameter eye	0.54-0.65 0.59 ± 0.03 n = 12	0.4-0.5 0.44 ± 0.02 n = 11
maximum width of head	3.7-4.1 3.88 ± 0.14 n = 7	3.4-3.9 3.61 ± 0.18 n = 6
ratio length of pronotum / maximum width of head	1.02-1.17 1.11 ± 0.05 n = 7	0.97-1.05 1.02 ± 0.03 n = 6

Table 24. Biometric data for males of *Chorthippus bornhalmi* and *C. brunneus brunneus*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of *C. brunneus brunneus* were taken from specimens from the northern Balkans, of *C. bornhalmi* from throughout Greece.

males	*bornhalmi*	*brunneus brunneus*
length of prozona	1.13-1.50 1.32 ± 0.09 n = 30	1.16-1.41 1.25 ± 0.07 n = 10
length of metazona	1.60-2.25 1.87 ± 0.14 n = 30	1.4-1.7 1.61 ± 0.09 n = 10
ratio length of prozona / length of metazona	0.58-0.82 0.71 ± 0.05 n = 30	0.71-0.88 0.78 ± 0.06 n = 10
minimum width of pronotal disc	0.85-1.01 0.91 ± 0.05 n = 30	0.73-0.92 0.86 ± 0.06 n = 10
maximum width of pronotal disc	2.15-2.70 2.39 ± 0.14 n = 30	1.96-2.21 2.07 ± 0.09 n = 10
ratio maximum / minimum width of pronotal disc	2.21-2.94 2.62 ± 0.19 n = 30	2.13-2.66 2.41 ± 0.17 n = 10
minimum diameter of tympanal opening	0.20-0.90 0.34 ± 0.11 n = 30	0.18-0.36 0.26 ± 0.06 n = 10
maximum diameter of tympanal opening	1.04-2.50 1.28 ± 0.23 n = 30	0.92-1.23 1.12 ± 0.08 n = 10
ratio maximum/ minimum diameter of tympanal opening	2.77-5.38 3.86 ± 0.55 n = 30	3.16-5.73 4.48 ± 0.82 n = 10
length of fore wing	13.39-16.9 15.34 ± 0.9 n = 30	12.9-15.3 13.8 ± 0.6 n = 10
distance from stigma to tip of fore wing	5.38-7.30 6.29 ± 0.52 n = 30	5.14-5.69 5.42 ± 0.20 n = 10

males	*bornhalmi*	*brunneus brunneus*
ratio distance from stigma to tip / length of fore wing	0.36-0.44 0.41 ± 0.02 n = 30	0.37-0.42 0.39 ± 0.01 n = 10
width of C area	0.57-0.75 0.66 ± 0.05 n = 28	0.58-0.63 0.61 ± 0.02 n = 10
width of Sc area	0.20-0.40 0.30 ± 0.05 n = 28	0.19-0.29 0.23 ± 0.02 n = 10
ratio width C / width Sc area	1.43-3.37 2.27 ± 0.48 n = 28	2.08-3.12 2.63 ± 0.29 n = 10
width combined C & Sc areas	0.80-1.05 0.92 ± 0.06 n = 28	0.79-0.91 0.83 ± 0.03 n = 10
ratio width combined C & Sc areas × 100 / length of fore wing	5.33-6.49 5.96 ± 0.31 n = 28	5.75-6.33 6.06 ± 0.21 n = 10
ratio length of ore wing / width of Sc area	34.00-77.00 52.74 ± 10.46 n = 28	52.1-70.9 60.01 ± 5.4 n = 10
ratio length of fore wing / width of C area	21.24-26.61 23.34 ± 1.41 n = 28	21.3-25.00 22.82 ± 1.1 n = 10
length of hind femur	8.39-10.70 9.86 ± 0.59 n = 30	7.6-9.8 9.1 ± 0.4 n = 30
ratio length of fore wing / length of hind femur	1.38-1.73 1.55 ± 0.07 n = 30	1.34-1.59 1.50 ± 0.06 n = 10
length of sridulatory file	3.25-4.50 4.00 ± 0.33 n = 30	2.35-3.30 2.78 ± 0.24 n = 30
distance from end of file to tip of knee	3.75-4.50 4.10 ± ◎0.21 n = 30	3.75-5.66 4.62 ± 0.35 n = 30
ratio length of file / distance from end of file to tip of knee	0.81-1.12 0.96 ± 0.08 n = 30	0.50-0.72 0.60 ± 0.06 n = 30
number of stridulatory pegs	105-153 124.2 ± 10.7 n = 34	55-89 71.3 ± 9.7 n = 30
number of stridulatory pegs per mm	25.55-36.61 31.24 ± 2.3 n = 30	20.2-31.8 25.7 ± 3.0 n = 30
length of tip of subgenital plate	0.49-0.71 0.59 ± 0.7 n = 20	

Table 25. Biometric data for females of *Chorthippus bornhalmi* and *C. brunneus brunneus*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of *C. brunneus brunneus* were taken from the northern Balkans, of *C. bornhalmi* from throughout Greece.

females	*bornhalmi*	*brunneus brunneus*
length of prozona	1.6-2.0	1.5-1.9
	1.80 ± 0.13	1.7 ± 0.13
	n = 7	n = 10
length of metazona	2.4-2.7	2.1-2.5
	2.57 ± 0.13	2.26 ± 0.14
	n = 7	n = 10
ratio length of prozona / metazona	0.66-0.74	0.64-0.87
	0.69 ± 0.03	0.75 ± 0.04
	n = 7	n = 10
minimum width of pronotal disc	1.0-1.4	1.0-1.4
	1.21 ± 0.09	1.19 ± 0.12
	n = 20	n = 10
maximum width of pronotal disc	3.0-3.9	2.7-3.2
	3.36 ± 0.21	2.95 ± 0.18
	n = 20	n = 10
ratio maximum / minimum width of pronotal disc	2.57-3.25	2.14-2.81
	2.78 ± 0.17	2.49 ± 0.21
	n = 20	n = 10
maximum diameter of tympanal openig	1.3-1.5	1.2-1.5
	1.4 ± 0.08	1.35 ± 0.10
	n = 7	n = 10
minimum diameter of tympanal opening	0.3-0.5	0.23-0.35
	0.38 ± 0.07	0.28 ± 0.04
	n = 7	n = 10
ratio maximum / minimum distance of tympanal opening	2.8-5.0	3.71-6.30
	3.73 ± 0.72	4.97 ± 0.95
	n = 7	n = 10
length of fore wing	18.0-20.9	16.9-19.0
	19.38 ± 0.05	17.93 ± 0.74
	n = 20	n = 10
distance from stigma to tip of fore wing	7.4-8.8	6.7-8.3
	7.99 ± 0.47	7.53 ± 0.59
	n = 10	n = 10
ratio distance from stigma to tip / length of fore wing	0.40-0.44	0.39-0.44
	0.42 ± 0.015	0.42 ± 0.01
	n = 10	n = 10
length of hind femur	11.6-14.8	11.6-13.6
	13.38 ± 1.06	12.46 ± 0.76
	n = 20	n = 10
ratio length of fore wing / length of hind femur	1.35-1.58	1.36-1.55
	1.45 ± 0.07	1.44 ± 0.06
	n = 20	n = 10
length of stridulatory file	4.8-6.0	3.2-4.2
	5.11 ± 0.41	3.78 ± 0.29
	n = 7	n = 10
distance from end of file to tip of knee	5.0-6.5	5.8-7.3
	5.60 ± 0.51	6.58 ± 0.54
	n = 7	n = 10

females	*bornhalmi*	*brunneus brunneus*
ratio length of file / distance from end of file to tip of knee	0.83-1.00 0.91 ± 0.05 n = 7	0.51-0.72 0.57 ± 0.07 n = 10
number of stridulatory pegs	83-118 103.4 ± 12 n = 7	45-78 56.5 ± 9.2 n = 10
number of stridulatory pegs per mm	16.6-22.3 20.24 ± 2.2 n = 7	11.8-18.5 14.9 ± 2.1 n = 10

Table 26. Biometric data for males of *Chorthippus biguttulus euhedickei*, *C. biguttulus parnassicus* and *C. biguttulus biguttulus*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of *C. biguttulus biguttulus* were taken from specimens from central and western Europe, of *C. biguttulus euhedickei* exclusively from Greece and those of *C. biguttulus parnassicus* from its typical site, Mt. Parnassos, Central Greece.

males	*biguttulus euhedickei*	*biguttulus parnassicus*	*biguttulus biguttulus*
length of prozona	1.22-1.6 1.39 ± 0.09 n = 22	1.29-1.41 1.35 ± 0.03 n = 10	1.2-1.5 1.36 ± 0.09 n = 17
length of metazona	1.5-2.03 1.67 ± 0.11 n = 22	1.35-1.7 1.57 ± 0.09 n = 10	1.55-1.9 1.71 ± 0.09 n = 17
ratio length prozona / length metazona	0.73-0.94 0.83 ± 0.06 n = 22	0.81-0.95 0.86 ± 0.03 n = 10	0.72-0.93 0.80 ± 0.05 n = 17
minimum width of pronotal disc	0.83-1.04 0.93 ± 0.05 n = 22	0.85-1.0 0.93 ± 0.04 n = 10	0.79-0.95 0.85 ± 0.05 n = 17
maximum width of pronotal disc	1.84-2.27 2.09 ± 0.11 n = 22	1.95-2.1 2.01 ± 0.05 n = 10	1.80-2.50 2.07 ± 0.15 n = 17
ratio maximum / minimum width of pronotal disc	2.05-2.59 2.26 ± 0.13 n = 22	2.0-2.35 2.15 ± 0.11 n = 10	2.21-2.95 2.45 ± 0.19 n = 17
minimum diameter of tympanal opening	0.18-0.42 0.28 ± 0.06 n = 22	0.175-0.325 0.238 ± 0.05 n = 10	0.125-0.25 0.194 ± 0.03 n = 17
maximum diameter of tympanal opening	1.16-1.35 1.24 ± 0.05 n = 22	1.0-1.21 1.12 ± 0.05 n = 10	1.0-1.23 1.14 ± 0.07 n= 17
ratio maximum / minimum diameter of tympanal opening	3.0-6.7 4.54 ± 0.9 n = 22	3.38-6.36 4.95 ± 1.0 n = 10	4.88-9.0 6.12 ± 1.20 n = 17
length of fore wing	11.0-15.5 13.3 ± 0.9 n = 30	10.6-12.1 11.3 ± 0.5 n = 16	12.0-14.8 13.1 ± 0.8 n = 17
distance from stigma to tip of fore wing	4.3-6.0 5.11 ± 0.39 n = 30	3.4-4.43 3.96 ± 0.32 n = 16	3.5-4.7 4.31 ± 0.29 n = 17

males	*biguttulus euhedickei*	*biguttulus parnassicus*	*biguttulus biguttulus*
ratio distance from stigma to tip / length of fore wing	0.34-0.49	0.32-0.38	0.29-0.36
	0.38 ± 0.03	0.35 ± 0.02	0.32 ± 0.02
	n = 30	n = 16	n = 17
width of C area	0.64-0.97	0.56-0.67	0.675-0.83
	0.84 ± 0.07	0.62 ± 0.03	0.745 ± 0.04
	n = 30	n = 16	n = 17
width of Sc area	0.28-0.62	0.19-0.30	0.42-0.56
	0.44 ± 0.08	0.233 ± 0.28	0.477 ± 0.04
	n = 30	n = 16	n = 17
ratio width C / width Sc area	1.36-3.14	2.21-3.25	1.26-1.84
	1.94 ± 0.44	2.68 ± 0.3	1.57 ± 0.15
	n = 30	n = 16	n = 17
width combined C & Sc areas	0.95-1.38	0.76-0.97	1.125-1.30
	1.15 ± 0.09	0.84 ± 0.05	1.21 ± 0.06
	n = 30	n = 16	n = 17
ratio width combined C & Sc areas × 100 / length of fore wing	7.55-9.75	6.74-8.55	8.27-9.89
	8.69 ± 0.59	7.49 ± 0.54	9.27 ± 0.37
	n = 30	n = 16	n = 17
ratio length of fore wing / width of Sc area	23.02-47.55	37.8-60.5	23.67-32.88
	30.82 ± 5.9	49.0 ± 6.4	27.56 ± 2.27
	n = 30	n = 16	n = 17
ratio length of fore wing / width of C area	14.01-19.68	16.48-19.94	16.40-18.93
	15.99 ± 1.27	18.26 ± 1.11	17.61 ± 0.82
	n = 30	n = 16	n = 17
length of hind femur	8.5-11.4	8.4-9.18	8.7-10.6
	9.7 ± 0.6	8.79 ± 0.3	9.41 ± 0.5
	n = 30	n = 16	n = 17
ratio length of fore wing / length of hind femur	1.17-1.58	1.18-1.38	1.24-1.49
	1.37 ± 0.08	1.28 ± 0.05	1.39 ± 0.05
	n = 30	n = 16	n = 17
length of stridulatory file	4.20-5.77	3.2-3.75	2.85-3.70
	5.12 ± 0.44	3.51 ± 0.13	3.24 ± 0.25
	n = 30	n = 16	n = 17
distance from end of file to tip of knee	2.30-3.58	3.2-4.05	4.0-5.03
	2.95 ± 0.34	3.68 ± 0.26	4.45 ± 0.31
	n = 30	n = 16	n = 17
ratio length of file / distance from end of file to tip of knee	1.24-2.19	0.85-1.09	0.63-0.88
	1.75 ± 0.26	0.95 ± 0.07	0.73 ± 0.07
	n = 30	n = 16	n = 17
number of stridulatory pegs	109-149	95-122	84-114
	127.2 ± 10.2	107.6 ± 6.5	98 ± 8.1
	n = 30	n = 16	n = 17
number of stridulatory pegs per mm	20.2-31.4	26.4-35.8	26.5-35.3
	25.0 ± 2.7	30.7 5 ± 2.1	30.25 ± 2.1
	n = 30	n = 16	n = 17

Table 27. Biometric data for females of *Chorthippus biguttulus euhedickei*, *C. biguttulus parnassicus* and *C. biguttulus biguttulus*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of *C. biguttulus biguttulus* were taken from specimens from central and western Europe, of *C. b. euhedickei* exclusively from Greece and those of *C. biguttulus parnassicus* from its typical site, Mt. Parnassos, Central Greece.

females	*biguttulus euhedickei*	*biguttulus parnassicus*	*biguttulus biguttulus*
length of prozona	1.75-2.0 1.85 ± 0.07 n = 10	1.7-1.9 1.78 ± 0.07 n = 6	1.7-1.9 1.77 ± 0.07 n = 7
length of metazona	2.1-2.4 2.25 ± 0.09 n = 10	1.9-2.3 2.1 ± 0.12 n = 6	1.95-2.3 2.13 ± 0.12 n = 7
ratio length prozona / length metazona	0.78-0.90 0.82 ± 0.04 n = 10	0.80-0.89 0.85 ± 0.03 n = 6	0.78-0.87 0.83 ± 0.03 n = 7
minimum width of pronotal disc	1.1-1.3 1.18 ± 0.7 n = 10	1.1-1.3 1.2 ± 0.08 n = 6	1.0-1.1 1.05 ± 0.04 n = 7
maximum width of pronotal disc	2.8-3.1 2.96 ± 0.11 n = 10	2.5-3.0 2.7 ± 0.17 n = 10	2.6-2.9 2.72 ± 0.11 n = 7
ratio maximum / minimum width of pronotal disc	2.33-2.72 2.51 ± 0.14 n = 10	2.01-2.61 2.32 ± 0.22 n = 6	2.36-2.80 2.58 ± 0.14 n = 7
minimum diameter of tympanal opening	1.3-1.6 1.45 ± 0.11 n = 10	1.4-1.5 1.46 ± 0.04 n = 6	1.1-1.3 1.23 ± 0.06 n = 7
maximum diameter of tympanal opening	0.2-0.40 0.29 ± 0.05 n = 10	0.18-0.25 0.21 ± 0.02 n = 6	1.18-0.30 0.21 ± 0.04 n = 7
ratio maximum / minimum diameter of tympanal opening	3.25-7.50 5.07 ± 1.10 n = 10	6.0-7.77 7.13 ± 0.62 n = 6	4.33-6.66 5.82 ± 0.78 n = 7
length of fore wing	15.1-18.2 16.42 ± 1.13 n = 10	14.1-14.8 14.4 ± 0.25 n = 6	14.7-16.2 15.6 ± 0.50 n = 7
distance from stigma to tip of fore wing	5.6-7.4 6.53 ± 0.37 n = 10	4.8-5.8 5.33 ± 0.37 n = 6	5.2-6.1 5.64 ± 0.31 n = 7
ratio distance from stigma to tip / length of fore wing	0.35-0.45 0.39 ± 0.03 n = 10	0.33-0.41 0.37 ± 0.03 n = 6	0.33-0.38 0.36 ± 0.02 n = 7
length of hind femur	11.1-13.1 12.38 ± 0.6 n = 10	11.4-12.4 11.73 ± 0.39 n = 6	11.5-12.2 11.84 ± 0.24 n = 7
ratio length of fore wing / length of hind femur	1.22-1.43 1.32 ± 0.07 n = 10	1.17-1.26 1.23 ± 0.03 n = 6	1.25-1.34 1.31 ± 0.03 n = 7
length of sridulatory file	5.2-6.3 5.71 ± 0.31 n = 10	4.3-4.7 4.5 ± 0.17 n = 6	3.7-4.4 3.97 ± 0.26 n = 7

females	*biguttulus euhedickei*	*biguttulus parnassicus*	*biguttulus biguttulus*
distance from end of file to tip of knee	3.6-5.0 4.27 ± 0.38 n = 10	4.7-5.5 5.16 ± 0.31 n = 6	5.1-6.1 5.54 ± 0.38 n = 7
ratio length of file / distance from end of file to tip of knee	1.14-1.63 1.35 ± 0.16 n = 10	0.78-0.95 0.87 ± 0.07 n = 6	0.61-0.83 0.72 ± 0.08 n = 7
number of stridulatory pegs	90-118 102.8 ± 9.6 n = 10	70-90 79.5 ± 8.9 n = 6	84-105 93.4 ± 6.9 n = 7
number of stridulatory pegs per mm	16.6-20.3 17.9 ± 1.1 n = 10	14.8-20.9 17.7 ± 2.5 n = 6	21-25 23.5 ± 1.4 n = 7

Table 28. Biometric data for males of typical *Chorthippus moreanus* and some non-identifiable, transitional populations between typical *C. moreanus* and *C. pulloides-crassiceps* complex. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of typical *C. moreanus* were taken from its type-locality Bassae, those of transitional forms of the populations from the pass over Mt. Taiyetos between Kalamata and Sparti and from Elati, south of Vitina, the high plateau of Arkadhia, respectively.

males	*moreanus* (typical)	transitional population: Mt. Taiyetos, pass between Kalamata-Sparti	transitional population: Elati, S of Vitina, Arkadhia
length of pronotum	2.9-3.5 3.15 ± 0.17 n = 20	2.6-3.0 2.83 ± 0.15 n = 5	2.7-3.1 2.9 ± 0.16 n = 5
length of prozona	1.5-1.8 1.59 ± 0.08 n = 20	1.4-1.55 1.47 ± 0.07 n = 5	1.4-1.55 1.45 ± 0.07 n = 5
length of metazona	1.4-1.7 1.56 ± 0.09 n = 20	1.2-1.45 1.36 ± 0.09 n = 5	1.3-1.55 1.45 ± 0.1 n = 5
ratio length of prozona / length of metazona	0.94-1.07 1.02 ± 0.04 n = 20	1.0-1.17 1.08 ± 0.06 n = 5	0.93-1.07 1.0 ± 0.05 n = 5
minimum diameter of tympanal opening	0.17-0.35 0.25 ± 0.05 n = 17	0.2-0.35 0.27 ± 0.07 n = 5	0.15-0.3 0.22 ± 0.05 n = 5
maximum diameter of tympanal opening	1.10-1.40 1.22 ± 0.08 n = 17	1.1-1.3 1.2 ± 0.08 n = 5	1.05-1.2 1.11 ± 0.05 n = 5
ratio maximum / minimum diameter of tympanal opening	3.57-7.14 4.95 ± 1.0 n = 17	4.5-9.0 6.01 ± 2.0 n = 5	4.0-7.33 5.35 ± 1.2 n = 5
length of fore wing	10.3-11.7 10.99 ± 0.44 n = 20	7.9-9.4 8.63 ± 0.66 n = 5	7.5-8.2 7.86 ± 0.27 n = 5

males	*moreanus* (typical)	transitional population: Mt. Taiyetos, pass between Kalamata-Sparti	transitional population: Elati, S of Vitina, Arkadhia
distance from stigma to tip of fore wing	2.7-3.32 2.89 ± 0.15 n = 20	1.7-2.0 1.88 ± 0.13 n = 5	1.2-1.8 1.38 ± 0.27 n = 5
ratio distance from stigma to tip / length of fore wing	0.23-0.29 0.26 ± 0.01 n = 20	0.21-0.25 0.22 ± 0.02 n = 5	0.15-0.23 0.17 ± 0.03 n = 5
width of C area	0.55-0.62 0.58 ± 0.02 n = 20	0.5-0.57 0.53 ± 0.03 n = 5	0.45-0.57 0.53 ± 0.05 n = 5
width of Sc area	0.22-0.32 0.26 ± 0.03 n = 20	0.21-0.27 0.24 ± 0.02 n = 5	0.25-0.27 0.26 ± 0.01 n = 5
ratio width of C / width of Sc area	1.69-2.67 2.23 ± 0.26 n = 20	2.00-2.22 2.10 ± 0.08 n = 5	1.8-2.3 2.05 ± 0.23 n = 5
width combined C & Sc areas	0.80-0.90 0.84 ± 0.03 n = 20	0.72-0.85 0.77 ± 0.05 n = 5	0.7-0.82 0.78 ± 0.05 n = 5
ratio width combined C & Sc areas × 100 / length of fore wing	7.13-8.18 7.69 ± 0.39 n = 20	8.42-9.45 9.07 ± 0.39 n = 5	8.75-10.71 9.99 ± 0.74 n = 5
length of hind femur	9.4-10.6 9.98 ± 0.3 n = 20	7.7-9.1 8.65 ± 0.58 n = 5	7.7-9.0 8.26 ± 0.5 n = 5
ratio length of fore wing / length of hind femur	1.0-1.23 1.10 ± 0.05 n = 20	0.95-1.03 1.01 ± 0.03 n = 5	0.91-1.00 0.95 ± 0.04 n = 5
length of sridulatory file	3.1-3.8 3.42 ± 0.19 n = 19	2.6-2.95 2.73 ± 0.15 n = 5	2.3-2.8 2.6 ± 0.2 n = 5
distance from end of file to tip of knee	4.2-5.0 4.67 ± 0.2 n = 19		3.8-4.0 3.87 ± 0.08 n = 5
ratio length of file / distance from end of file-tip of knee	0.67-0.82 0.73 ± 0.04 n = 19		0.57-0.72 0.67 ± 0.06 n = 5
number of stridulatory pegs	100-136 115.7 ± 10.3 n = 19	92-101 95.7 ± 3.7 n = 5	99-103 101.6 ± 1.6 n = 5
number of stridulatory pegs per mm	29.4-36.3 33.8 ± 2.0 n = 19	35.4-44.8 37.8 ± 3.9 n = 5	36.6-44.3 39.2 ± 3.2 n = 5
maximum width of head	2.75-3.1 2.92 ± 0.1 n = 17	2.6-3.1 2.79 ± 0.19 n = 5	2.5-2.65 2.55 ± 0.07 n = 5
ratio length of pronotum / max. width of head	1.01-1.14 1.07 ± 0.03 n = 17	1.0-1.12 1.02 ± 0.05 n = 5	1.07-1.2 1.13 ± 0.06 n = 5

Table 29. Biometric data for females of *Chorthippus moreanus*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of typical *C. moreanus* were taken from its type-locality Bassae.

females	*moreanus* (typical)
length of pronotum	3.8-4.5 4.1 ± 0.25 n = 7
length of prozona	1.8-2.2 2.02 ± 0.12 n = 7
length of metazona	2.0-2.3 2.07 ± 0.12 n = 7
ratio length of prozona / length of metazona	0.9-1.05 0.98 ± 0.05 n = 7
minimum width of pronotal disc	1.1-1.4 1.2 ± 0.1 n = 7
maximum width of pronotal disc	2.7-3.0 2.8 ± 0.11 n = 7
ratio maximum / minimum width of pronotal disc	2.14-2.72 2.39 ± 0.19 n = 7
maximum diameter of tympanal openig	1.3-1.6 1.44 ± 0.09 n = 7
minimum diameter of tympanal opening	0.15-0.28 0.18 ± 0.04 n = 7
ratio maximum / minimum diameter tympanal opening	5.0-10.6 8.0 ± 1.7 n = 7
length of fore wing	12.8-14.2 13.5 ± 0.45 n = 7
distance from stigma to tip of fore wing	4.0-4.5 4.2 ± 0.17 n = 7
ratio distance stigma to tip / length of fore wing	0.29-0.35 0.31 ± 0.02 n = 7
length of hind femur	11.9-13.6 12.7 ± 0.67 n = 7
ratio length of fore wing / length of hind femur	1.02-1.13 1.06 ± 0.04 n = 7
interocular distance	1.0-1.2 1.11 ± 0.06 n = 7

females	*moreanus* (typical)
maximum diameter eye	2.2-2.4 2.27 ± 0.07 n = 7
ratio interocular distance / maximum diameter eye	0.45-0.53 0.49 ± 0.03 n = 7
maximum width of head	3.8-4.2 4.0 ± 0.13 n = 7
ratio length of pronotum / maximum width of head	0.97-1.02 1.02 ± 0.04 n = 7

Table 30. Biometric data for males of *Chorthippus mollis mollis*, typical *C. mollis lesinensis* and *C. mollis pechevi*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of *C. m. mollis* were taken from Greece, of typical *C. m. lesinensis* from Dalmatian islands and of *C. m. pechevi* from the type series.

males	*mollis mollis* (Greece)	*mollis lesinensis* (typical)	*mollis pechevi* (type series)
length of pronotum	2.6-3.3 2.95 ± 0.2 n = 20	2.9-3.1 2.94 ± 0.09 n = 7	
length of prozona	1.25-1.65 1.45 ± 0.12 n = 20	1.45-1.60 1.5 ± 0.05 n = 7	1.3-1.5 1.4 ± 0.07 n = 5
length of metazona	1.35-1.70 1.50 ± 0.11 n = 20	1.40-1.5 1.44 ± 0.04 n = 7	1.46-1.6 1.52 ± 0.05 n = 5
ratio length of prozona / length of metazona	0.89-1.11 0.97 ± 0.05 n = 20	1.0-1.07 1.04 ± 0.04 n = 7	0.87-0.96 0.92 ± 0.03 n = 5
minimum width of pronotal disc	0.75-1.10 0.87 ± 0.09 n = 20	0.90-1.05 0.97 ± 0.06 n = 6	0.81-0.95 0.89 ± 0.05 n = 5
maximum width of pronotal disc	1.7-2.1 1.90 ± 0.12 n = 20	1.9-2.0 1.97 ± 0.05 n = 6	2.0-2.2 2.08 ± 0.08 n = 5
ratio maximum / minimum width of pronotal disc	1.9-2.4 2.18 ± 0.15 n = 20	1.9-2.2 2.03 ± 0.12 n = 6	2.10-2.59 2.33 ± 0.18 n = 5
minimum diameter of tympanal opening	0.15-0.325 0.24 ± 0.05 n = 20	0.16-0.25 0.2 ± 0.03 n = 7	0.22-0.30 0.27 ± 0.03 n = 5
maximum diameter of tympanal opening	1.02-1.25 1.12 ± 0.05 n = 20	1.07-1.3 1.18 ± 0.06 n = 7	1.04-1.15 1.09 ± 0.04 n = 5
ratio maximum / minimum diameter tympanal opening	3.38-7.33 4.89 ± 1.04 n = 20	4.8-7.18 5.98 ± 0.76 n = 7	3.62-4.72 4.10 ± 0.46 n = 5

males	*mollis mollis* (Greece)	*mollis lesinensis* (typical)	*mollis pechevi* (type series)
length of fore wing	8.7-12.7 10.7 ± 1.1 n = 28	10.0-10.9 10.4 ± 0.3 n = 7	12.5-13.8 13.22 ± 0.51 n = 5
distance from stigma to tip of fore wing	2.8-5.0 3.46 ± 0.58 n = 28	2.6-3.45 3.21 ± 0.28 n = 7	4.9-5.4 5.12 ± 0.18 n = 5
ratio distance stigma to tip / length of fore wing	0.28-0.39 0.32 ± 0.02 n = 28	0.26-0.33 0.31 ± 0.02 n = 7	0.37-0.41 0.39 ± 0.01 n = 5
width of C area	0.44-0.60 0.52 ± 0.04 n = 28	0.41-0.5 0.46 ± 0.03 n = 7	0.49-0.60 0.523 ± 0.04 n = 5
width of Sc area	0.22-0.35 0.28 ± 0.03 n = 28	0.22-0.30 0.25 ± 0.03 n = 7	0.23-0.27 0.25 ± 0.01 n = 5
ratio width C / width Sc area	1.53-2.22 1.85 ± 0.18 n = 28	1.46-2.18 1.86 ± 0.24 n = 7	1.92-2.40 2.11 ± 0.18 n = 5
width combined C & Sc areas	0.665-0.95 0.80 ± 0.06 n = 28	0.7-0.8 0.72 ± 0.04 n = 7	0.72-0.85 0.77 ± 0.05 n = 5
ratio width combined C & Sc areas × 100 / length of fore wing	5.95-8.67 7.55 ± 0.64 n = 28	6.42-7.62 6.89 ± 0.38 n = 7	5.29-6.44 5.85 ± 0.47 n = 5
ratio length of fore wing / width of Sc area	32.66-50.8 38.17 ± 4.6 n = 28	35-46.8 41.8 ± 4.8 n = 7	48.1-59.1 53.47 ± 4.0 n = 5
length of hind femur	7.7-11.1 8.9 ± 0.83 n = 28	9.1-10.9 9.63 ± 0.62 n = 7	9.1-10.7 9.84 ± 0.58 n = 5
ratio length of fore wing / length of hind femur	1.09-1.40 1.19 ± 0.07 n = 28	0.96-1.15 1.08 ± 0.06 n = 7	1.27-1.43 1.34 ± 0.06 n = 5
ratio length of fore wing / width of C area	17.6-25.2 20.62 ± 2.04 n = 28	21-24.6 22.53 ± 1.3 n = 7	24.5-27.7 25.37 ± 2.4 n = 5
length of sridulatory file	2.6-3.65 3.07 ± 0.29 n = 28	3.1-3.8 3.37 ± 0.23 n = 7	3.2-4.1 3.73 ± 0.4 n = 5
distance from end of file to tip of knee	3.55-5.20 4.23 ± 0.41 n = 28	4.1-5.1 4.41 ± 0.39 n = 7	4.3-5.2 4.76 ± 0.35 n = 5
ratio length of file / distance from end of file to tip of knee	0.61-0.83 0.72 ± 0.05 n = 28	0.73-0.83 0.76 ± 0.03 n = 7	0.69-0.94 0.78 ± 0.1 n = 5
number of stridulatory pegs	94-134 112.5 ± 11 n = 23	105-138 116.2 ± 11.4 n = 7	110-135 119.4 ± 9.7 n = 5
number of stridulatory pegs per mm	28.5-40.0 36.1 ± 3 n = 23	27.6-39.4 34.5 ± 4.2 n = 7	29.5-35.9 32.1 ± 2.5 n = 5

males	*mollis mollis* (Greece)	*mollis lesinensis* (typical)	*mollis pechevi* (type series)
length of tip of subgenital plate	0.60-0.85 0.72 ± 0.06 n = 20		
maximum width of head	2.45-3.0 2.62 ± 0.16 n = 20	2.73-3.0 2.85 ± 0.11 n = 7	2.6-2.9 2.76 ± 0.19 n = 5
ratio length of pronotum / maximum width of head	1.0-1.22 1.12 ± 0.05 n = 20	1.01-1.06 1.03 ± 0.01 n = 7	1.03-1.10 1.07 ± 0.04 n = 5
interocular distance			0.78-0.80 0.79 ± 0.01 n = 5
maximum diameter eye			1.65-1.70 1.67 ± 0.03 n = 5
ratio interocular distance / maximum diameter eye			0.45-0.48 0.47 ± 0.01 n = 5

Table 31. Biometric data for females of *Chorthippus mollis mollis*, and typical *C. mollis lesinensis*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of *C. m. mollis* were taken from Greece and of typical *C. m. lesinensis* from Dalmatian islands.

females	*mollis mollis* (Greece)	*mollis lesinensis* (typical)
length of pronotum	3.1-4.2 3.84 ± 0.18 n = 10	3.3-4.3 3.75 ± 0.36 n = 7
length of prozona	1.6-2.0 1.83 ± 0.11 n = 10	1.75-2.1 1.94 ± 0.15 n = 5
length of metazona	1.75-2.2 2.00 ± 0.13 n = 10	1.75-2.0 1.89 ± 0.11 n = 5
ratio length of prozona / length of metazona	0.76-1.06 0.91 ± 0.08 n = 10	-1.05 1.02 ± 0.02 n = 5
minimum width of pronotal disc	0.9-1.3 1.09 ± 0.09 n = 20	1.15-1.3 1.20 ± 0.05 n = 5
maximum width of pronotal disc	2.4-3.0 2.69 ± 0.17 n = 20	2.5-3.0 2.68 ± 0.19 n = 5
ratio maximum / minimum width of pronotal disc	2.15-2.80 2.46 ± 0.17 n = 20	2.16-2.30 2.22 ± 0.07 n = 5
maximum diameter of tympanal openig	1.25-1.40 1.31 ± 0.06 n = 10	1.19-1.5 1.42 ± 0.13 n = 5

females	*mollis mollis* (Greece)	*mollis lesinensis* (typical)
minimum diameter of tympanal opening	0.15-0.25 0.195 ± 0.04 n = 10	0.13-0.3 0.19 ± 0.06 n = 5
ratio maximum / minimum diameter tympanal opening	5.0-9.33 6.96 ± 1.52 n = 10	5-11.1 7.9 ± 2.6 n = 5
length of fore wing	12.1-16.0 13.63 ± 1.3 n = 21	12.3-14.6 13.18 ± 0.88 n = 5
distance from stigma to tip of fore wing	4.0-5.7 4.77 ± 0.68 n = 10	4.7-6.3 5.58 ± 0.61 n = 5
ratio distance stigma to tip / length of fore wing	0.31-0.39 0.35 ± 0.03 n = 10	0.38-0.48 0.42 ± 0.05 n = 5
length of hind femur	10.2-13.2 11.7 ± 0.75 n = 21	10.8-13.3 12.26 ± 1.0 n = 5
ratio length of fore wing / length of hind femur	1.01-1.31 1.16 ± 0.07 n = 21	1.03-1.313 1.07 ± 0.37 n = 5
interocular distance	0.95-1.1 1.02 ± 0.06 n = 7	0.98-1.25 1.08 ± 0.11 n = 5
maximum diameter eye	1.97-2.16 2.05 ± 0.07 n = 7	2.13-2.53 2.29 ± 0.15 n = 5
ratio interocular distance / maximum diameter eye	0.46-0.55 0.50 ± 0.028 n = 7	0.45-0.49 0.47 ± 0.01 n = 5
maximum width of head	3.4-4.0 3.61 ± 0.19 n = 10	3.35-4.45 3.89 ± 0.33 n = 7
ratio length of pronotum / maximum width of head	1.01-1.16 1.06 ± 0.04 n = 10	0.89-1.10 0.98 ± 0.06 n = 7

Table 32. Biometric data for males of typical *Chorthippus crassiceps*, its morphologically slightly and more atypical forms and of *C. parnon*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of typical *C. crassiceps* were taken from its type locality, the island of Poros, its slightly atypical forms from Epidavros & Mt. Dhidhimotikon, its more atypical forms from Sofikon & Limnes respectively (figs 268-269) and those of *C. parnon* from the topotypical area of Monemvasia.

males	*crassiceps* (typical)	*crassiceps* (slightly atypical)	*crassiceps* (strongly atypical)	*parnon*
length of pronotum	2.8-3.2 2.97 ± 0.11 n = 20	2.7-3.2 2.9 ± 0.15 n = 8	2.7-3.11 2.87 ± 0.12 n = 9	2.7-3.3 3.03 ± 0.15 n = 20

males	*crassiceps* (typical)	*crassiceps* (slightly atypical)	*crassiceps* (strongly atypical)	*parnon*
length of prozona	1.45-1.70 1.54 ± 0.07 n = 20	1.4-1.65 1.48 ± 0.08 n = 8	1.4-1.55 1.47 ± 0.05 n = 9	1.4-1.7 1.57 ± 0.07 n = 20
length of metazona	1.35-1.53 1.42 ± 0.05 n = 20	1.28-1.55 1.41 ± 0.08 n = 8	1.25-1.6 1.4 ± 0.1 n = 9	1.27-1.65 1.46 ± 0.1 n = 20
ratio length of prozona / length of metazona	1.04-1.15 1.09 ± 0.03 n = 20	1.0-1.1 1.05 ± 0.04 n = 8	0.94-1.16 1.05 ± 0.07 n = 9	0.93-1.23 1.07 ± 0.07 n = 20
minimum width of pronotal disc	0.84-1.10 0.97 ± 0.08 n = 19	0.85-0.9 0.88 ± 0.02 n = 3	0.78-0.95 0.84 ± 0.07 n = 4	
maximum width of pronotal disc	1.8-2.1 1.96 ± 0.08 n = 19	1.8-2.0 1.93 ± 0.11 n = 3	1.8-1.9 1.83 ± 0.04 n = 4	
ratio maximum / minimum width of pronotal disc	1.82-2.35 2.02 ± 0.15 n = 19	2.0-2.35 2.19 ± 0.18 n = 3	1.0-2.3 2.18 ± 0.13 n = 4	
minimum diameter of tympanal opening	0.3-0.4 0.34 ± 0.03 n = 16	0.2-0.43 0.31 ± 0.08 n = 8	0.15-0.4 0.25 ± 0.07 n = 9	0.30-0.45 0.36 ± 0.04 n = 20
maximum diameter of tympanal opening	1.1-1.25 1.18 ± 0.05 n = 16	1.0-1.2 1.09 ± 0.06 n = 8	1.0-1.15 1.05 ± 0.06 n = 9	1.0-1.24 1.13 ± 0.05 n = 20
ratio maximum / minimum diameter tympanal opening	2.87-4.17 3.51 ± 0.43 n = 16	2.55-5.25 3.7 ± 0.86 n = 8	2.5-7.13 4.44 ± 1.3 n = 9	2.5-3.83 3.12 ± 0.4 n = 20
length of fore wing	9.6-11.5 10.67 ± 0.44 n = 20	8.4-10.3 9.5 ± 0.57 n = 8	6.9-9.1 7.48 ± 0.38 n = 9	9.7-11.1 10.5 ± 0.36 n = 20
distance from stigma to tip of fore wing	2.9-3.5 3.32 ± 0.17 n = 20	2.5-2.9 2.74 ± 0.17 n = 8	0.9-1.5 1.17 ± 0.3 n = 3	2.9-3.7 3.26 ± 0.17 n = 20
ratio distance stigma to tip / length of fore wing	0.29-0.33 0.31 ± 0.01 n = 20	0.27-0.29 0.28 ± 0.01 n = 8	0.12-0.20 0.16 ± 0.04 n = 3	0.27-0.33 0.31 ± 0.01 n = 20
width of C area	0.50-0.62 0.56 ± 0.03 n = 20	0.5-0.58 0.54 ± 0.03 n = 8	0.45-0.55 0.50 ± 0.04 n = 9	0.47-0.62 0.54 ± 0.045 n = 20
width of Sc area	0.2-0.28 0.23 ± 0.02 n = 20	0.2-0.27 0.23 ± 0.02 n = 8	0.2-0.28 0.237 ± 0.02 n = 9	0.15-0.25 0.19 ± 0.03 n = 20
ratio width C / width Sc area	1.91-3.0 2.42 ± 0.32 n = 20	2.0-2.75 2.36 ± 0.34 n = 8	1.8-2.75 2.15 ± 0.29 n = 9	2.0-4.0 2.91 ± 0.6 n = 20
width combined C & Sc areas	0.75-0.88 0.81 ± 0.04 n = 20	0.75-0.825 0.77 ± 0.03 n = 8	0.67-0.83 0.74 ± 0.05 n = 9	0.67-0.80 0.73 ± 0.03 n = 20
ratio width combined C & Sc areas × 100 / length of fore wing	6.61-8.42 7.56 ± 0.49 n = 20	7.57-8.92 8.21 ± 0.49 n = 8	9.46-10.87 9.93 ± 0.49 n = 9	6.31-7.73 6.97 ± 0.44 n = 20

males	*crassiceps* (typical)	*crassiceps* (slightly atypical)	*crassiceps* (strongly atypical)	*parnon*
ratio length of fore wing / width of Sc area	36.1-53.5	33.6-47.8	27.6-39	
	46.1 ± 5.4	41.4 ± 4.5	32 ± 3.6	
	n = 20	n = 8	n = 8	
length of hind femur	9.5-10.7	8.2-10.3	8.5-9.8	9.0-10.3
	9.98 ± 0.38	9.12 ± 0.65	9.23 ± 0.47	9.73 ± 0.3
	n = 20	n = 8	n = 9	n = 20
ratio length of fore wing / length of hind femur	1.0-1.14	1.0-1.1	0.78-0.83	0.96-1.14
	1.07 ± 0.03	1.04 ± 0.03	0.81 ± 0.02	1.08 ± 0.05
	n = 20	n = 8	n = 9	n = 20
ratio length of fore wing / width of C area	17.6-22.5	15.8-19.8	14.1-16.4	
	19.08 ± 1.3	17.6 ± 1.3	15.1 ± 0.8	
	n = 20	n = 8	n = 8	
length of stridulatory file	2.7-3.56	2.6-3.2	2.2-2.7	2.8-3.4
	3.07 ± 0.23	2.88 ± 0.19	2.55 ± 0.17	3.09 ± 0.16
	n = 20	n = 8	n = 8	n = 20
distance from end of file to tip of knee	4.3-5.1	3.9-5.2	4.25-4.9	4.2-5.0
	4.82 ± 0.22	4.35 ± 0.39	4.52 ± 0.21	4.66 ± 0.2
	n = 20	n = 8	n = 8	n = 20
ratio length of file / distance from end of file to tip of knee	0.54-0.73	0.59-0.71	0.5-0.62	0.57-0.78
	0.64 ± 0.05	0.66 ± 0.04	0.56 ± 0.04	0.67 ± 0.05
	n = 20	n = 8	n = 8	n = 20
number of stridulatory pegs	89-122	94-120	74-96	97-138
	106.5 ± 10.15	105.3 ± 8.9	84.6 ± 7.2	116.5 ± 12.4
	n = 20	n = 8	n = 8	n = 20
number of stridulatory pegs per mm	30.7-40.0	32.4-41.8	27.4-38.2	31.3-43.1
	34.5 ± 2.5	36.6 ± 3.4	33.3 ± 3.5	37.6 ± 3.1
	n = 20	n = 8	n = 8	n = 20
maximum width of head	2.94-3.29	2.7-3.2	2.9-3.3	2.95-3.45
	3.13 ± 0.10	2.95 ± 0.16	3.0 ± 0.12	3.17 ± 0.1
	n = 20	n = 8	n = 9	n = 20
ratio length of pronotum / maximum width of head	0.88-0.99	0.92-1.04	0.93-1.01	0.83-1.03
	0.95 ± 0.03	0.98 ± 0.04	0.95 ± 0.02	0.96 ± 0.04
	n = 20	n = 8	n = 9	n = 20

Table 33. Biometric data for females of typical *Chorthippus crassiceps* and *C. parnon*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of typical *C. crassiceps* were taken from its type locality, the island of Poros, those of *C. parnon* from the topotypical area of Monemvasia.

females	*crassiceps* (typical)	*parnon*
length of pronotum	3.6-4.1	3.7-4.3
	3.76 ± 0.15	4.00 ± 0.19
	n = 10	n = 7
length of prozona	1.9-2.1	1.9-2.1
	1.99 ± 0.06	1.98 ± 0.06
	n = 7	n = 7
length of metazona	1.7-2.1	1.8-2.2
	1.87 ± 0.12	2.02 ± 0.14
	n = 7	n = 7

females	*crassiceps* (typical)	*parnon*
ratio length of prozona / length of metazona	1.0-1.18 1.07 ± 0.05 n = 10	0.9-1.05 0.98 ± 0.05 n = 7
minimum width of pronotal disc	1.1-1.3 1.22 ± 0.07 n = 7	1.1-1.4 1.31 ± 0.08 n = 7
maximum width of pronotal disc	2.5-3.0 2.7 ± 0.16 n = 7	2.7-3.1 2.7 ± 0.12 n = 7
ratio maximum / minimum width of pronotal disc	2.03-2.45 2.20 ± 0.14 n = 7	2.03-2.58 2.22 ± 0.21 n = 7
maximum diameter of tympanal openig	1.35-1.55 1.45 ± 0.06 n = 7	1.2-1.5 1.33 ± 0.09 n = 7
minimum diameter of tympanal opening	0.28-0.45 0.36 ± 0.05 n = 7	0.28-0.44 0.37 ± 0.06 n = 7
ratio maximum / minimum diameter tympanal opening	3.3-5.5 4.04 ± 0.76 n = 7	3.02-5.2 3.67 ± 0.74 n = 7
length of fore wing	12.3-14.6 13.09 ± 0.5 n = 10	13.2-14.9 13.9 ± 0.6 n = 7
distance from stigma to tip of fore wing	4.0-4.8 4.47 ± 0.28 n = 7	3.9-5.3 4.8 ± 0.47 n = 7
ratio distance stigma to tip / length of fore wing	0.28-0.35 0.33 ± 0.02 n = 7	0.29-0.37 0.34 ± 0.02 n = 7
length of hind femur	11.3-13.6 12.19 ± 0.5 n = 19	11.7-13.7 12.7 ± 0.69 n = 7
ratio length of fore wing / length of hind femur	0.98-1.13 1.07 ± 0.04 n = 10	1.02-1.13 1.09 ± 0.03 n = 7
interocular distance	0.93-1.1 1.03 ± 0.06 n = 7	1.0-1.2 1.09 ± 0.06 n = 7
maximum diameter eye	2.3-2.48 2.36 ± 0.08 n = 7	2.3-2.5 2.42 ± 0.07 n = 7
ratio interocular distance / maximum diameter eye	0.40-0.47 0.43 ± 0.02 n = 7	0.42-0.48 0.44 ± 0.02 n = 7
maximum width of head	3.8-4.2 4.03 ± 0.15 n = 10	3.9-4.6 4.24 ± 0.23 n = 7
ratio length of pronotum / maximum width of head	0.88-0.98 0.93 ± 0.03 n = 10	0.89-0.97 0.94 ± 0.02 n = 7

Table 34. Biometric data for males of *Chorthippus pulloides* and *C. sangiorgii*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of *C. pulloides* were taken from the typical populations of the Peloponnese and the Pindhos range and separately of specimens from Mt. Akarnanika, southwestern mainland of Greece and those of *C. sangiorgii* from the island of Kefallonia

males	*pulloides* (Peloponnese & Pindos range)	*pulloides* (Mt. Akarnanika)	*sangiorgii* (Island of Kefallinia)
length of pronotum	2.6-3.7 3.14 ± 0.22 n = 41	2.9-3.3 3.07 ± 0.14 n = 10	2.6-2.8 2.67 ± 0.06 n = 12
length of prozona	1.3-1.9 1.61 ± 0.11 n = 41	1.48-1.70 1.57 ± 0.08 n = 10	1.3-1.4 1.35 ± 0.04 n =12
length of metazona	1.2-1.8 1.53 ± 0.12 n = 41	1.37-1.60 1.50 ± 0.07 n = 10	1.2-1.4 1.30 ± 0.07 n = 12
ratio length of prozona / length of metazona	0.93-1.16 1.06 ± 0.06 n = 41	0.94-1.12 1.04 ± 0.05 n = 10	0.93-1.16 1.03 ± 0.08 n = 12
minimum width pronotal disc	0.95-1.1 1.03 ± 0.06 n = 5	0.90-0.95 0.91 ± 0.02 n = 4	0.80-0.91 0.87 ± 0.04 n = 5
maximum width pronotal disc	2.0-2.5 2.27 ± 0.19 n = 5	1.9-2.1 2.03 ± 0.11 n = 4	1.8-2.0 1.90 ± 0.06 n = 5
ratio maximum / minimimum width pronotal disc	2.0-2.5 2.21 ± 0.22 n = 5	2.1-2.3 2.23 ± 0.09 n = 4	2.03-2.31 2.18 ± 0.12 n = 5
minimum diameter of tympanal opening	0.08-0.40 0.19 ± 0.06 n = 41	0.12-0.16 0.13 ± 0.02 n = 10	0.2-0.3 0.24 ± 0.03 n = 12
maximum diameter of tympanal opening	1.0-1.3 1.12 ± 0.08 n = 41	1.0-1.35 1.17 ± 0.09 n = 10	0.88-1.25 1.09 ± 0.1 n = 12
ratio maximum / minimum diameter of tympanal opening	3.0-13.1 6.34 ± 2.2 n = 41	6.8-10.8 8.81 ± 1.2 n = 10	3.5-6.25 4.69 ± 0.9 n = 12
length of fore wing	6.2-8.8 7.52 ± 0.68 n = 44	5.5-6.8 6.05 ± 0.3 n = 10	5.6-7.1 6.48 ± 0.3 n = 23
maximum width of fore wing	1.9-2.9 2.2 ± 0.3 n = 9	1.7-2.0 1.85 ± 0.12 n = 8	1.5-2.1 1.76 ± 0.19 n = 10
ratio length / width fore wing	2.17-3.89 3.41 ± 0.52 n = 9	3.1-3.57 3.33 ± 0 2 n = 8	3.33-4.46 3.78 ± 0.36 n = 10
distance from stigma (if recognisable) to tip of fore wing	0.6-1.3 0.93 ± 0.14 n = 25	n = 0 of 10	0.6-1.0 0.8 ± 0.16 n = 5 of 19

males	*pulloides* (Peloponnese & Pindos range)	*pulloides* (Mt. Akarnanika)	*sangiorgii* (Island of Kefallinia)
ratio distance stigma to tip / length of fore wing	0.08-0.18 0.12 ± 0.02 n = 25		0.11-0.16 0.13 ± 0.02 n = 5
width of C area	0.36-0.60 0.49 ± 0.05 n = 41	0.35-0.45 0.39 ± 0.04 n = 10	0.40-0.51 0.45 ± 0.03 n = 10
width of Sc area	0.20-0.37 0.29 ± 0.04 n = 41	0.24-0.30 0.27 ± 0.02 n = 10	0.20-0.28 0.23 ± 0.02 n = 10
ratio width of C / width of Sc area	1.26-2.5 1.72 ± 0.26 n = 41	1.17-1.87 1.44 ± 0.2 n = 10	1.75-2.5 1.97 ± 0.2 n = 10
width of combined C & Sc areas	0.65-0.95 0.79 ± 0.07 n = 41	0.60-0.75 0.65 ± 0.04 n = 10	0.60-0.79 0.69 ± 0.05 n = 10
ratio width of combined C & Sc areas × 100 / length of fore wing	9.26-12.32 10.55 ± 0.80 n = 41	8.82-12.71 10.70 ± 0.9 n = 10	9.37-11.79 10.63 ± 0.7 n = 10
length of hind femur	8.1-10.3 9.12 ± 0.55 n = 44	8.4-9.9 8.92 ± 0.3 n = 13	7.9-8.9 8.35 ± 0.29 n = 12
ratio length of fore wing / length of hind femur	0.71-0.99 0.82 ± 0.06 n = 43	0.62-0.74 0.67 ± 0.03 n = 13	0.74-0.84 0.78 ± 0.03 n = 10
length of sridulatory file	2.5-4.3 3.13 ± 0.41 n = 44	2.2-3.0 2.61 ± 0.23 n = 13	2.5-3.2 2.78 ± 0.2 n = 10
distance from end of file to tip of knee	3.7-5.1 4.35 ± 0.28 n = 41	4.1-4.9 4.40 ± 0.25 n = 10	3.7-4.3 4.04 ± 0.21 n = 10
ratio length of file / distance from end of file to tip of knee	0.57-0.95 0.72 ± 0.08 n = 41	0.54-0.73 0.60 ± 0.05 n = 10	0.63-0.81 0.69 ± 0.06 n = 10
number of stridulatory pegs	71-141 99.7 ± 19 n = 44	52-67 59.7 ± 4.0 n = 13	85-104 93.1 ± 5.9 n = 10
number of stridulatory pegs per mm	25.5-40.9 31.7 ± 4.0 n = 44	19.6-26.8 22.9 ± 1.9 n = 13	29.7-38.0 33.7 ± 2.8 n = 10
minimum distance between eyes	0.79-0.90 0.83 ± 0.04 n = 10	0.75-0.80 0.78 ± 0.02 n = 6	0.54-0.69 0.62 ± 0.06 n = 4
maximum diameter eye	1.7-1.9 1.83 ± 0.09 n = 10	1.8-2.0 1.83 ± 0.08 n = 6	1.6-1.8 1.69 ± 0.08 n = 4
ratio interocular distance / diameter eye	0.41-0.50 0.45 ± 0.03 n = 10	0.40-0.44 0.43 ± 0.01 n = 6	0.33-0.38 0.36 ± 0.02 n = 4

males	*pulloides* (Peloponnese & Pindos range)	*pulloides* (Mt. Akarnanika)	*sangiorgii* (Island of Kefallinia)
maximum width of head	2.7-3.2 2.96 ± 0.15 n = 36	2.78-3.2 2.92 ± 0.18 n = 7	2.4-2.7 2.59 ± 0.1 n = 10
ratio length of pronotum / maximum width of head	0.95-1.16 1.06 ± 0.05 n = 36	0.96-1.08 1.04 ± 0.04 n = 7	0.97-1.05 1.03 ± 0.05 n = 10

Table 35. Biometric data for females of *Chorthippus pulloides* and *C. sangiorgii*. Minimum, maximum, mean, standard deviation and number of specimens are given. The measurements (in mm) of *C. pulloides* were taken from typical populations of the Peloponnese and Pindhos range and separately of specimens from Mt. Akarnanika, southwestern mainland of Greece and those of *C. sangiorgii* from the island of Kefallinia.

females	*pulloides* (Peloponnese & Pindos range)	*pulloides* (Mt. Akarnanika)	*sangiorgii* (Island of Kefallinia)
length of pronotum	3.7-4.7 4.26 ± 0.3 n = 8	3.5-4.0 3.8 ± 0.18 n = 11	3.1-4.1 3.64 ± 0.3 n = 5
length of prozona	2.1-2.8 2.35 ± 0.23 n = 8	1.8-2.1 1.98 ± 0.08 n = 11	1.5-2.2 1.88 ± 0.24 n = 5
length of metazona	1.8-2.4 2.1 ± 0.17 n = 8	1.6-2.0 1.83 ± 0.12 n = 11	1.5-1.8 1.74 ± 0.1 n = 5
ratio length of prozona / length of metazona	1.0-1.5 1.12 ± 0.18 n = 8	1.0-1.25 1.08 ± 0.07 n = 11	1.0-1.2 1.07 ± 0.09 n = 5
minimum width pronotal disc	1.1-1.5 1.2 ± 0.12 n = 8	1.0-1.2 1.08 ± 0.07 n = 11	1.05-1.3 1.85 ± 0.1 n = 5
maximum width pronotal disc	2.6-3.4 3.01 ± 0.26 n = 8	2.4-3.0 2.70 ± 0.16 n = 11	2.4-2.8 2.6 ± 0.15 n = 5
ratio maximum / minimum width pronotal disc	2.16-2.81 2.46 ± 0.21 n = 8	2.33-2.66 2.48 ± 0.09 n = 11	2.07-2.54 2.27 ± 0.19 n = 5
minimum diameter of tympanal opening	0.05-0.25 0.15 ± 0.06 n = 8	0.03-0.18 0.095 ± 0.04 n = 11	0.2-0.44 0.28 ± 0.1 n = 5
maximum diameter of tympanal opening	1.2-1.8 1.43 ± 0.17 n = 8	1.03-1.50 1.23 ± 0.15 n = 11	1.3-1.5 1.38 ± 0.08 n = 5
ratio maximum /minimum diameter of tympanal opening	5.6-24 11.4 ± 5.6 n = 8	7-46 17 ± 11 n = 11	3.0-7.5 5.4 ± 1.9 n = 5
length of fore wing	6.5-8.0 7.22 ± 0.5 n = 8	4.0-5.7 4.93 ± 0.58 n = 11	4.9-7.1 6.1 ± 0.8 n = 5

females	*pulloides* (Peloponnese & Pindos range)	*pulloides* (Mt. Akarnanika)	*sangiorgii* (Island of Kefallinia)
maximum width of fore wing	2.3-2.8 2.42 ± 0.2 n = 8	1.8-2.3 2.04 ± 0.15 n = 11	1.8-2.5 2.1 ± 0.27 n = 5
ratio length / width fore wing	2.6-3.3 2.98 ± 0.8 n = 8	2.15-2.84 2.40 ± 0.24 n = 11	2.1-3.6 2.98 ± 0.5 n = 5
length of hind femur	10.6-13.2 11.8 ± 0.55 n = 8	9.7-12 10.9 ± 0.65 n = 11	10.0-12.1 10.8 ± 0.8 n = 5
ratio length of fore wing / length of hind femur	0.50-0.65 0.59 ± 0.04 n = 8	0.38-0.53 0.45 ± 0.04 n = 11	0.47-0.61 0.56 ± 0.05 n = 5
minimum distance between eyes	1.1-1.4 1.23 ± 0.08 n = 12	1.0-1.16 1.06 ± 0.05 n = 11	0.8-1.01 0.92 ± 0.07 n = 8
maximum diameter eye	2.0-2.2 2.1 ± 0.07 n = 12	2.0-2.2 2.13 ± 0.07 n = 11	1.9-2.3 2.1 ± 0.1 n = 8
ratio interocular distance / diameter eye	0.52-0.67 0.58 ± 0.04 n = 12	0.45-0.52 0.50 ± 0.01 n = 11	0.36-0.46 1.03 ± 0.03 n = 8
maximum width of head	4.0-4.6 4.16 ± 0.22 n = 8	3.4-4.1 3.85 ± 0.23 n = 8	3.2-4.0 3.7 ± 0.34 n = 4
ratio length of pronotum / maximum width of head	0.90-1.12 1.03 ± 0.06 n = 8	0.97-1.03 1.02 ± 0.02 n = 8	0.97-1.09 1.03 ± 0.05 n = 4

Appendix 4. Content cd

CD1, *Chorthippus vagans africanus*, calling song (Tunesia, 1997, leg. D. Dachlauer), diagram: fig. 223.

CD2, *Chorthippus vagans dissimilis*, calling song (Greece, 1986, leg. O. von Helversen), diagram: fig. 224.

CD3, *Chorthippus vagans dissimilis*, courtship song (Greece, 1982, leg. Zilch), diagram: fig. 225.

CD4, *Chorthippus vagans cypriotus*, calling song (Cyprus, 1996, leg. H. Kriegbaum), diagrams: figs 15, 226.

CD5, *Chorthippus willemsei*, calling song (Greece, 1981, leg. O. von Helversen), diagram: fig. 227.

CD6, *Chorthippus willemsei*, courtship song (Greece, 1981, leg. O. von Helversen), diagram: fig. 228.

CD7, *Chorthippus willemsei*, rivalry song (Greece, 1981, leg. O. von Helversen), diagram: fig. 229.

CD8 , *Chorthippus biroi*, calling song (Greece, 1999, leg. O. von Helversen), diagram: fig. 230.

CD9, *Chorthippus biroi*, rivalry song (Greece, 1989, leg. O. von Helversen), diagram: fig. 231.

CD10, *Chorthippus bornhalmi*, calling song (Greece, 1981, leg. O. von Helversen), diagram: fig. 232.

CD11, *Chorthippus biguttulus biguttulus*, calling song (Germany, 2002, leg. B. Gottsberger), diagrams: figs 16, 233.

CD12, *Chorthippus biguttulus euhedickei*, courtship song (Greece, 2001, leg. O. von Helversen), diagram: fig. 234.

CD13, *Chorthippus biguttulus euhedickei*, calling song (one fore wing removed) (Greece, 1997, leg. O. von Helversen), diagram: fig. 235.

CD14, *Chorthippus biguttulus parnassicus*, calling song (Greece, 1988, leg. F. Willemse), diagram: fig. 236.

CD15, *Chorthippus moreanus*, calling song (Greece, 1995, leg. O. von Helversen), diagram: fig. 237.

CD16, *Chorthippus moreanus*, courtship song (Greece, 1986, leg. O. von Helversen), diagrams: figs 16, 238.

CD17, *Chorthippus mollis mollis*, calling song (Greece, 2004, leg. O. von Helversen), diagrams: figs 15, 239.

CD18, *Chorthippus mollis mollis*, calling song (Greece, 1990, leg. O. von Helversen), diagram: fig. 240.

CD19, *Chorthippus mollis lesinensis*, calling song and rivalry song (Montenegro, 1999, leg. unknown), diagram: fig. 241.

CD20, *Chorthippus mollis lesinensis*, courtship song (Croatia, 1996, leg. R. Kleukers), diagram: fig. 242.

CD21, *Chorthippus crassiceps*, calling song (one fore wing removed) (Greece, 1979, leg. W. Elegast), diagrams: figs 15, 243.

CD22, *Chorthippus crassiceps*, morphologically atypical, calling song (Greece, 1991, leg. F. Willemse), diagram: fig. 244.

CD23, *Chorthippus parnon*, calling song (Greece, 1990, leg. O. von Helversen), diagram: fig. 245.

CD24, *Chorthippus parnon*, courtship song (Greece, 1998, leg. F. Mayer), diagram: fig. 246.

CD25, *Chorthippus parnon*, rivalry song (Greece, 1990, leg. O. von Helversen), diagram: fig. 247.

CD26, *Chorthippus pulloides*, calling song (Greece, 1990, leg. O. von Helversen), diagrams: figs 15, 248.

CD27, *Chorthippus pulloides*, morphologically atypical, calling song (Greece, 1990, leg. O. von Helversen), diagram: fig. 249.

CD28, *Chorthippus pulloides*, calling song just after removing female, (Greece, 2004, leg. O. von Helversen), diagram: fig. 250.

CD29, *Chorthippus pulloides*, courtship song (Greece, 2004, leg. O. von Helversen), diagram: fig. 251.

CD30, *Chorthippus sangiorgii*, calling song (Greece, 1996, leg. J. Schul), diagram: fig. 252.

CD31, *Chorthippus pulloides*, bioacoustically atypical, calling song (Greece, 1989, leg. O. von Helversen), diagram: fig. 253.

CD32, *Chorthippus pulloides*, bioacoustically & morphologically atypical, courtship song (Greece, 1998, leg. F. Mayer), diagram: fig. 254.

CD33, *Chorthippus pulloides*, bioacoustically & morphologically atypical, courtship song (one-legged) (Greece, 1991, leg. F. Willemse), diagram: fig. 255.

CD34, *Chorthippus moreanus*, bioacoustically atypical, courtship song (Greece, 1986, leg. O. von Helversen), diagrams: figs 16, 256

CD35, *Chorthippus moreanus*, bioacoustically atypical, calling song (Greece, 1986, leg. O. von Helversen), diagram: fig. 257.

CD36 *Chorthippus moreanus* × *pulloides-crassiceps*, transitional population, calling song (Greece, 1989, leg. O. von Helversen), diagrams: figs 16, 258.

CD37, *Chorthippus moreanus* × *pulloides-crassiceps*, transitional population, calling song (Greece, 1986, leg. O. von Helversen), diagram: fig. 259.

CD38, *Chorthippus apricarius*, calling song (Netherlands, 1993, recorded B. Odé), no diagram.

CD39, *Chorthippus brunneus*, calling song (Netherlands, 1993, recorded B. Odé), no diagram.