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Revision of the *Poecilimon ornatus* group (Orthoptera: Phaneropteridae) with particular reference to the taxa in Bulgaria and Macedonia*

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Abstract. The *Poecilimon ornatus* group has an exclusively European distribution and includes the largest species in the genus. A revision of the taxa belonging to this group in Bulgaria and Macedonia (Central and Eastern Balkan Peninsula) is presented. Nine taxa described from Bulgaria are synonymised with 3 previously known species, as follows: *Poecilimon ornatus* (= *P. mistshenkoi marzani*, syn. n., *P. mistshenkoi tinkae*, syn. n., *P. mistshenkoi vlachinensis*, syn. n.), *P. affinis* s. str. (= *P. mistshenkoi mistshenkoi*, syn. n., *P. affinis ruenensis*, syn. n., *P. affinis rilensis*, syn. n., *P. affinis medimontanus*, syn. n., *P. harzi*, syn. n.) and *P. hoelzeli* (= *P. kisi*, syn. n.). The synonymy of *P. poecilus* with *P. affinis* and the subspecific status of *P. affinis komareki* are confirmed. One species, *Poecilimon jablanicensis*, sp. n., is described as new to science. A tabulated key, lists and maps of all known localities and oscillograms of the songs of all the species in this group are presented. The phylogenetic relationships and evolutionary trends in the *Poecilimon ornatus* group are discussed.

INTRODUCTION

Poecilimon Fischer, 1853 is a group of short-winged herbivorous bushcrickets, distributed from the Apennines to Eastern Siberia and Central Tien-Schan (Bey-Bienko, 1954), and the largest genus of the suborder Ensifera in the Palaearctic. Its centre of speciation and diversity, however, is restricted to the Pontic region with only a few taxa occuring outside the Balkans, Asia Minor and the Caucasus region. They have poor dispersal ability due to their microptery and this along with the diverse geomorphological and climatic aspects and history of the area where they occur has resulted in rapid morphological and behavioural evolution. Within the genus there are many groups of apparently related taxa. Despite the few full or partial revisions (e.g. Ramme, 1933; Bey-Bienko, 1954; Willemse, 1982; Heller, 1984; Heller & Lehmann, 2004; Heller & Sevgili, 2005; Heller et al., 2006; Heller et al., 2008) the phylogeny and systematics of *Poecilimon* is only partly resolved. Even a recent partial review of the genus based on molecular data (Ullrich et al., 2010) has not clarified all questions.

One group for which the phylogeny and systematics is poorly known is the *Poecilimon ornatus* group. The species belonging here were listed in group I ("Gruppe I"; containing two sections) by Ramme (1933) in the first revision of the genus. The group's taxa are characterized by large or moderate body size, posteriorly widened and more or less upcurved pronotum, well visible tegmina and moderately incurved cerci with a single tooth. The *Poecilimon ornatus*-group after Heller (1984), consists of 8 taxa, namely *P. nobilis* Brunner von Wattenwyl, 1878*, P. obesus obesus* Brunner von Wattenwyl, 1878*, P. obesus artedentatus* Heller, 1984, *P. affinis affinis* (Frivaldszky, 1867), *P. affinis komareki* Čejchan, 1957, *P. affinis hoelzeli* Harz, 1966, *P. ornatus* (Schmidt, 1850) and *P. pancici* Karaman, 1958, distributed mainly in the Balkans. Later on, *P. artedentatus* and *P. hoelzeli* was given specific status (Willemse, 1985; Willemse & Heller, 1992), *P. pancici* synonymised (Willemse, 1985) and a few new taxa, somewhat resembling the latter species, described (*P. pindos* F. Willemse, 1982, *P. soulion* L. Willemse, 1987 and *P. gracilioides* F. Willemse et Heller, 1992). The last species connect the group morphologically with *P. gracilis* (Fieber, 1853). *P. schmidtii* (Fieber, 1853), forming together with *P. gracilis* the second section of Ramme's (1933) group I, is not closely related to the others (e.g. Ullrich et al., 2010) and is not included in this study. In this group, however, the following 9 taxa, described by Peshev (1980) from Bulgaria should be included: *P. mistshenkoi mistshenkoi, P. mistshenkoi marani, P. mistshenkoi tinkae, P. mistshenkoi vlachinensis, P. affinis ruenensis, P. affinis rilensis, P. affinis medi-*

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* While this paper was in press, a study by Ingrisch and Pavicevic [2010; Seven new Tettigoniidae (Orthoptera) and a new Blattellidae (Blattodea) from the Durmitor area of Montenegro with notes on previously known taxa. *Zootaxa* 2565: 1–41] was published, also dealing with taxa of the *P. ornatus* group. The authors describe some new forms and change the rank of others. In contrast to the ideas presented in that paper we still consider the form *P. rumijae* as an infrasubspecific variation of *P. affinis komareki*. Judging from the extent of the differences we do not exclude the possibility that some of the newly described forms are local variants of *P. affinis* (compare with the morphological and bioacoustic variation described here).

montanus, P. kisi and *P. harzi*. These forms, though described in detail, lack a well defined differential diagnosis and their taxonomic status and systematic relationships are still doubtful. After studying the type material and investigating the morphology, behaviour and bioacoustics of topotypic populations, some changes in the systematics and taxonomy of the group from Bulgaria became necessary. These taxa are the subject of the present work. The rest of the species in this group are restricted to Greece. Their distribution and systematic position have been studied by Willemse and co-authors (Willemse, 1982, 1985; Willemse & Heller, 1992) and only the most important facts are repeated here for comparison. Due to the lack of song recordings for the two subspecies of *P. affinis* described by Karaman (1974), *P. affinis serbicus* Karaman, 1974 and *P. affinis hajlensis* Karaman, 1974, these taxa are not discussed in detail. In addition, during field studies, a new taxon from the *Poecilimon ornatus* group was discovered. While all other species of the group have a bidirectional sound-communication system (ancestral condition in *Poecilimon*), this species possesses a unidirectional acoustic communication system (loss of female tegmina together with stridulatory organs). This new species, *Poecilimon jablanicensis*, sp. n., is described and some conclusions about the evolutionary trends in the group are presented in this paper.

MATERIAL AND METHODS

During the present study material from several collections were surveyed, including the National Museum of Natural History (at that time containing also the former collection of Orthoptera of the Institute of Zoology), Bulgarian Academy of Sciences, Sofia; collection of the Natural History Section of the Regional History Museum in Blagoevgrad; collection of the Macedonian Museum of Natural History, Skopje; collection of Dragan Chobanov; collection of Klaus-Gerhard Heller, abbreviated as NMNH, HMB, MMNH, CC and CH, respectively. In addition, material from some private collections was examined.

Concerning the systematics and distribution of species only references with original or supplementary information are presented. For each taxon a distributional map is prepared including both literature (localities revised when material available) and unpublished data. Data on altitude were added, if missing, using the co-ordinates and the GPSVisualizer online (Scheider; www.gpsvisualizer.com).

Songs of the species investigated were recorded with an electret condenser microphone (Knowles BT-1759-000) equipped with a custom-made preamplifier, connected to a PC through an external soundcard (TransitUSB, "M-Audio") (96 kHz sampling rate). Song measurements were obtained manually in WaveLab5 (Steinberg). For the spectrum of *P. jablanicenis* (due to a reduced sampling rate of 48 kHz only up to 24 kHz) the response curve of the Knowles microphone was corrected using a comparison with a Brüel & Kjaer 4133 microphone. Recordings were processed and oscillograms of the songs were prepared using Turbolab 4.0 (Bressner Technology, Germany). The recordings for the comparative figures were made using different types of equipment. For sound recording in the field most often a Uher tape recorder 4200 IC with a Uher M645 microphone (frequency response flat up to 20 kHz) and in the laboratory a Racal store 4 D tape recorder with Brüel & Kjaer 4133 and 4135 microphones (frequency response flat up to 40, respectively 70 kHz), were used.

Bioacoustic terminology: calling song – the song produced by an isolated male; syllable – the sound produced by one opening-and-closing movement of the tegmina; syllable duration – the time measured from the beginning of the first to the end of last impulse in a syllable; syllable period – the span including a syllable and the following interval; impulse – a undivided transient train of sound waves produced by the stridulatory tooth striking the plectrum (the anal edge of the opposite tegmen).

Appendix with detailed distribution of individual species is available online at:
<http://www.eje.cz/supplfiles/eje1575suppl.pdf>

RESULTS

A. Species of the *Poecilimon ornatus* group occurring in Bulgaria and Macedonia

All species in this group on the Central and Eastern Balkan Peninsula and adjacent territories in the North fall into two groups: either large and bulky animals or small and slender ones (see Table 2). The first group can morphologically (and by song) be separated into three subgroups, which are considered here to be three separate species (although they rarely occur sympatrically or syntopically), *P. ornatus*, *P. affinis* and *P. hoelzeli*. The second is made up of two distinct species, one widespread (*P. gracilis*) and one very local, which is a new species.

Poecilimon ornatus (Schmidt, 1850)

Ephippigera ornata Schmidt, 1850 (184), type locality Slovenia [northern part = S Kärnten, Kamnik (see Willemse, 1985)].

Barbitistes fieberi Fieber, 1853 (175), type locality Italy, Trieste; synonymized with *P. ornatus* by Krauss (1878); Brunner von Wattenwyl (1878, 1882) used the younger name *fieberi* including *P. ornatus*.

Odontura ornata; Schmidt, 1866 (81).

Poecilimon ornatus; Krauss, 1878 (497); Ramme, 1933 (511, Pl. 6, Fig. 2., Pl. 7, Fig. 1, Pl. 8, Fig. 1, Pl. 11, Fig. 1, Pl. 12, Fig. 1); Bey-Bienko, 1954 (270–271); Harz, 1969 (119–120, Figs 32, 268, 270, 271, 319, 322); Willemse, 1982 (partim; 156–158, Figs 1, 2, 5, 9); Heller, 1984 (83, 85, Figs 5–D, 7–E–G, 9–B); Willemse, 1985 (11–12, Figs 1–5, 34); Heller, 1988 (50–51, Pls 34–G, 88, 120–D).

Poecilimon pancici Karaman, 1958 (36, Figs 1–7), type locality Macedonia, Gradishtanska Planina Mt., Gabresh vill.; Harz, 1969 (122); Willemse, 1982 (158, Fig. 10). Synonym of *P. ornatus* after Heller (1988).

Poecilimon greini Harz, 1977 (27–28). Synonym of *P. ornatus* after Heller (1984).

Poecilimon mistshenkoi marzani Peshev, 1980 (33–34), type locality Bulgaria, Alibotush Mt., Kosharite Locality, 1800–1900 m, syn. n.

Poecilimon mistshenkoi tinkae Peshev, 1980 (34), type locality Bulgaria, Belassitsa Mt., northeastern slope of Kalabak Peak, 1700 m, syn. n.

Poecilimon mistshenkoi vlachinensis Peshev, 1980 (34, 36), type locality Bulgaria, Vlakhina Mts, eastern slope, near the state boundary between Yugoslavia and Bulgaria, 1600–1700 m [Kadiytsa Peak], syn. n.

Variation (general appearance – Fig. 1A). The populations from different parts of the range and different altitudes vary significantly in body size and colouration (compare Fig. 1J and 1K). Generally, the melanistic col-

TABLE 2. Tabulated key for distinguishing the species of the *Poecilimon ornatus* group.

species / character	auditory spiracle	female tegmina	male cerci (see Figs 2, 3)	metazona of male pronotum	hind femur length (mm)	stridulatory file shape	stridulatory teeth distribution	stridulatory teeth number	syllables shape	syllable duration (20–30°C)	distribution (see Figs 10, 11, 12, 13)
P. jablanicensis	small	small, non-overlapping	>2.5 mm, tooth distinct	strongly raised fig. 8C	11.5–14.0	arcuate	size evenly decreasing	175–210	compact, crescendo	>350–~1000 ms	Jablanica Mt. SW Macedonia
P. gracilis	large	overlapping	>2.5 mm, tooth distinct	strongly raised	11.5–18.5	arcuate	size evenly decreasing	135–160	bipartite	>250–400 ms	W & NW Balkans to Austria
P. gracilioides	large	overlapping	<2.5 mm, tooth distinct	strongly raised	14.3–15.6	arcuate	size abruptly decreasing at 2/3 from base	~120	tripartite	>250–?ms	NW Greece
P. soulion	large	overlapping	<2.5 mm, tooth distinct	slightly raised	17.0–19.2	arcuate	size abruptly decreasing at 2/3 from base	~140	tripartite	300–650 ms	Mountains in Pindos range, Greece
P. nobilis	large	overlapping	<2 mm, tooth distinct	slightly raised	15.5–18.0	arcuate	size evenly decreasing	115–120	bipartite	~500–800 ms	Peloponnesos (S Greece)
P. obesus	large	overlapping	>2.5 mm, tooth distinct	slightly raised	21.0–23.0	arcuate	size slightly decreasing at the very apex	~120	bipartite	>500–1000 ms	W Continental Greece (W & S Greece)
P. artedentatus	large	overlapping	>2.5 mm, tooth distinct	slightly raised	18.3–22.0	arcuate	size very gently decreasing	~280	compact, crescendo	>~500 ms	Peloponnesos (S Greece)
P. pindos	large	overlapping	<2.5 mm, tooth indistinct	slightly raised	15.1–18.2	arcuate	size very gently decreasing	115–135	compact, crescendo	>100–150 ms	N Pindos range (NW Greece)
P. hoelzeli	large	overlapping	=2.5 mm, tooth indistinct	strongly raised	16.5–21.0	arcuate	size very gently decreasing	235–270	compact, crescendo	>100–150 ms	S Macedonia, SW Bulgaria and N Greece
P. affinis affinis	large	overlapping	>2.5 mm, tooth indistinct	strongly raised (variable)	13.0–25.0	slightly bulged in the middle	size evenly decreasing	180–240	compact, crescendo	>100–500 ms	N & C Balkans and Carpathians
P. affinis komareki	large	overlapping	>3 mm, tooth indistinct	strongly raised (variable)	21.0–25.0	slightly bulged in the middle	size evenly decreasing	~250	compact, crescendo	within the range of *P. a. affinis*	Coastal Albania and Montenegro
P. ornatus	large	overlapping	>3 mm, tooth indistinct	strongly raised (variable)	19.0–24.0	distinctly bulged in the distal part	size decreasing after the bulge	158–220	compact, rectangular	<50 ms	C & NW Balkans to Austria and Italy

ouration varies within a population, while there is a tendency for body size to be smaller at higher altitudes (see Discussion). The pronotal shape, mostly the elevation of the metazona, and the part of the tegmina covered by the pronotum vary even between animals from the same place. Strongly raised metazona of pronotum and strong development of a melanistic colouration are also observed in animals from high-density populations. All these characters cannot be used as distinctive. The cercus shape may be a better character, the cerci being gently incurved at the ends, but here also there can be confusion with *P. affinis* (compare Figs 2O1–O10 and 3A1–A14). The most stable morphological feature is the shape of the stridulatory file (Heller, 1984; Willemse, 1985) (Figs 4 and 5: O1–O3), which has a distinct bulge distally. The number of stridulatory teeth also varies considerably, though there are generally fewer teeth than in *P. affinis*. Heller (1988) reports 158–212 stridulatory teeth in *P. ornatus*, which is well supported by new observations, with some large specimens having up to 220 teeth. Usually the number of teeth does not exceed 200. The song (Figs 6O1, O2, 7B) is the most striking characteristic of this species, consisting of very short syllables with high amplitude from the abrupt beginning to the end (often with a longer, low-amplitude fading end resulting from echoes). The syllable lasts only about 10 ms and even with echoes it is still much shorter than 100 ms. The female responds to the male song 40 ms after its beginning (at 30°C; Heller et al., 1997) and the male song must have ended if it is to hear her response. Also the stridulatory movement is much faster and shorter than in all other species of the group (Heller, 1988).

Synonymy. The two sibling species, *P. ornatus* and *P. affinis*, vary greatly throughout their range (horizontally and altitudinally) in morphological features, which previously were thought to be distinctive (e.g. Ramme, 1951; Harz, 1969; Karaman, 1974; Willemse, 1984), e.g. width of fastigium in relation to scapus, pronotal and cercal shape, general body size, etc. Heller (1984) shows that the definition of both species and their relatives on the basis of these characters is often unreliable. He (l.c.) also indicates that the song and structure of the stridulatory file are stable characters that can be reliably used to differentiating between the species in the *Poecilimon ornatus* group, and this was confirmed by subsequent studies (e.g. Willemse, 1985; Heller, 1988). Some valuable differences in the shape of the cercus were pointed out by Willemse (1985), but there is overlap between species (see “Variation”; *P. affinis*; Figs 2, 3).

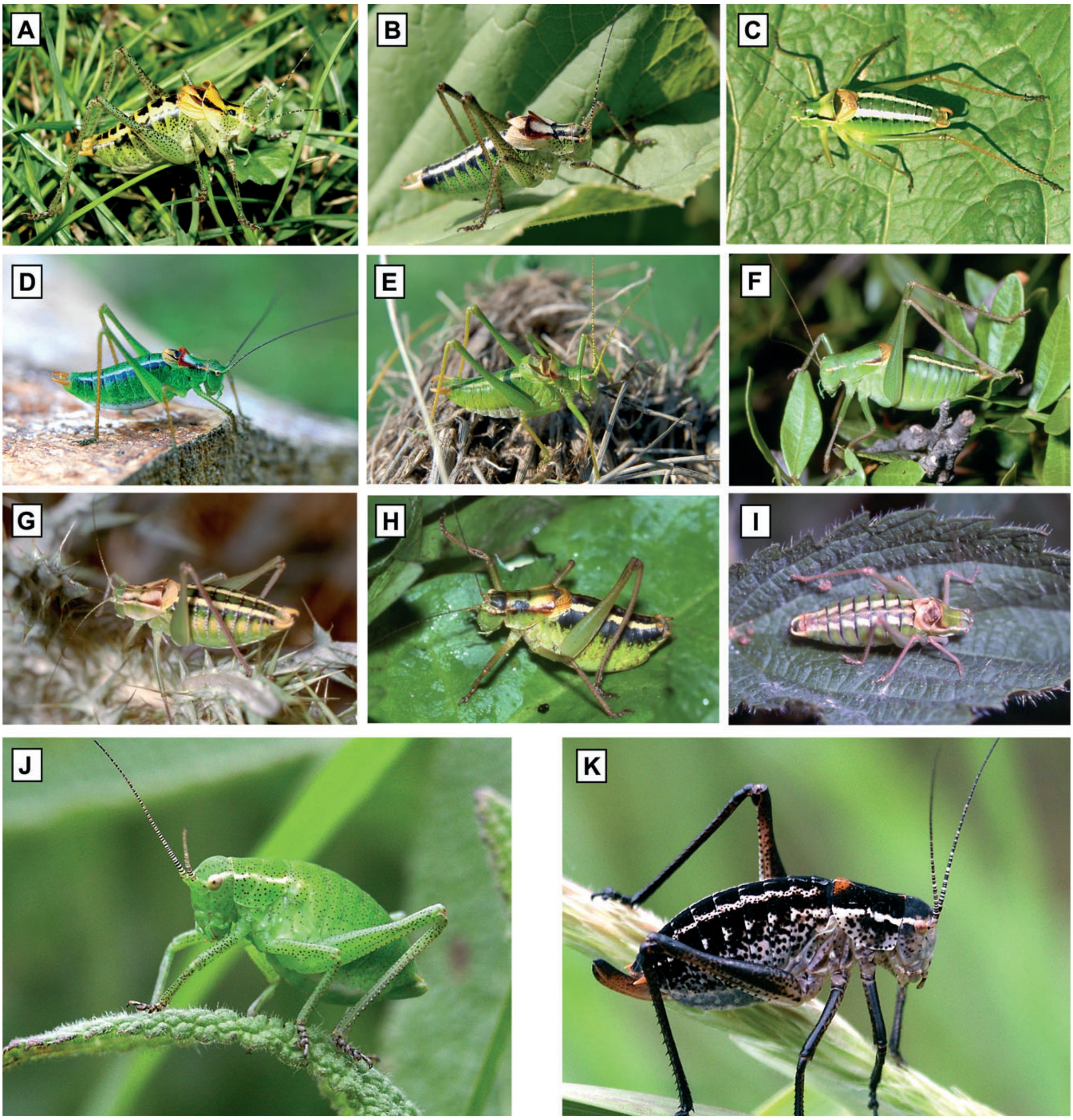

Fig. 1. Appearance of some of the species of the *Poecilimon ornatus* group (relative sizes of the species not maintained). A – *P. ornatus*, Bulgaria, Alibotoush, 1750 m (M. Langourov); B – *P. affinis*, Macedonia, Shar, 1800 m (L. Stefanov); C – *P. hoelzeli*, Macedonia, Kozhuf, 1750 m; D – *P. gracilis*, Macedonia, Shar, 1400 m (L. Stefanov); E – *P. jablanicensis*, Macedonia, Jablanica, 1800–1950 m; F – *P. obesus*, Greece; G – *P. artedentatus*, Greece; H – *P. nobilis*, Greece; I – *P. gracilioides*, Greece; J – *P. ornatus* (nymph from a low-density population), Macedonia, Mariovo (L. Stefanov); K – *P. ornatus* (nymph from a high-density population), Macedonia, Mariovo (L. Stefanov).

In his study on *Poecilimon*, Peshev (1980) describes nine new taxa (including species and subspecies) in the *Poecilimon ornatus* group from Bulgaria. The morphological descriptions, though detailed, are insufficient for the determination of even abundant material. The short differential diagnoses are based mostly on pronotal shape and relative proportions of tegmina, cerci, genital plate and ovipositor, which are unreliable taxonomic features in this group (see above; Heller, 1984; Willemse, 1985), especially in comparison with *P. affinis*. Peshev (1980) emphasized the similarity of *P. mistshenkoi* and *P. ornatus* without citing well defined differences. Study of material from various localities showed that the morphological features characterizing *P. ornatus*, like the shape of the cercus (Fig. 2O1–O10) and stridulatory file (Figs 4 and 5: O1–O3), are present in specimens from well defined regions in Bulgaria and Macedonia, connected with the species' range in neighbouring territories in

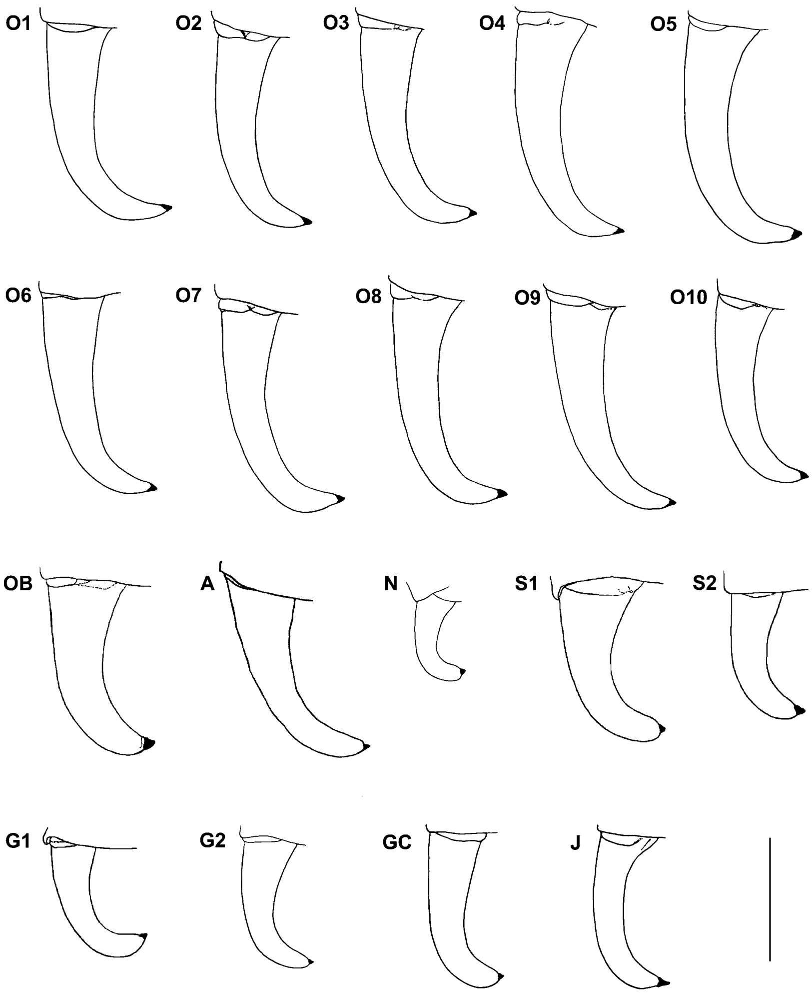

Fig. 2. *Poecilimon ornatus* group, dorsal view of male cercus: O1–O10 – *P. ornatus* (O1 – Bulgaria, Pirin, Demir Kapiya Pass, 1800 m; O2 – Bulgaria, Pirin, Begovishki Rid Ridge, 2200 m; O3 – Bulgaria, Pirin, Pirin Chalet, 1700 m; O4 – Bulgaria, Pirin, Orelek Peak; O5 – Bulgaria, Alibotoush, 1750 m; O6 – Bulgaria, Belassitsa, 1700–1900 m; O7 – Bulgaria, Ograzhden, 1500 m; O8 – Bulgaria, Maleshevska Planina; O9 – Bulgaria, Vlakhina, 1600–1900 m; O10 – Macedonia – Jakupica); OB – *P. obesus*, Greece, Koutsilaris, 200 m, CH2938; A – *P. artedentatus*, Greece, Peloponnesos, Metaxion, 840 m; N – *P. nobilis*, Greece, Peloponnesos, Mainalon (redrawn from Willemse, 1987); S1 – *P. soulion*, Greece, Tomaros, 900–1900 m, CH6510; S2 – *P. soulion*, Greece, Timfristos, CH2475; G1 – *P. gracilioides*, Greece, Tsoumerka, 1850 m, CH6921; G2 – *P. gracilioides*, Greece, Karava Range; GC – *P. gracilis*, Macedonia, Radika, 900 m; J – *P. jablanicensis*, Jablanica, 1850 m. Scale = 2 mm.

Greece. The latter is true both for the type material and newly collected specimens from the type localities and known distributional range of *P. mistshenkoi marzani, P. mistshenkoi tinkae, P. mistshenkoi vlachinensis* and populations from reported localities of *P. mistshenkoi mistshenkoi* (see *P. affinis*). Song analysis (see Fig. 4O1, O2) proved these taxa clearly belong to *P. ornatus* and support the proposed synonymy.

Distribution (Figs 10, 11, Appendix). In the literature before Heller (1984) and even later, *P. ornatus* is frequently confused with *P. affinis*, thus many records will remain doubtful until the collected material is revised or until new material is collected in the respective localities. This is epecially true for some territories in Bosnia and Hercegovina, Serbia, Montenegro and Albania.

The species' range covers the western half of the Balkan Peninsula (Northwestern Greece – North of Tsoumerka Mt., Southwestern Bulgaria, Central and Eastern Macedonia, Montenegro, Bosnia and Hercegovina, Croatia, Slovenia) and the easternmost part of the Alps (Italy and Austria). Interestingly the range appears to be divided into a northern (from Austria to Montenegro) and southern part (south- and eastwards of Central Macedonia) separated by a gap. This gap is probably the result of less intensive collecting in this area as it is recorded in other species, e.g. *Eupholidoptera chabrieri* (Ciplak et al., 2007). In addition, associated with this gap is the serious problem of this species being misidentified as *P. affinis*. There are no obvious differences between the northern and the southern populations. The range of the southern population covers the easternmost edge of the Pindo-Dinaric mountain group, including the mountains of the Northern Vardar zone (e.g. Vodno) and the eastern part of the Pelagonian horst anticline (Yakupitsa, Babuna, Goleshnitsa etc. in Macedonia), dipping into the southwestern part of the Rhodope group (the bordering mountains of Vlakhina, Maleshevska, Ograzhden, Belassitsa, as well as Pirin, Alibotush, Vrontou and Pangaion in Bulgaria and Greece). Further southwestwards there is another gap, separating a small population in Northwestern Greece (the mountains of Smolikas and Tzoumerka).

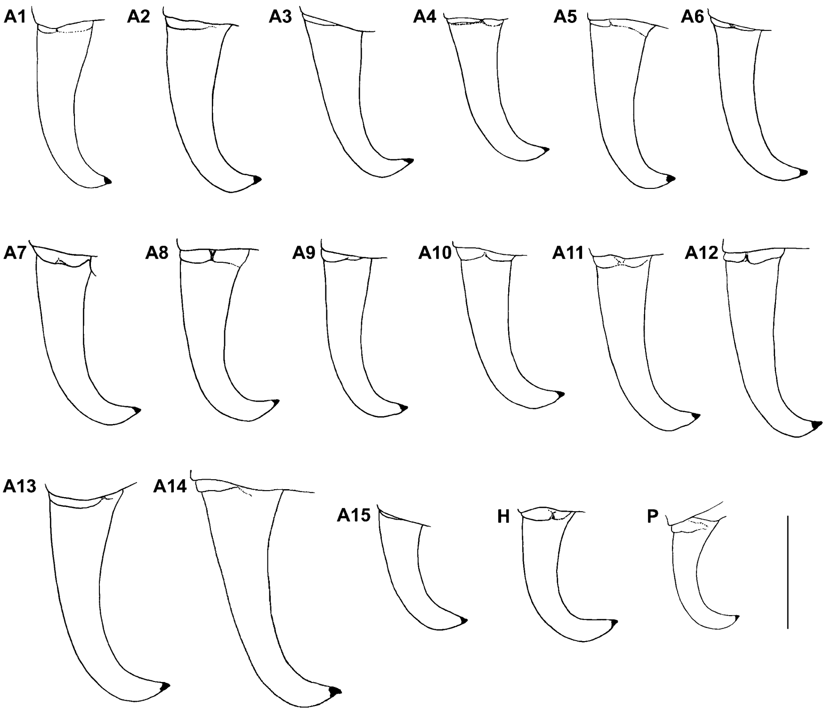

Fig. 3. *Poecilimon ornatus* group, dorsal view of male cercus: A1–A13 – *P. affinis affinis* (A1 – Bulgaria, W Stara Planina, Kom Peak, 1500 m; A2 – Bulgaria, Sredna Gora, Bratiya Peak, 1450 m; A3 – Bulgaria, Ossogovska Planina, Tri Bouki Hotel, 1400–1600 m; A4 – Bulgaria, Rila, Parangalitsa Reserve, >1900 m, A5 – Bulgaria, Rila, Septemvriyche Resort; A6 – Bulgaria, Pirin, Sedelets Peak, 1700–1900 m; A7 – Bulgaria, Pirin, Pirin Peak; A8 – Bulgaria, Pirin, Dautov Vruh Peak; A9 – Bulgaria, Pirin, Dzhindzhiritsa Cirque; A10 – Bulgaria, Pirin, Byala Reka Reserve; A11 – Bulgaria, Pirin, Bayuvi Doupki Reserve; A12 – Bulgaria, Pirin, Strazhite Peak; A13 – Macedonia, Radika Valley, 900 m); A14 – *P. affinis komareki*, Montenegro, Rumija, CH1128; A15 – *P.* cf. *affinis*, Montenegro, Durmitor; H – *P. hoelzeli* – Bulgaria, Belassitsa, 1700–1900 m; P – *P. pindos*, Greece, Timfi (redrawn from Willemse, 1987). Scale = 2 mm.

Poecilimon affinis **(Frivaldszky, 1867)**

P. affinis has the largest range of the taxa within this group. It extends from Northern Greece to the Carpathians in Romania and covers a relatively compact area. An isolated locality is known from the Ukraine. All over this range, the species exhibits nearly no differences in song pattern and the morphological variation is mainly connected with altitude (see below). As a result of this variation, many subspecies are described based on subtle differences (see under *P. affinis affinis*). Although generally a mountainous species, one population has adapted to living in Mediterranean scrub along the Adriatic coast of Northern Albania and Montenegro. Though retaining the same song characteristics, these animals are significantly larger and much stouter than those in most other populations of the species. This population was described by Čejchan (1957) as a distinct species, *P. komareki*, but Heller (1984) regarded it as a subspecies of *P. affinis* because of its great similarity with the latter. Revision of the available material and song recordings, and taking into account the poorly investigated transitional populations between typical *P. affinis* and the coastal populations, indicates that the species *P. affinis* consists of two subspecies.

Poecilimon affinis affinis **(Frivaldszky, 1867)**

Odontura affinis Frivaldszky, 1867 (91, Fig. 2), type locality SW Romania, Mehadia.

Poecilimon affinis; Brunner von Wattenwyl, 1878 (37, 39); Ramme, 1933 (512, Pl. 6, Fig. 1., Pl. 8, Fig. 2, Pl. 11, Fig. 2, Pl. 12, Fig. 2); Bey-Bienko, 1954 (273–274); Harz, 1969 (121, Figs 275, 276, 321, 354, 355–358).

Poecilimon poecilus Ramme, 1951 (94–95), type locality Macedonia, Shar Mts, Popova Shapka resort, 2000 m. Synonym of *P. affinis affinis* after Heller (1984).

Poecilimon affinis poecilus; Karaman, 1974 (27–29, Figs 4–6, 12, 17, 20, 22, 23, 29, 30, 36).

Poecilimon ornatus (Schmidt); Willemse, 1984 (partim; 156, Figs 3, 4, 6–8, 199, 200).

Poecilimon affnis s. str.; Heller, 1984 (82, Figs 5–C, 7–D, 8–A, 9–A); Willemse, 1985 (12–14, Figs 6–10, 35); Heller, 1988 (48–49, Pls 34–E, 35–D, 88, 120–C).

Poecilimon mistshenkoi mistshenkoi Peshev, 1980 (30–33), type locality Bulgaria, Pirin Mts, along the road from the town of Bansko to the Bunderitsa tourist hostel, about 1600 m, syn. n.

Poecilimon affinis affinis (Friv.): Peshev, 1980 (37–39).

Poecilimon affinis ruenensis Peshev, 1980 (39), type locality Bulgaria, Ossogovo Mts, the foot of Ruen Peak, Kolonite Locality, 1560 m, syn. n.

Poecilimon affinis rilensis Peshev, 1980 (39–40), type locality Bulgaria, Rila Mts, the valley of Rilska River, 1600 m, syn. n.

Poecilimon affinis medimontanus Peshev, 1980 (40), type locality Bulgaria, Sredna Gora Mt., Bratia Peak, 1450 m, syn. n.

Poecilimon harzi Peshev, 1980 (41–42), type locality Bulgaria, Pirin Mts, Suhodol Locality, near Yavorov tourist hostel, 1750 m, syn. n.

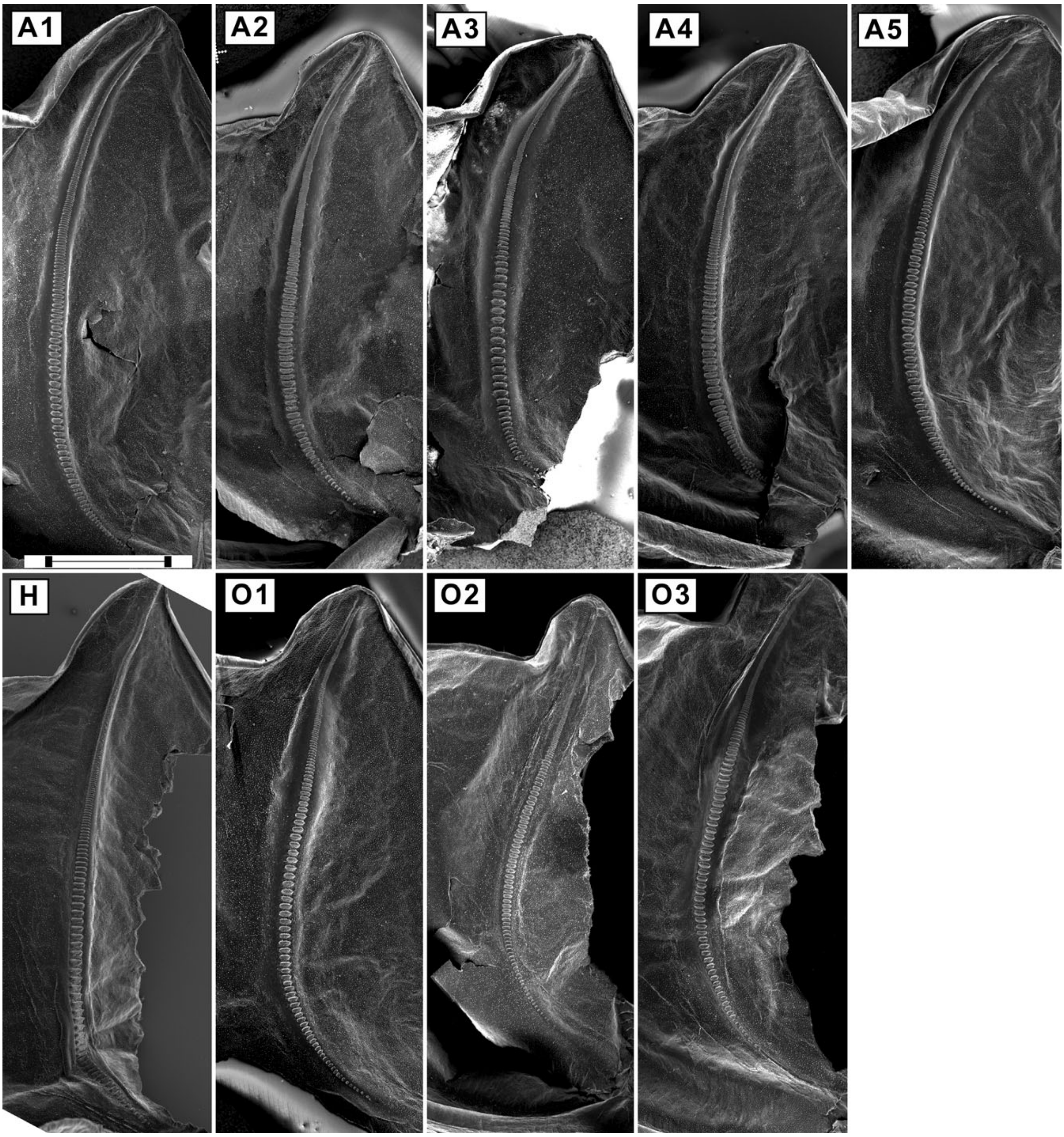

Fig. 4. SEM-photographs of the stridulatory files of *P. affinis* (A1–A5), *P. hoelzeli* (H) and *P. ornatus* (O1–O3) from Bulgaria: A1 – paratype of *P. affinis medimontanus*, Sredna Gora Mts, Bratiya peak, 1400–1500 m, 23.vii.1973, Peshev leg. (NMNH), 220 stridulatory teeth; A2 – paratype of *P. affinis ruenensis*, Ossogovo Mts, 1335–1550 m, 3.viii.1974, Andreeva leg. (NMNH); A3 – Andreeva det. as *P. affinis rilensis*, Rila Mts, Parangalitsa Preserve, 12.ix.1980, Andreeva leg. (NMNH), 180 stridulatory teeth; A4 – topotype of *P. harzi*, Pirin Mts, Byala Reka Preserve, 14.viii.1986, Andreeva leg. (NMNH); A5 – topotype of *P. mistshenkoi mistshenkoi*, Pirin Mts, Bunderitsa chalet, ~1850 m, 22.vii.2001, Chobanov & Heller leg. (CC), 200–210 stridulatory teeth; H – paratype of *P. kisi*, Belassitsa Mt., Demir Kapiya pass, 1800 m, 25.vii.1977, Slaveykov leg. (NMNH), 250–255 stridulatory teeth; O1 – topotype of *P. mistshenkoi marani*, Alibotoush Mt., Livade place, 1700 m, 9.viii.2006, Chobanov leg. (CC); O2 – paratype of *P. mistshenkoi tinkae*, Belassitsa Mt., Demir Kapiya pass, 1800 m, 23.vii.1977, Slaveykov leg. (NMNH); O3 – syntype of *P. mistshenkoi vlachinensis*, Vlakhina Mts, 1700–1900 m, 31.vii.1974, Andreeva leg. (NMNH). Scale = 1 mm.

Poecilimon affinis komareki Čejchan, 1957

Poecilimon komareki Čejchan, 1957 (5, Figs 1–5), type locality Albania, Linze near Tirana; Harz, 1969 (121–122, Figs 274, 277). Subspecies of *P. affinis* after Heller (1984).

Poecilimon komareki rumijae Karaman, 1972 (10, Figs), type locality Montenegro, Runija Mountain. Synonym of *P. affinis komareki* by lowering the latter to a subspecific status.

Poecilimon affinis komareki; Heller, 1984 (82).

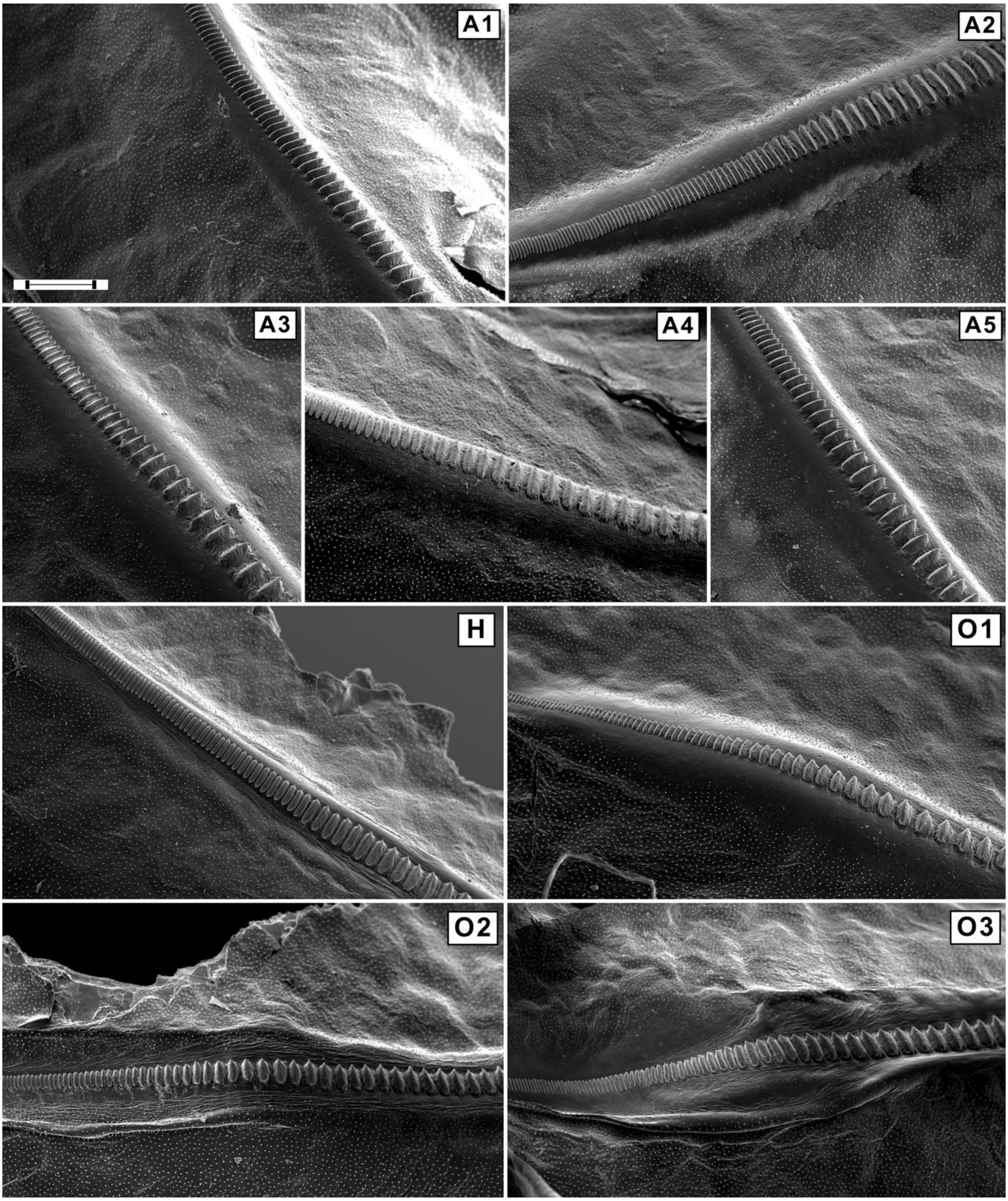

Fig. 5. SEM-photographs of the middle part of the stridulatory files of *P. affinis* (A1–A5), *P. hoelzeli* (H) and *P. ornatus* (O1–O3) (symbols and corresponding material as in Fig. 4). Scale = 200 µm.

Variation (general appearance – Fig. 1B). Similar to *P. ornatus* and the other widely distributed species in this group in terms of the variation in body size, width of fastigium in relation to scapus, upcurving of pronotum and colouration. This is generally connected with altitude (see above; Discussion). Sometimes, however, both small and large animals were observed together (e.g. at 1950 m in Rila Mountains), which is one reason for assuming these as different taxa (e.g. Pavićević & Karaman, 2001). The pronotal shape is also quite variable and cannot be used as a distinctive feature within the group. The incurvation of cerci (Fig. 3A1–A14) is stronger than in *P. ornatus*, with the apical parts almost at right angles to the longitudinal body axis. However, at some places, especially in

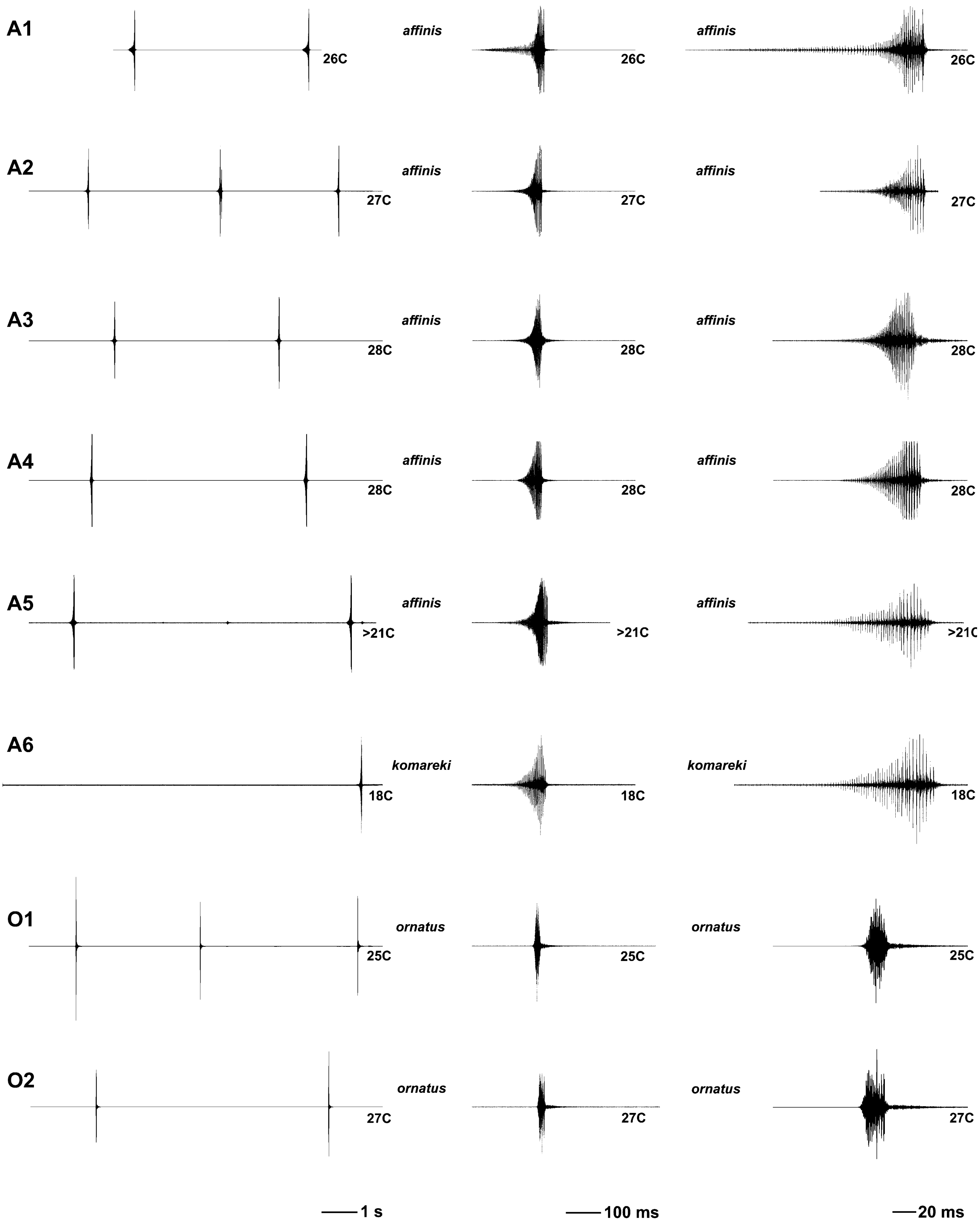

Fig. 6. Oscillograms of the song of *P. affinis affinis* (A1–A5), *P. affinis komareki* (A6) and *P. ornatus* (O1, O2) recorded at three different speeds: A1 – *P. affinis*, Bulgaria, Ruy Mt. foothills, road between Trun and Lomnitsa vill., 750 m, 16.vi.2007, Chobanov & Ilieva leg. (CC), rec. 2007P186; A2 – *P. affinis*, Bulgaria, Rila Mts, above Rilski Manastir Monastery, 2000–2400 m, 17.viii.2008, Chobanov & Ilieva leg. (CC), rec. 2008P203; A3 – *P. affinis*, Bulgaria, Pirin Mts, Shiligarnika place, 1800–2000 m, 27.–28.vii.2009, Chobanov leg. (CC), rec. 2009P063 (unspecified male); A4 – *P. affinis*, data as in A3, rec. 2009P080 (male No. 5); A5 – *P. affinis*, Ukraine, Cherkaska Oblast, Kanev Forest Reserve (49°44′N, 31°30′E), 18.–23.vi.1996, Heller leg., rec. POAF9604 (CH3308); A6 – *P. affinis komareki*, Montenegro, Lovcen Pass (42°25′N, 18°47′E), 800 m, 26.vii.1982, Heller leg., rec. POAF8206; O1 – *P. ornatus*, Bulgaria, Alibotoush Mt., Livade place, 1700 m, 9.viii.2006, Chobanov leg. (CC), rec. 2006P306; O2 – *P. ornatus*, Bulgaria, Maleshevska Planina Mts, above Gorna Breznitsa vill., 800 m, 6.vii.2006, Chobanov leg. (CC), rec. 2006P292.

the North Pirin Mountains, where *P. affinis* and *P. ornatus* occur parapatrically, the cercal shape of both species is more similar (compare Fig. 3A12 with Fig. 2O1–O10). Still, in some animals the shape of cercus deviates markedly from the normal range of variation

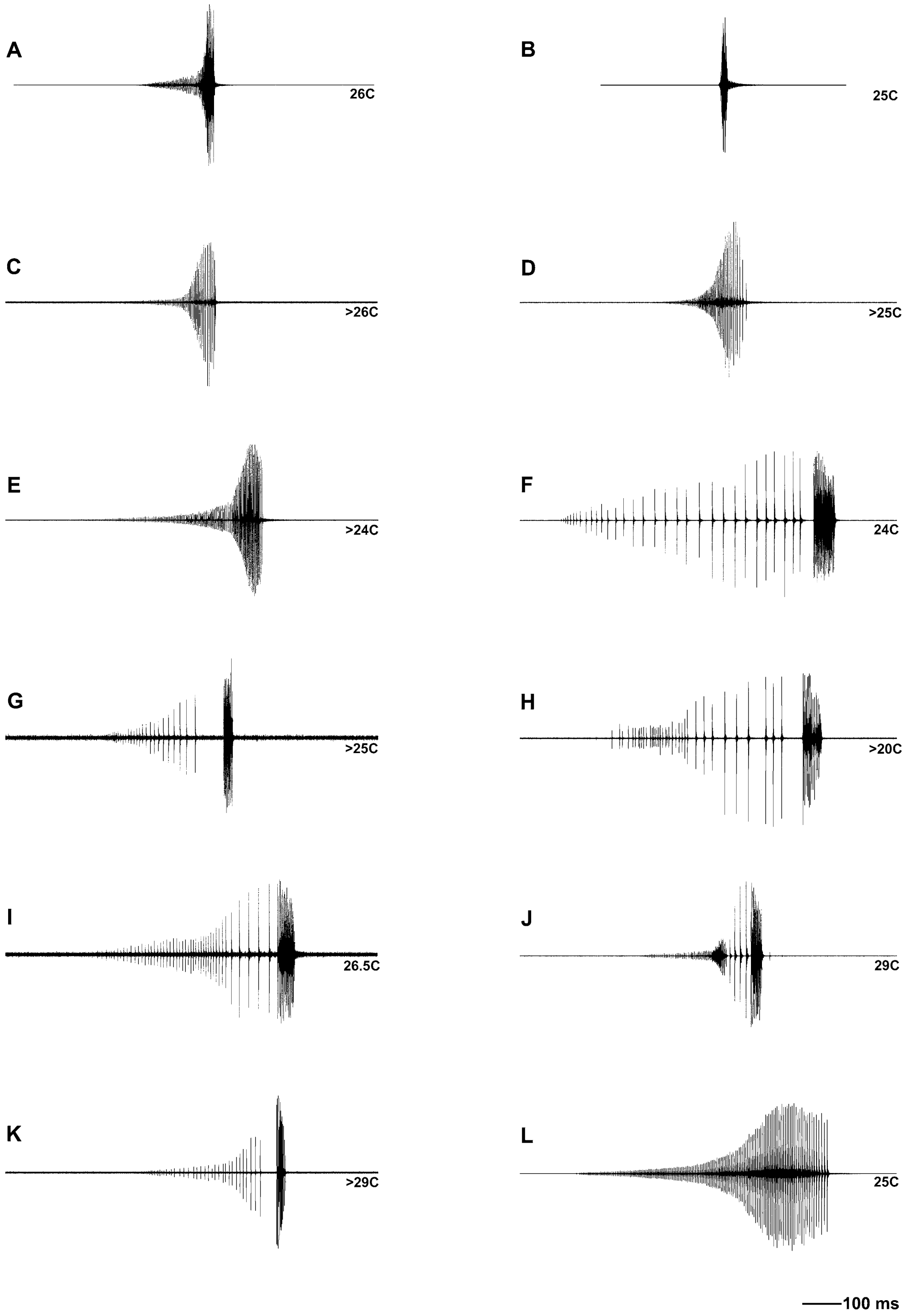

Fig. 7. Oscillograms of the song: A – *P. affinis*, Bulgaria, Ruy Mt. foothills, road between Trun and Lomnitsa vill., 750 m, 16.vi.2007, Chobanov & Ilieva leg. (CC), rec. 2007P186; B – *P. ornatus*, Bulgaria, Alibotoush Mt., Livade place, 1700 m, 9.viii.2006, Chobanov leg. (CC), rec. 2006P306; C – *P. hoelzeli*, Greece, Pieria Mt., (40°15′N, 22°9′E), 1680 m, 27.vi.1986, Heller leg., rec. POHO8206 (CH0157); D – *P. pindos*, Greece, Mavrovouni Mt. (39°51′N, 21°7′E), 25.viii.1988, Heller leg., rec. POPI8809 (CH2317); E – *P. artedentatus*, Greece, Peloponnesos, Mykene (37°44′N, 22°45′E), 4.iv.1983, Blümm leg., rec. POAR8315 (CH1175); F – *P. obesus*, Greece, Amfilohia (38°51′N, 21°10′E), 10.vi.1980, Heller leg., rec. POOB8020 (CH1151); G – *P. nobilis*, Greece, Peloponnesos, Taigetos, (36°57′N, 22°22′E), 1020 m, 15.vi.1980, Heller & Volleth leg., rec. PONO8018 (CH1176); H – *P. soulion*, Greece, Soulion Mt. (39°23′N, 20°39′E), 1300–1400 m, 27.vi.1999, Heller & Volleth leg., rec. POSO9903 (CH4825); I – *P. soulion*, Greece, Timfristos (38°54′N, 21°54′E), 1.–30.vi.1989, Heller leg., rec. POOB8901 (CH2475); J – *P. gracilioides*, Greece, Tsoumerka (39°24′N, 21°9′E), 1850 m, 6.–7.viii.2003, K.-G. Heller, M. Heller & M. Volleth leg., rec. POGC0302 (CH6291); K – *P. gracilis*, Austria, Kärnten (46°27′N, 14°23′E), 20.viii.1989, Heller leg., rec. POGR8905 (CH2555); L – *P. jablanicensis*, locality and date as in description, rec. 2006P332 (male No. 2).

(Fig. 3A15), as similarly recorded for the stridulatory row by Willemse (1985).

The distinctive features are again in the shape of the stridulatory file (Heller, 1984; Willemse, 1985) (Figs 4 and 5: A1–A5) and the song (Heller, 1984) (Figs

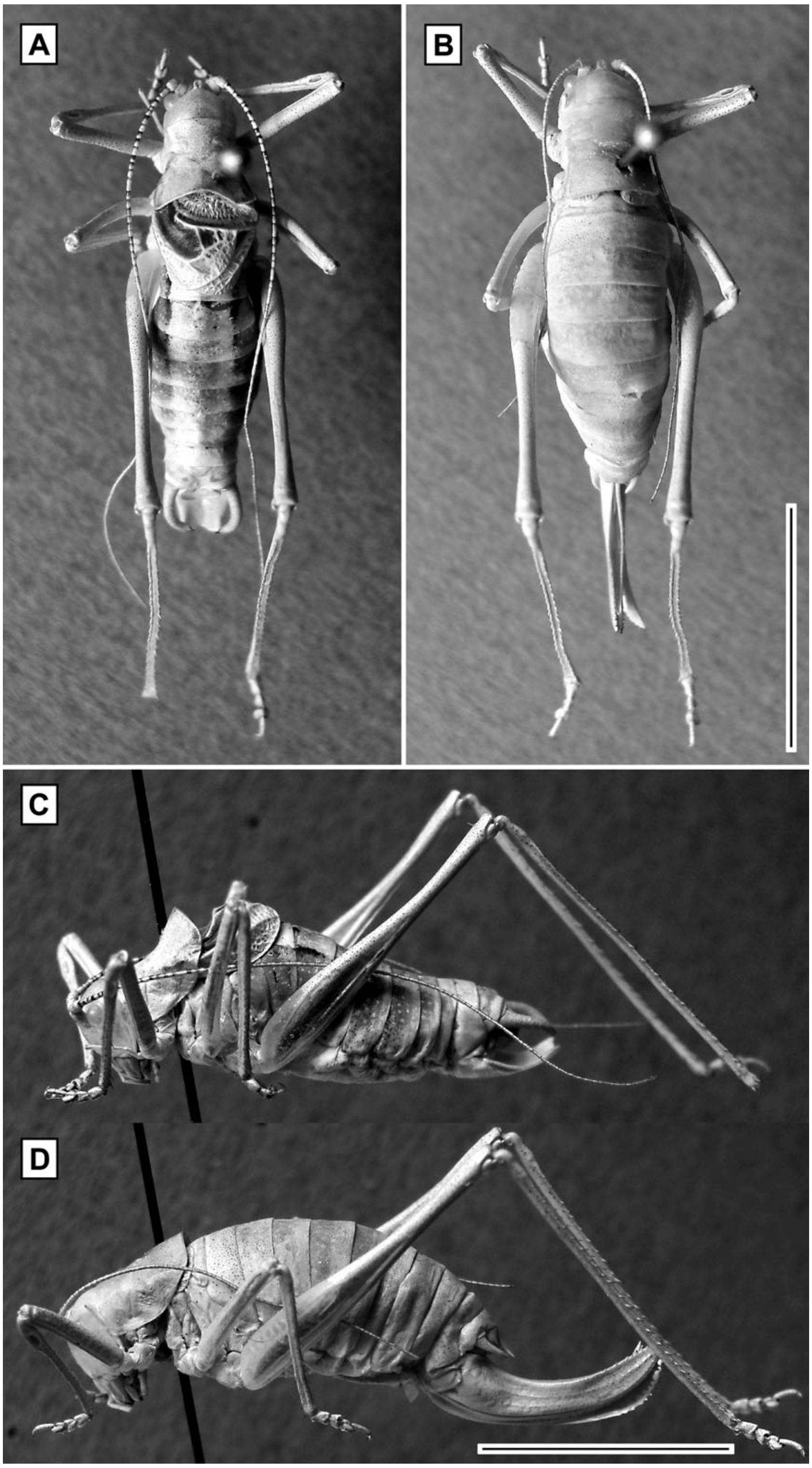

Fig. 8. *Poecilimon jablanicensis*: A – male (holotype), dorsal view; B – female (paratype), dorsal view; C – male (holotype), lateral view; D – female (paratype), lateral view. Scale = 1 cm.

6A1–A6, 7A). The stridulatory file is bearing a high number of teeth (usually more than 200) and has a small bulge at the middle. However, though Heller (1988) reports 220–230 teeth in this species we observed 180–240 teeth and the number is generally more variable in the southeastern populations (SW Bulgaria). The lowest number of teeth is found in small specimens from high altitudes. Thus, the number of teeth is not a good character for distinguishing *P. affinis* from *P. ornatus* but the shape of the stridulatory file is a more reliable morphological feature for separating these species. The song also distinguishes *P. affinis* from *P. ornatus* (Fig. 6: compare A1–A6 with O1, O2; Fig. 7: compare A with B), the former produces long syllables (100–500 ms) with a

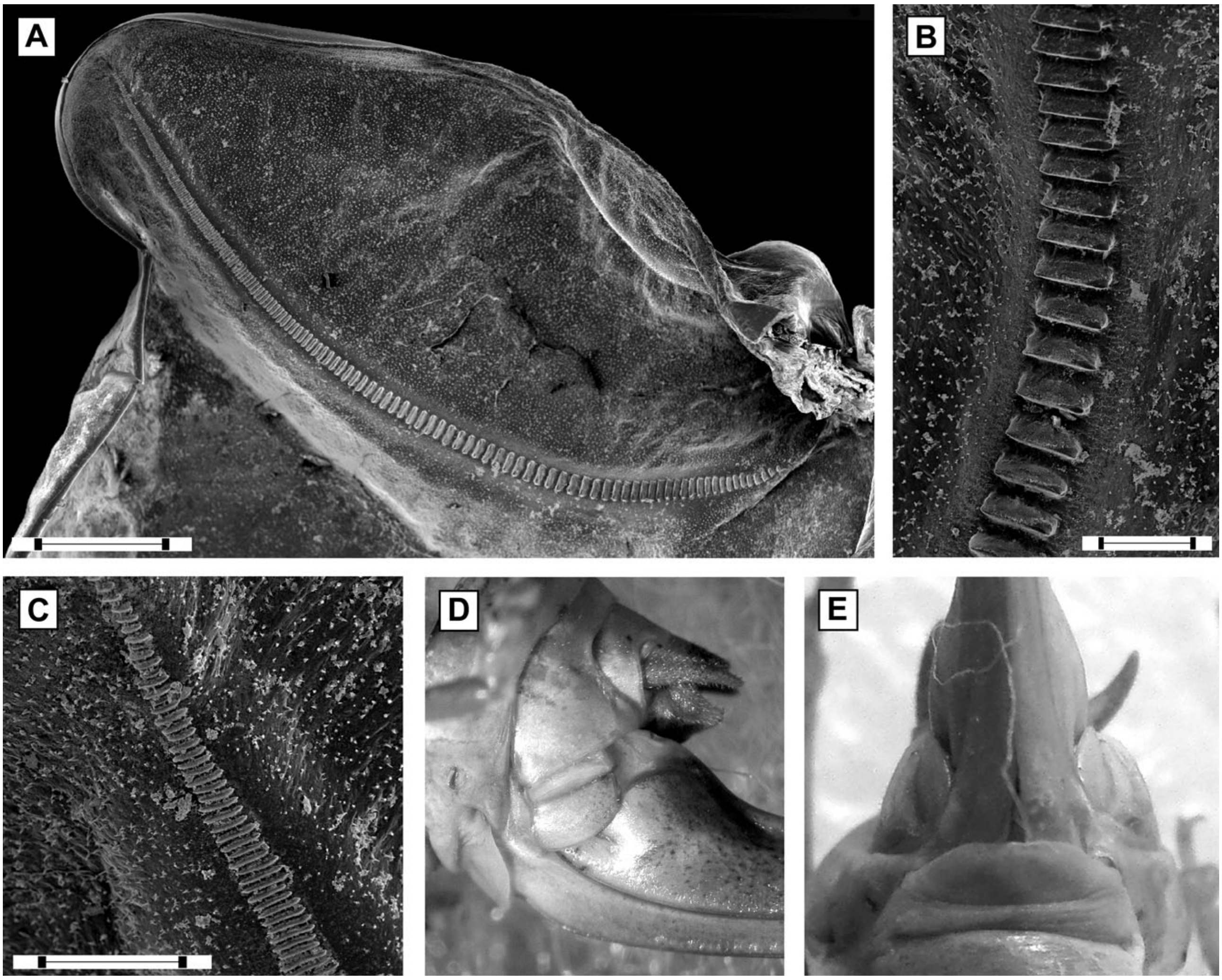

Fig. 9. *Poecilimon jablanicensis*: A – male stridulatory file (scale = 500 µm); B – middle part of male stridulatory file (scale = 100 µm); C – apical part of male stridulatory file (scale = 100 µm); D – base of the ovipositor in lateral view; C – same in ventral view.

gentle and continuous increase in amplitude at the beginning and a following high-amplitude section of 30–40 ms.

Synonymy. The study of the rich material (including types) of the *Poecilimon ornatus* group indicated that the populations from the mountain regions of Western and Northeastern Macedonia and Middle and central part of Western Bulgaria (see Distribution; Figs 10–11) show the same variation in morphology as *Poecilimon affinis affinis* (see for example Fig. 3A1–A13, Figs 4 and 5: A1–A5). The sound recordings are also similar. The song (Figs 6A1–A6, 7A) consists of single syllables, each syllable having a long, low-amplitude beginning, followed without interruption by a steep increase in amplitude to the second high-amplitude part. Again the fading of the final low-amplitude part is a result of echoes (see *P. ornatus*). At a temperature of 26–28°C the syllables of the songs of individuals from these populations usually last 150–200 ms with a high-amplitude part of 30–40 ms. The song duration tends to decrease east- and southwards, being shortest in populations from the northern slopes of the Pirin Mountans in Bulgaria, which border the populations of *P. ornatus*. Whether this is a result of geneflow is still a matter of speculation. The song of one individual, which did not differ in morphology, was aberrant with a shorter low-amplitude part of the syllable (Fig. 6A4) and syllables hardly longer than 100 ms.

These results indicate the synonymy of *P. mistshenkoi mistshenkoi*, *P. affinis ruenensis, P. affinis rilensis, P. affinis medimontanus* and *P. harzi* with *P. affinis affinis* (*P. affinis* s. str. sensu Heller, 1984).

Recently, Pavićević & Karaman (2001) again raised *P. poecilus* to species level, pointing out that it is "… a good species, which can be supported by our supposition that it was found together with *P. affinis serbicus* on the same bush of *Juniperus* on Prokletije Mts". This was not confirmed by a diagnostic comparison of morphological, bioacoustic or other characters. Heller (1984) noted the tendency for body size to decrease (the small body size and pronotum shape being characteristics of *P. poecilus* by Ramme, 1951) with increasing altitude in the populations of *P. affinis* on the western slopes of Shar Mountains (locus typicus of *P. poecilus*). Karaman (1974) discusses the general tendency for the pronotal metazona to be raised and black colouration to predominate where this species is abundant and in populations of *P. affinis* from high altitudes (with increased humidity). Indeed,

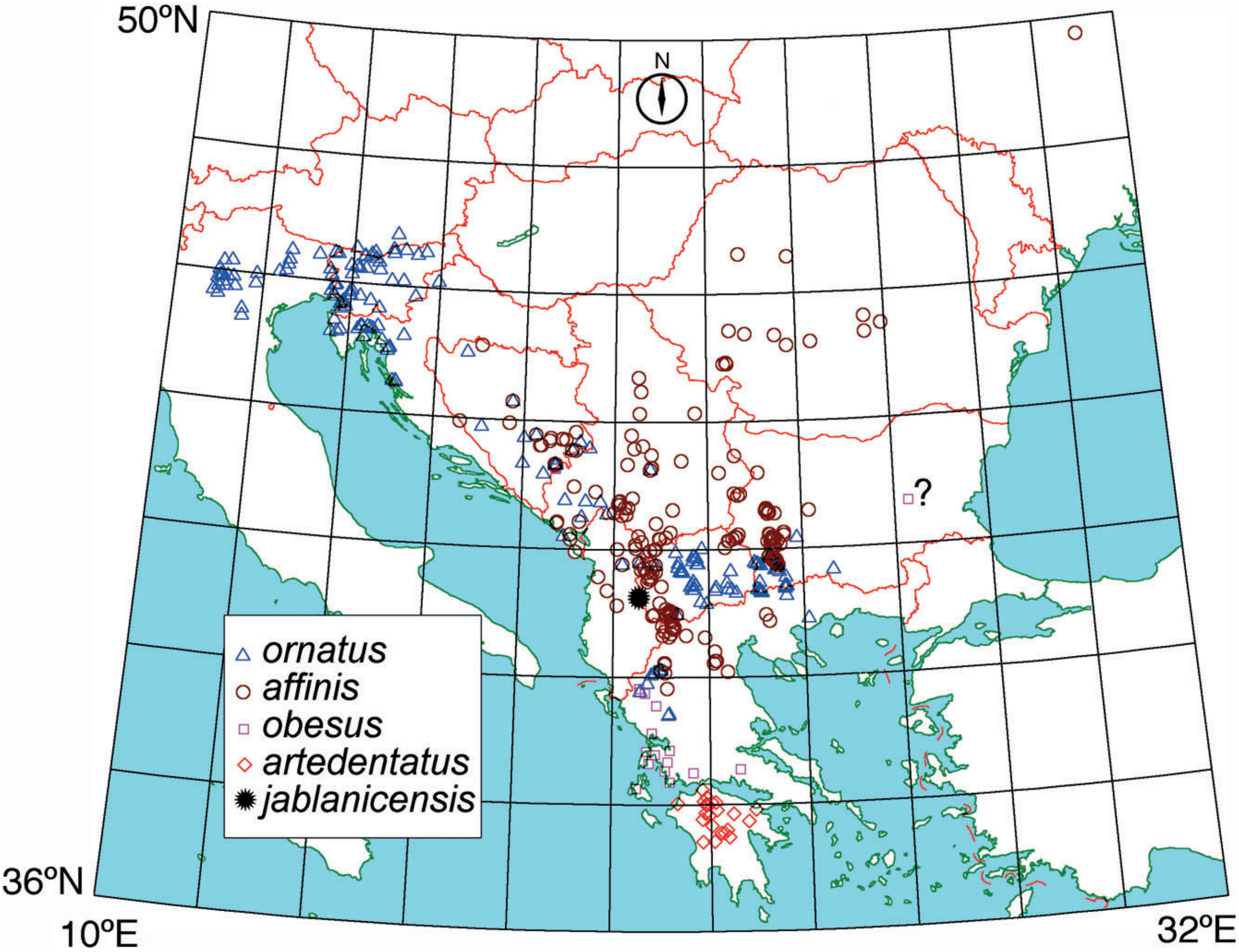

Fig. 10. Distribution of *P. ornatus, P. affinis, P. obesus, P. artedentatus* and *P. jablanicensis*.

small melanistic individuals occur at the upper altitudes of the distributions of both *P. affinis* (above 2000 m in the Shar Mountains in Macedonia and Rila and Pirin Mountains in Bulgaria) and *P. ornatus* (e.g., above 2000 m in the Jakupica Mountains in Macedonia), while large greenish *P. affinis* with a weakly raised pronotum were observed at 900 m in the valley of the Radika River (Macedonia). This tends to support Heller's (1984) suggestion that *P. poecilus* and *P. affinis* are synonymous. Karaman (1972) described *Poecilimon komareki rumijae* on the basis of already mentioned generally variable morphological characters like the shape of the pronotum and body size. Because of the lowering *P. komareki* to a subspecies of *P. affinis* by Heller (1984), the weakly differing *P. komareki rumijae*, considered by Eades & Otte (OSF online, 2009) as a subspecies of *P. affinis*, becomes an infra-subspecific category. Thus (see also Heller, 1984), it is here considered synonymous with *P. affinis komareki* (= *P. komareki rumijae*, syn.). Karaman (1974) describes a further two subspecies of *P. affinis – P. affinis serbicus* and *P. affinis hajlensis*, which are distinguished by subtle differences in the shape of the pronotum and cerci, and body dimensions. In addition, the shape of the stridulatory file of individuals in some populations in Serbia differs from that typical for *P. affinis* (Willemse, 1985). The shape of the cerci of one specimen from Durmitor (Montenegro) differed from that of individuals in all other populations of *P. affinis* investigated (Fig. 3A15). However, its taxonomic position will remain speculative until the songs of individuals from these populations are recorded.

Distribution (Figs 10, 11, Appendix). The main part of this species' range covers the Balkan Peninsula (Western and Central Bulgaria, Northwestern Greece, Western Macedonia, Albania, Serbia, Montenegro, Bosnia and Hercegovina), reaching also Romania and, in an isolated spot, the Kanev region in Southern Ukraine. *P. affinis* occurs throughout the Southwestern Carpathians (Romania) and the Western Stara Planina (Bulgaria) and the mountains in Southeastern Serbia and the central part of Western Bulgaria, where the distribution divides into two arms – western and eastern, which encompass the southern population of *P. ornatus*. The western, more extensive, arm runs through the Kosovo Highlands into the Pindo-Dinaric mountain group north to Bosnia and Hercegovina, and south to the North Pindos (Greece), and in the west reaching the Pelagonian horst anticline on the Baba (Pelister) Mountain (Macedonia). The eastern arm, encompassing the population of *P. ornatus* from the North, extends into the Rhodopean mountain group

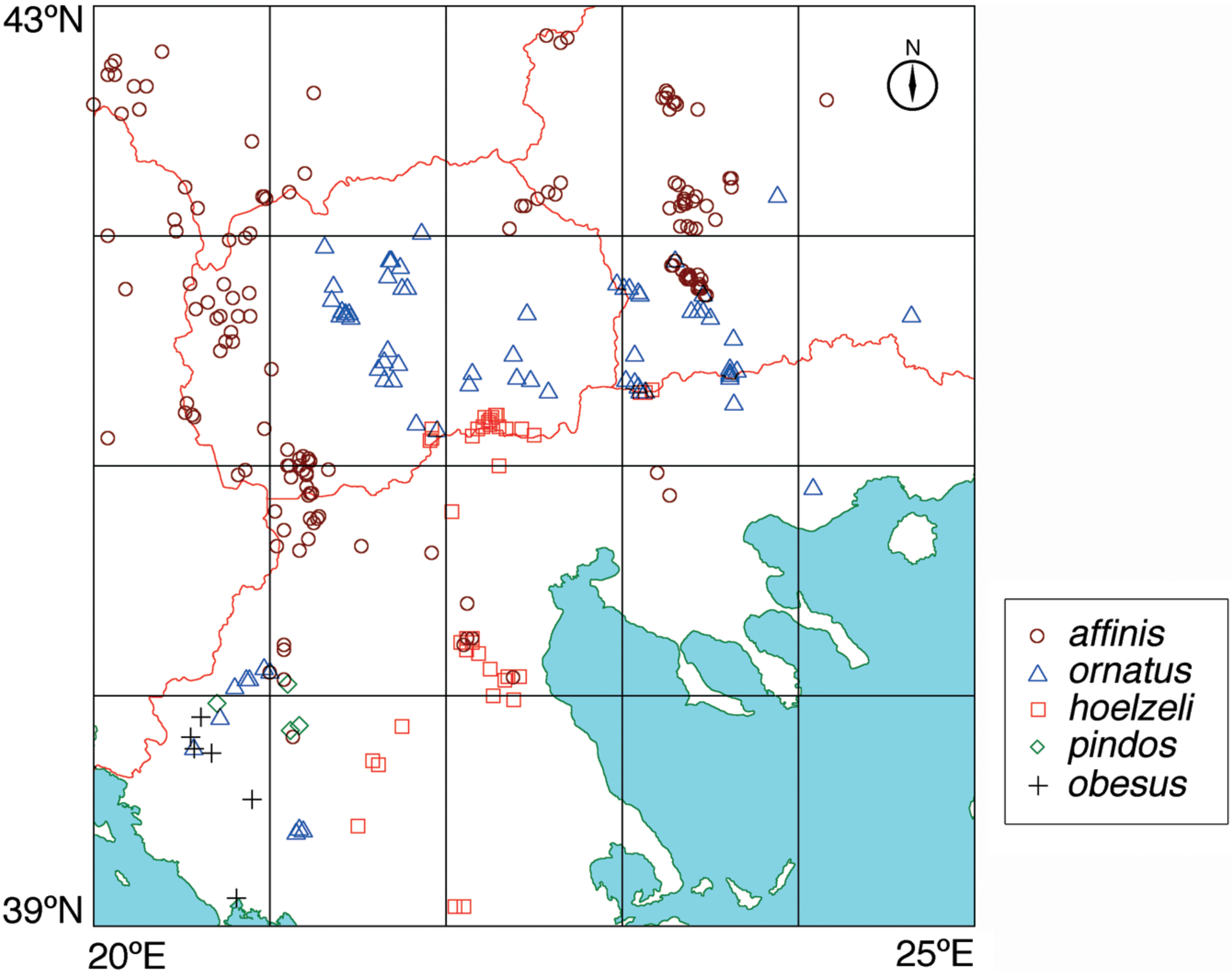

Fig. 11. Distribution of *P. affinis, P. ornatus, P. hoelzeli, P. pindos* and *P. obesus* on the Central Balkan Peninsula.

reaching Rila and North Pirin Mountains (Bulgaria) in the east. Isolated localities are recorded for the Lakhanas and Vertiskos Mountains (Greece: Makedhonia).

Along the borders between the ranges of *P. ornatus* and *P. affinis* these species are not recorded as occurring sympatrically. However, there seems to be a narrow, southeast-northwest oriented contact zone between populations of these species in the Northern Pirin Mountains, where they may occur both sympatrically and even syntopically. Moreover, Köhler (1988) reports both species from the same area. Other possible areas of contact are the Treska River Valley in Macedonia and some places in Greece.

Poecilimon hoelzeli Harz, 1966

Poecilimon ornatus hoelzeli Harz, 1966 (23, Figs 10–14), type locality Macedonia, Kožuf Mt., Mala Rupa, 1200 m; Harz, 1969 (120, Fig. 349). Subspecies of *P. affinis* after Heller, 1984.

Poecilimon hoelzeli; Willemse, 1982 (158, 160, Figs 11–14, 128–130, 184–186, 201, 202); Heller, 1988 (49, Figs 34–F, 35–E, 88).

Poecilimon affinis hoelzeli; Heller, 1984 (82–83, Figs 6, 8–B).

Poecilimon kisi Peshev, 1980 (36–37), type locality Bulgaria, Belassitsa Mt., northeastern slope of Kalabak Peak, Demirkapiya Locality, 1700–1900 m, syn. n.

Variation (general appearance – Fig. 1C). This species usually inhabits mountains and exhibits little morphological variation. However, at some places at altitudes between 600–700 m quite large animals with a less elevated pronotal metazona and little melanistic colour are recorded (e.g. Kozhuf Mountain, Macedonia). Thus, generally its variation falls within that of *P. ornatus* and *P. affinis* (see Discussion). The incurvation of the cerci (Fig. 3H) is marked and typical of this species. The stridulatory file (Figs 4 and 5: H) and song (Fig. 7C; Heller, 1984) differ slightly from those of *P. affinis* and are more uniform. The number of stridulatory teeth is high and ranges between 235 and 270.

Synonymy. This species is closely related to *P. pindos* and *P. affinis* although initially described as a subspecies of *P. ornatus*. Its specific features include the shape of male cerci, pronotum and tegmina, the shape of the stridulatory row and number of stridulatory teeth. A unique characteristic of *P. hoelzeli* is the basal fold on dorsal margin of the lower ovipositor valve, which bears a highly visible knob-shaped process. A new distinctive

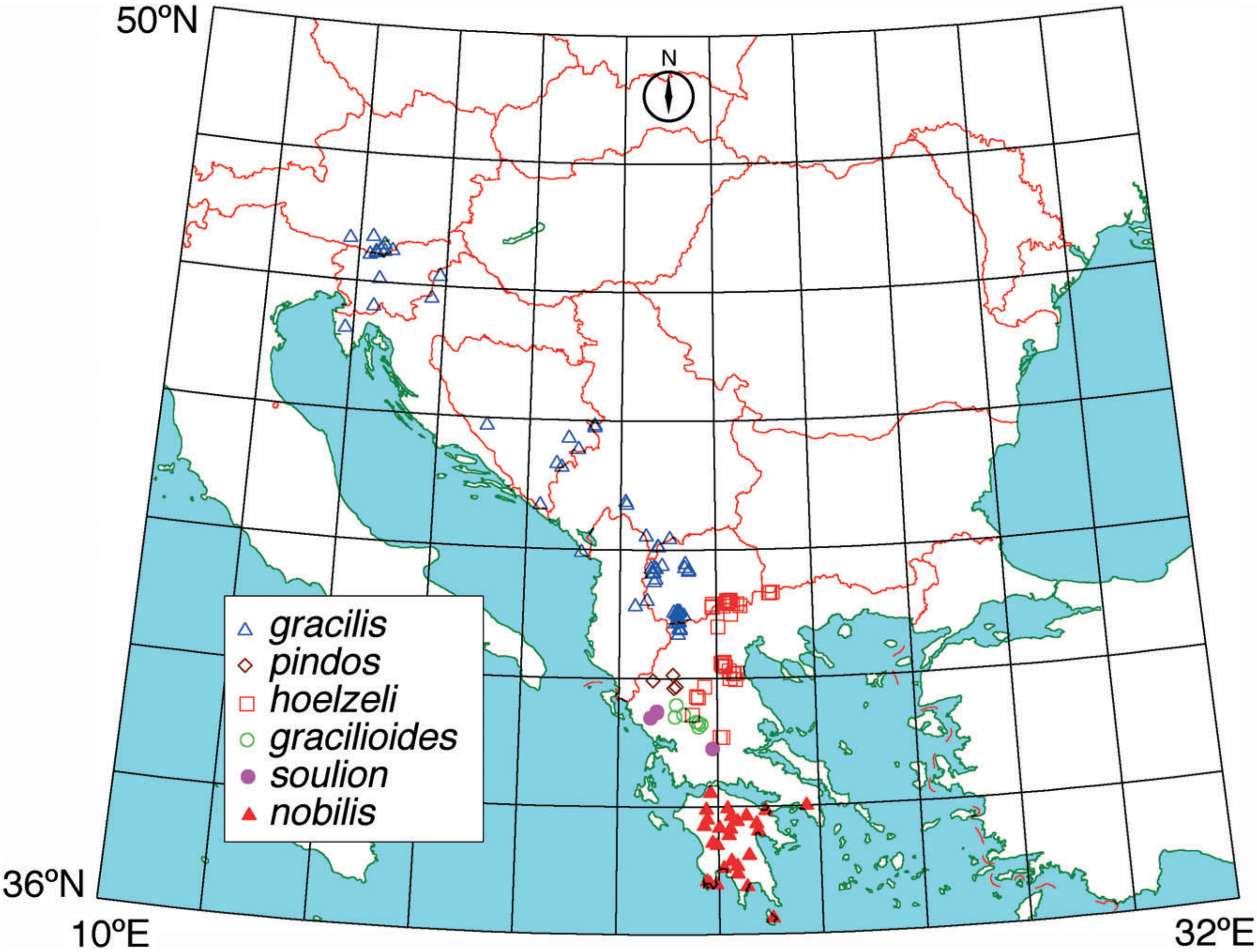

Fig. 12. Distribution of *P. gracilis, P. pindos, P. hoelzeli, P. gracilioides, P. soulion* and *P. nobilis*.

feature is the number of stridulatory teeth, which is generally higher than in its relatives (usually more than 240). The specific status of *P. hoelzeli* was confirmed both by the stability of its distinctive characters (see Willemse, 1982; Heller, 1988), its syntopic occurrence with *P. ornatus* on the Belassitsa Mountain (SW Bulgaria) and para- and sympatric occurrence with *P. affinis* (Willemse, 1985) in Greece (Pieria Mt., 1500 m) (Willemse, 1982 as *P. ornatus*). The results of the study of the type material and newly collected specimens of *P. kisi* from Belassitsa Mt. (Bulgaria) clearly support its synonymy with *P. hoelzeli*.

Distribution (Figs 11, 12, Appendix). The range of this species is restricted to a small area in the Central Balkans, covering Southeastern Macedonia, extreme Southwestern Bulgaria and the central part of Northern Greece southwest to Pieria Mt.

Poecilimon gracilis (Fieber, 1853)

Barbitistes gracilis Fieber, 1853 (261), type locality "Illyrien".

Isophya tölgi Ebner, 1908 (332), type locality Bosnia and Hercegovina, Cajniza (Ramme, 1933). Synonym of *P. gracilis* after Ramme (1933).

Poecilimon gracilis; Ramme, 1933 (515, Pl. 6, Fig. 5, Pl. 8, Fig. 6, Pl. 11, Fig. 5); Bey-Bienko, 1954 (277); Harz, 1969 (123, Figs 280, 324, 363–365); Willemse, 1982 (158, 160, Figs 11–14, 128–130, 184–186, 201, 202); Heller, 1984 (85, Figs 8–C, 9–C, 10–E); Heller, 1988 (51–52, Figs 36B, 88, 121C).

Poecilimon mavrovi Karaman, 1958 (38–39, Figs 8–12), type locality Macedonia, Bistra Mt., Careva Cheshma and Verbenska Gora. Synonym of *P. gracilis* after Heller (1984).

Poecilimon mavrovi; Harz, 1969 (123–124).

Variation (general appearance – Fig. 1D, frequency spectrum – Fig. 15). This species is morphologically variable within its wide range (Willemse, 1982) in terms of body size and shape of the pronotum and cercus (Fig. 2G, C) etc. The differences are of a similar scale to the differences in these characteristics in *P. ornatus* and *P. affinis*, though it is difficult to connect them to microclimate or other factors. The song (Fig. 7K; Heller, 1984), however, is typical and clearly specific to this species.

Distribution (Figs 12, 13, Appendix). S Austria, Slovenia, Croatia, Bosnia and Hercegovina, Serbia, Montenegro, Albania, Macedonia, Northeastern Greece (Florina).

Poecilimon jablanicensis, sp. n.

Diagnosis. *Poecilimon jablanicensis*, sp. n., is readily defined by the shape of its pronotum, tegmina, cerci (Figs 1E, 2J, 8, 9) and song (Figs 7L, 14A) of the male, by the reduced, non-overlapping tegmina in the female (see Fig. 8B, D) and the reduced size of the auditory spiracle in both sexes (see Fig. 8C, D).

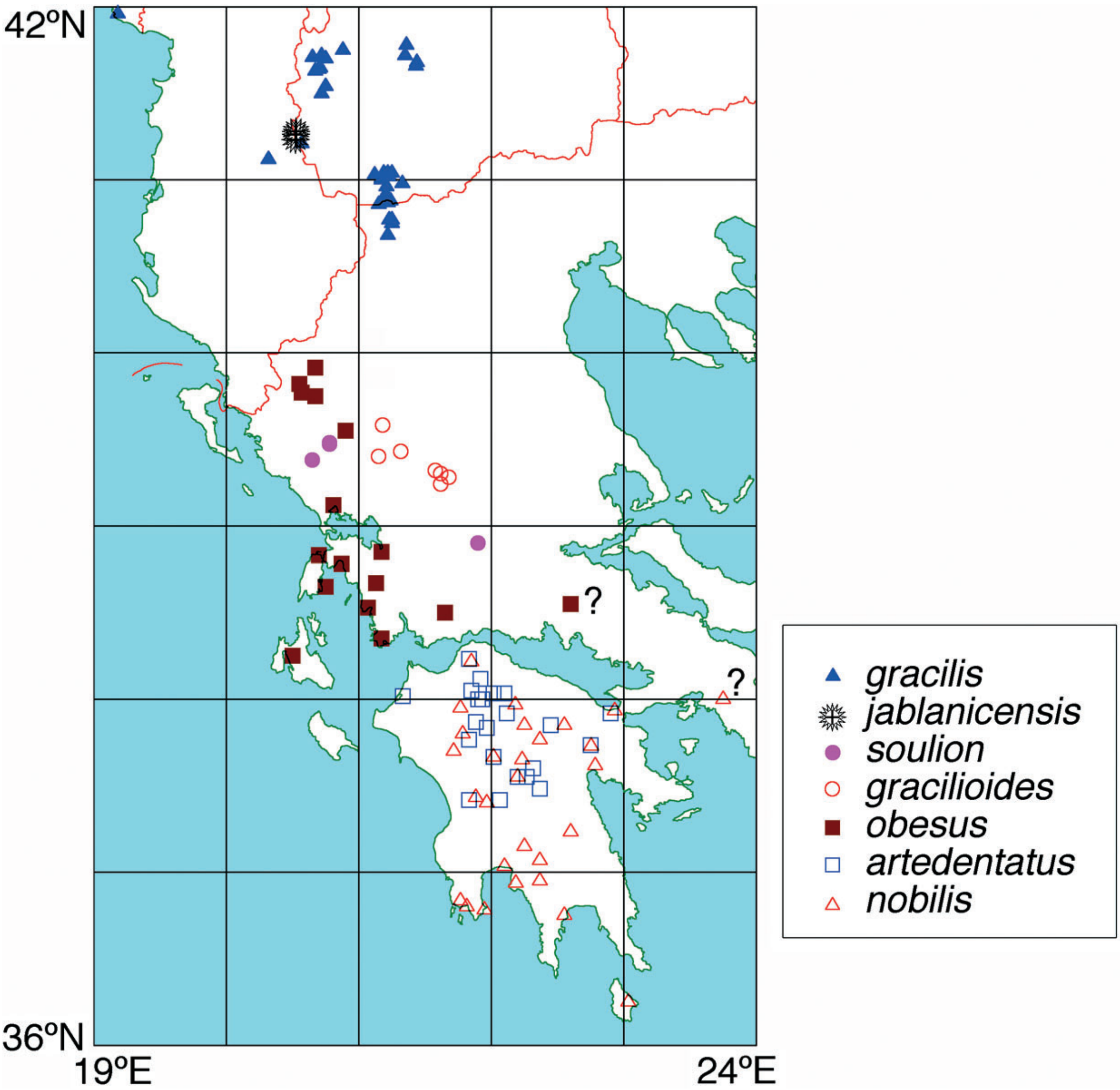

Fig. 13. Distribution of *P. gracilis, P. jablanicensis, P. soulion, P. gracilioides, P. obesus, P. artedentatus* and *P. nobilis* in the Central and Southern Balkans.

This species is one of the slender species of the *Poecilimon ornatus* group. It is most closely related to *P. gracilis* and *P. gracilioides*, the first being probably the ancestral taxon that gave rise to this specialized mountain form, which inhabits only open (pseudo-) subalpine areas. The unique morphological autapomorphies of *P. jablanicensis* are the reduced size of the auditory spiracle in both the male and female, and the rudimentary tegmina in the female, which do not overlap. Other characters differentiating this new species from *P. gracilioides* are the wider and strongly upcurved metazona of the pronotum, bigger and strongly bulging male tegmina, clearly longer stridulatory file with a greater number of teeth, smaller body size, shape of cerci, and length of subgenital plate. In addition, on the stridulatory file (Fig. 9A–C) of this new species the teeth gradually change in size, while in *P. gracilioides* (and *P. soulion*) there is an abrupt change in the size of the teeth. The colouration of *P. jablanicensis* resembles that of *P. gracilis,* but the integument is much duller and the general colour has usually more yellowish green than fresh-green (compare Fig. 1: D with E).

The song of *Poecilimon jablanicensis* differs greatly from the two- to three-partitioned and shorter song of its closest relatives, *P. gracilis* and *P. gracilioides*. The few recordings of the song of *P. gracilioides* indicate that the syllables are produced at much longer intervals. Generally the song resembles that of the sympatric *P. affinis* (compare Fig. 6A1–A6 with Figs 7L, 14A). In *P. jablanicensis* the syllables are regularly repeated over a long period, while in *P. affinis* they are normally separated by long intervals, irregularly repeated or sometimes a few syllables are produced with short intervals. The syllable has a similar shape in both taxa, but in *P. jablanicensis* it is much longer (750–350 ms at 26–30°C, probably up to more than 1 s at lower temperatures) than in *P. affinis* (500–100 ms at 18–30°C). In *P. jablanicensis* the highest amplitude-part (~100–150 ms) is about 3–5 times longer than in *P. affinis* (30–40 ms) and includes a greater number of impulses. The song of *P. jablanicensis* resembles that of *P. artedentatus* (Fig. 7E; Heller, 1984), which is endemic in the Peloponnesos in Southern Greece, and even more so by having a smaller number of impulses. The frequency spectrum of *P. jablanicensis* covers lower frequencies than that of its relatives, with a maximum at about 22 kHz (but see below) compared to the 30 kHz in *P. gracilis* (Heller, 1988; see Fig. 15).

Description

Male (Figs 1E, 8A, C). Medium sized and considerably slender. Integument moderately shiny to dull (especially that of the pronotum).

Head: fastigium of vertex extended anteriorly, lateral margins parallel, length and width about equal to those of second antennal segment, width about half to two-thirds of that of scapus, with strong longitudinal groove. Antennae with second segment conspicuously swollen, about one-third wider than the third segment.

Thorax: pronotum saddle shaped both in dorsal and lateral view; prozona slightly raised anteriorly, metazona dome-raised and very broad above tegmina, transverse sulcus cutting the median line of pronotum before its middle at the start of its backward extension. Posterior margin is concave to barely emarginated. Lower margin of pronotal lateral lobe slightly wavy, its hind margin rounded. Auditory spiracle small for this species-group, much smaller than in its relatives, *P. gracilis* and *P. gracilioides*; its vertical diameter smaller than the diameter of one eye (similar to that in the females of the latter two species; see Fig. 1 in Stumpner & Heller, 1992), aperture narrow elliptical, only slightly covered by the pronotal lateral lobe. Tegmina conspicuously large, wider than pronotum, anal margin protruding at the lateral edge of pronotum with the tip of the stridulatory vein forming an acutely-rounded lobe. Apical margin of tegmina reaches from the middle of second to the beginning of third abdominal tergite. Visible length of tegmina is equal to or slightly shorter than that of pronotum, complete length greater than that of pronotum. Texture of tegmina is rough, not mostly membranous as in *P. gracilis*. Stridulatory vein (CuP) is strong. The medio-cubital area is dome-raised. Medial field forms large, thick, membranous resonator. Stridulatory file of left tegmen (Fig. 9A–C) about 3.3 (178 teeth) – 3.4 mm long, bearing 175–210 teeth (6 males, mean ± SD = 193 ± 12, median = 194; the basal part of file frequently bears 2–6 narrower, sometimes spine-like and somewhat isolated teeth, which also were counted), almost reaching the edge of the tegmen at the apical part of the file. Fore femur longer than pronotum. Hind femora lack ventral spines.

Abdomen: margins of tergites straight or weakly excised, especially the first tergite. Long stout cerci (Fig. 2J) slightly and evenly curved inwards and downwards after the middle; basally strongly dorso-ventrally thicker. Apical part of cerci slightly flattened dorso-ventrally, in lateral view slightly S-shaped (Fig. 8C) and tapering to the tip, in dorsal view almost equally thick along whole length. Cercus tip shortly tapering to a wide end, bearing a large tooth. Cercus tooth long, wide, with an inner crest bordering an inner ventrolateral groove. Epiproct large, slightly broader than long, with an ovally obtuse hind margin. Subgenital plate (see Fig. 8A, C) long, reaching tip of cerci, wide, lateral margins almost parallel, only slightly converging posteriorly, posterolateral edges triangularly protruding, posterior margin with slightly wavy excision.

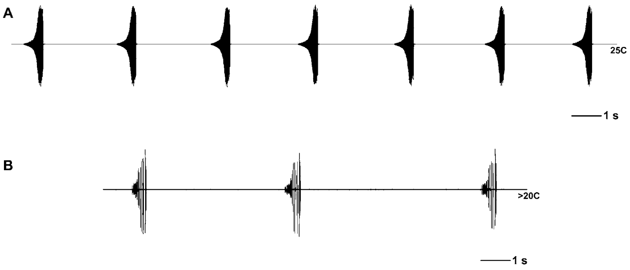

Fig. 14. Oscillograms of the male calling songs of *P. jablanicensis*, rec. 2006P332 (A) and *P. soulion*, rec. POSO9903 (B) (data as in Fig. 7).

Colouration (see Fig. 1E): light green to yellowish-green. Vertex, pronotum, tergites and legs finely speckled rusty brown. Antennae yellowish with black rings. Head and pronotal dorsum with two lateral thin pale yellowish stripes, which on metazona of pronotum broaden posteriorly and meet at the hind margin; there is a similar pale yellow median sripe along the vertex. Dorsolateral corners of pronotum on metazona with red triangular stripes, on the outside border of the yellow stripes. Sometimes rusty-red spots or stripes are present on fastigium of vertex, vertex, legs, etc. Tegmina yellowish with mediocubital area brown. Tibiae yellowish-green to yellowish-brown. Abdomen of the same general colouration with two broad pale yellowish dorsal stripes, sometimes laterally bordered with black spots starting from the base of terga but not reaching their posterior margins. Sometimes, shorter and smaller black spots medially border the stripes. Cercus yellowish, tooth black.

Female (Figs 8B, D, 9D, E). Integument dull. Pronotum almost cylindrical and straight dorsally with the transverse sulcus cutting the median line after the middle of pronotum. Hind margin of pronotum slightly concave to slightly convex. Metazona weakly widened. Auditory spiracle very small, its diameter much smaller than the eye. Tegmina fully covered by pronotum, not overlapping each other and reaching at most to the middle of first tergite, roundly-triangular, with a transverse, almost straight apical margin. Stridulatory apparatus reduced. Cerci long, surpassing the epiproct, conical, apical fourth slightly angularly incurved. Epiproct elongated and oval. Subgenital plate (Fig. 9D, E) short, almost oval, with a barely angled tip. Ovipositor more than twice as long as pronotum, apical part with short, stout teeth dorsally, ventrally and laterally, as in allied species. Gonangulum flattened. Basal fold of dorsal margin of lower ovipositor valve (Fig. 9D) flattened, lamelliform, forming with gonangulum a small, shallow, laterally-facing groove.

Colouration: unicolourous green, weakly speckled rusty brown, lateral pale yellow stripes present on head and pronotum; in some specimens there are small dorsolateral pronotal red spots and dorsal abdominal pale stripes, rarely bordered with black.

Measurements (mm). Body ♂ 19.0–21.2 (mean 20.2, n = 7), ♀ 17.5–20.2 (mean 19.2, n = 3); pronotum ♂ 3.4–3.9 (mean 3.5, n = 7), ♀ 3.5–4.1 (mean 3.9, n = 3); male tegmen ~4–4.5, visible part ~3–4; hind femur ♂ 11.4–14.0 (mean 13.0, n = 7), ♀ 13.1–13.5 (mean 13.3, n = 3); male subgenital plate 3.9–4.4 (mean 4.1, n = 7) ovipositor 9.2–9.6 (mean 9.4, n = 3). Measurements were taken between the mid-lines of the structures (in the case of the pronotum and male subgenital plate this is not the longest part).

Bioacoustics. Male calling song (Figs 7L, 14A) consists of single syllables, repeated regularly for a long time without noticeable pauses, with comparatively short syllables periods. The syllables have a goblet-like shape starting with a very quiet part and gently increasing to a crescendo in the last fourth, which has the highest amplitude.The songs of two males placed in different environmental situations were studied (Table 1).

At 26°C (male labelled No. 2 in CC) the syllables lasted 524–747 ms (mean 634 ± 71, n = 62), with the syllables longer at the beginning of the song and gradually decreasing with time. The syllables consisted of 143–162 (mean 157 ± 6, n = 30) impulses with an impulse period of 3–10 ms (mean 4.1 ms). The impulse period at the beginning and in the middle of the song is shorter (about 3–4 ms, except the first impulse, which has a period of up to 9 ms) than in the last fourth of the song (4–5 ms, reaching up to 6–10 ms in the last 4–5 impulses). Typical of the shape of the syllables is the gentle increase in the amplitude over the first ~100–110 impulses, with an abrupt crescendo at impulses 110–125 (130th) and maximum amplitude achieved in the last 30 impulses.

The same specimen at 29–30°C produced syllables lasting 362–428 ms (mean 396 ± 17, n = 54), with the shortening caused by the shorter impulse period (2–6 ms, mean 2.6) while retaining the same number of impulses.

Another male (labelled No. 1 in CC) at 29–30°C differed slightly in having a similar syllable duration but lower number of impulses. However, at this temperature the first impulses of a syllable are quickly produced, which in combination with the low amplitude, make it difficult to distinguish single impulses. In this case an isolated impulse also frequently followed the syllables at an interval of more than 10 ms and up to 85 ms.

Additional variation in the song was observed in male No1 (CC) when singing in duet with another male. In this case, the song consisted of longer syllables, separated by shorter intervals. Thus, while the syllable period is not (significantly) affected by body temperature, it could be influenced by competition for mates. In addition, the mean impulse period was longer due to the longer intervals between the last impulses in a syllable. This could be due to competition between sexually active males and hence song plays a part in the competiton for mates.

Tegmen movements were not recorded but observations indicate they consist of a simple fast opening and slow closing movement. The sound is produced during the closing of tegmina.

Table 1. Characteristics of the male song of *P. jablanicensis*, sp. n., recorded from two males in different conditions and situations.

Specimen T°C	Character			
	Syllables duration (ms)	Syllables period (s)	Imulse period (ms; mean)	Number of impulses
Male No. 2 26°C	634 ± 71 (524–747) Mode = 735 Median = 640 n = 62	3.3 ± 0.5 (2.7–4.8) Mode = N/A Median = 3.2 n = 62	4.1	157 ± 6 (143–162) Mode = 161 Median = 159 n = 30
Male No. 2 29–30°C	396 ± 17 (362–428) Mode = 411 Median = 394 n = 54	3.0 ± 0.9 (1.1–5.8) Mode = 3.0 Median = 2.8 n = 62	2.6	~150–160
Male No. 1 29–30°C calling	408 ± 39 (351–475) Mode = 373 Median = 401 n = 50	2.4 ± 1.2 (1.4–7.2) Mode = 1.7 Median = 2.0 n = 46	3.3	133 ± 4 (126–140) Mode = 133 Median = 133 n = 17
Male No. 1 29–30°C in duet	552 ± 37 (484–638) Mode = 547 Median = 547 n = 31	1.7 ± 0.3 (1.3–2.4) Mode = N/A Median = 1.7 n = 31	4.3	~140

The song frequencies (Fig. 15) are between 15 and 24 kHz, possibly artificially restricted by the low sampling rate (48 kHz), with a maximum of about 21–22 kHz.

Variation. As this species only inhabits the subalpine low-vegetation belt and possibly has a quite restricted range, it shows little morphological and bioacoustic variation. However, there is some slight variation in the size of the body parts and sometimes insignificant differences in the shape of the male pronotum. The song may also differ slightly under different conditions (Table 1), such as temperature and male activity.

Material. Holotype ♂ (dry preparation; NMNH) (Fig. 8A, C), paratypes: 2♂, 2♀ (NMNH), 9♂, 4♀, 2♂ nymphs last instar, 1♀ nymph 5th instar, 1♂ nymph 4th instar (CC), 2♂, 2♀ (CH): Macedonia (FYROM), Struga district, Mt. Jablanica (Yablanitsa), NW of Gorna Belica village: (UTM: 34TDL56) localities around Crn Vrv Peak (Krstec Place), Chuma Peak and Golem Kokal Peak; (UTM: 34TDL66) Vevchansko Ezero Lake; (UTM: 34TDL56/66) Podgorechko Ezero lake; (UTM: 34TDL57/67) Srizhjak peak; above the timberline (*Fagus sylvatica*), montaneous/subalpine meadows (limestone and siliceous soils), mostly in mesophyte herbaceous thickets, 1800–2100 m alt., 18.–20.vii.2006, leg. D. Chobanov (NMNH).

Etymology. Named after its type locality, Jablanica Mountain.

Distribution (Figs 10, 13) **and ecology**. This species is known from high parts of Jablanica Mountain, above the timberline, at an altitude of 1800–2100 m a.s.l. Here it inhabits lush pseudosubalpine and subalpine meadows with *Rumex* spp., *Rubus idaeus*, etc. The animals were relatively abundant and stayed on the vegetation or within it. At the end of July most of the individuals were already adult and sexually active, though at the highest places nymphs still occurred. Around snow patches, where the snow had recently melted, nymphs of all instars, including recently hatched, were found.

Jablanica Mt., together with Korab Mt., forms a small group of young mountains with alpine relief and is part of the

Southern Dinaric mountain group of the Pindo-Dinaric system. Jablanica is well isolated from the North, East and South by deep river valleys or low passes (lower than 1000 m a.s.l.), although considering historic events this is not an absolute criterion for isolation. The western crest of Jablanica Mt. (situated in Albania) parallel to the main ridge is well connected not only with Jablanica but also with Chermenika Mt., thus the species range is likely to include also areas in Central Western Albania.

B. Species of the *Poecilimon ornatus* group known only from Greece

Systematics and distribution of the Greek species are covered in the papers of F. Willemse (1982, 1985), L. Willemse (1987), F. Willemse & Heller (1992) and F. Willemse & L. Willemse (2008). Here only a short summary is given plus some additional new results.

Poecilimon pindos F. Willemse, 1982

Poecilimon pindos Willemse, 1982 (160–161, Figs 15, 16, 131–133, 187–189, 203, 204), type locality Greece, Pindos Mts, Timfi Mt. above Papikon, 1800–2000 m; Willemse, 1985 (15, Fig. 36); Heller, 1988 (50, Abb. 34–H, 107, 121–B).

This species' cercus shape is shown in Fig. 3P and song in Fig. 7D.

Distribution (Figs 9, 10, Appendix). This species is restricted in its distribution to the Northern Pindos Range in Greece, hitherto only recorded from the high parts of the mountains of Timfi and Mavrovouni, between 1800 and 2100 m a.s.l.

Poecilimon obesus Brunner von Wattenwyl, 1878

Poecilimon obesus Brunner von Wattenwyl, 1878 (38), type locality Greece, "Epirus" and "Parnass"; Ramme, 1933 (513, plates 6–2, 8–3, 11–3, 12–3, 3a, 3b); Harz, 1969 (118, Figs 269, 345–348); Willemse, 1982 (161–162, Figs 19–22, 136–138, 207, 208).

Poecilimon beieri Ramme, 1933 (514, Pls 6–4, 8–5, 11–4), type locality Greece, Meganisi Island; Harz, 1969 (120, Figs 272, 320, 350); Willemse, 1982 (162, Figs 23, 209, 210). Synonym of *P. obesus obesus* after Heller (1984).

Poecilimon obesus obesus; Heller, 1984 (77–78, Abb. 3–C, 5–B, 7–B); Willemse, 1985 (15–16, Figs 30, 32); Heller, 1988 (47, Abb. 34–B, 88, 120–B).

This species' general appearance is shown in Fig. 1F, the cercus shape in Fig. 2OB and the song in Fig. 7F.

Distribution (Figs 10, 11, 13, Appendix). This species was obviously misidentified as *Polysarcus scutatus* by Szijj (1992), which was confirmed by our findings at one of Szijj's localities. Like *P. obesus* species of the genus *Polysarcus* also have a very wide fastigium. *Polysarcus scutatus* is currently known from only one area in Greece (located above 1600 m a.s.l.; Willeme & Willemse, 2008).

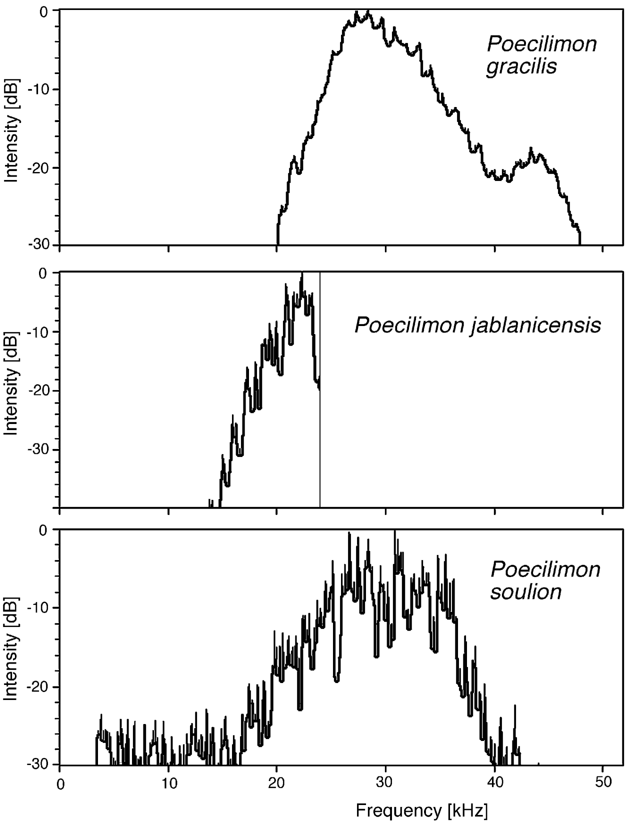

Fig. 15. Frequency spectra of the male calling songs of *P. gracilis*, rec. POGR8905 (CH2555), *P. jablanicensis* (male No. 2, recorded 7.viii.2006) and *P. soulion*, rec. POOB8901 (CH2475) (other data as in Fig. 7).

The range of this species covers the western parts of Central and Northern Greece; recorded on Parnass Mountain by Brunner von Wattenwyl (1878), but not since so this high mountain locality is considered doubtful. The localities in Bosnia and Hercegovina (Mikšić, 1973) in Maglich Mountain are equally doubtful both because of their remoteness from the range of *P. obesus* and their high altitude (see Discussion for the species' ecological preferences). Most probably they are of a taxon related to *P. ornatus* or *P. affinis*. The record of *P. obesus* from Sliven (Central East Bulgaria) (Frey-Gessner, 1893: p. 401 – 1♀; Nedelkov, 1908: p. 426 – not clear whether this is quoting information in Frey-Gessner, 1893 or referring to a new material) cannot be referred to any of the species of this group, both because of its great remoteness from the group's range and the low altitude, until the material is found or more specimens are collected. In contrast to all other species in this group *P. obesus* is found at low altitudes, with many of the localities below 200 m a.s.l. and never above 1500 m a.s.l.

Poecilimon artedentatus Heller, 1984

Poecilimon obesus artedentatus Heller, 1984 (78–79, Abb. 3–D, 4, 5–A, 7–C), type locality Greece, Peloponnes, Akhaia, E of Kato Vlassia vill. (Umg. Metaxion) on the road to Kalavrita, 840 m; Willemse, 1985 (16–17); Heller, 1988 (47, Abb. 34–C, 35–B, 88, 120–A).

Poecilimon artedentatus; Willemse & Heller, 1992 (301, 303) (stat. n.).

This species' general appearance is shown in Fig. 1G, the cercus shape in Fig.2A and song in Fig. 7E.

Distribution (Figs 10, 13, Appendix). *Poecilimon artedentatus* is restricted to the Peloponnesos (Greece), where it occurs mainly between 500 and 1000 m a.s.l. and never above 1500 m a.s.l.

Poecilimon nobilis Brunner von Wattenwyl, 1878

Poecilimon nobilis Brunner von Wattenwyl, 1878 (50), type locality Greece, "Athen" and "Taygetes"; Ramme, 1933 (513, Pls 6–3, 8–4, 12–4, 4a); Harz, 1969 (118, Figs 267, 342–344); Willemse, 1982 (162–163, Figs 24–26, 182, 183, 211, 212); Heller, 1984 (76–77, Abb. 3–A, 7–A); Heller, 1988 (46, Abb. 34–A, 35–A, 88, 121–E).

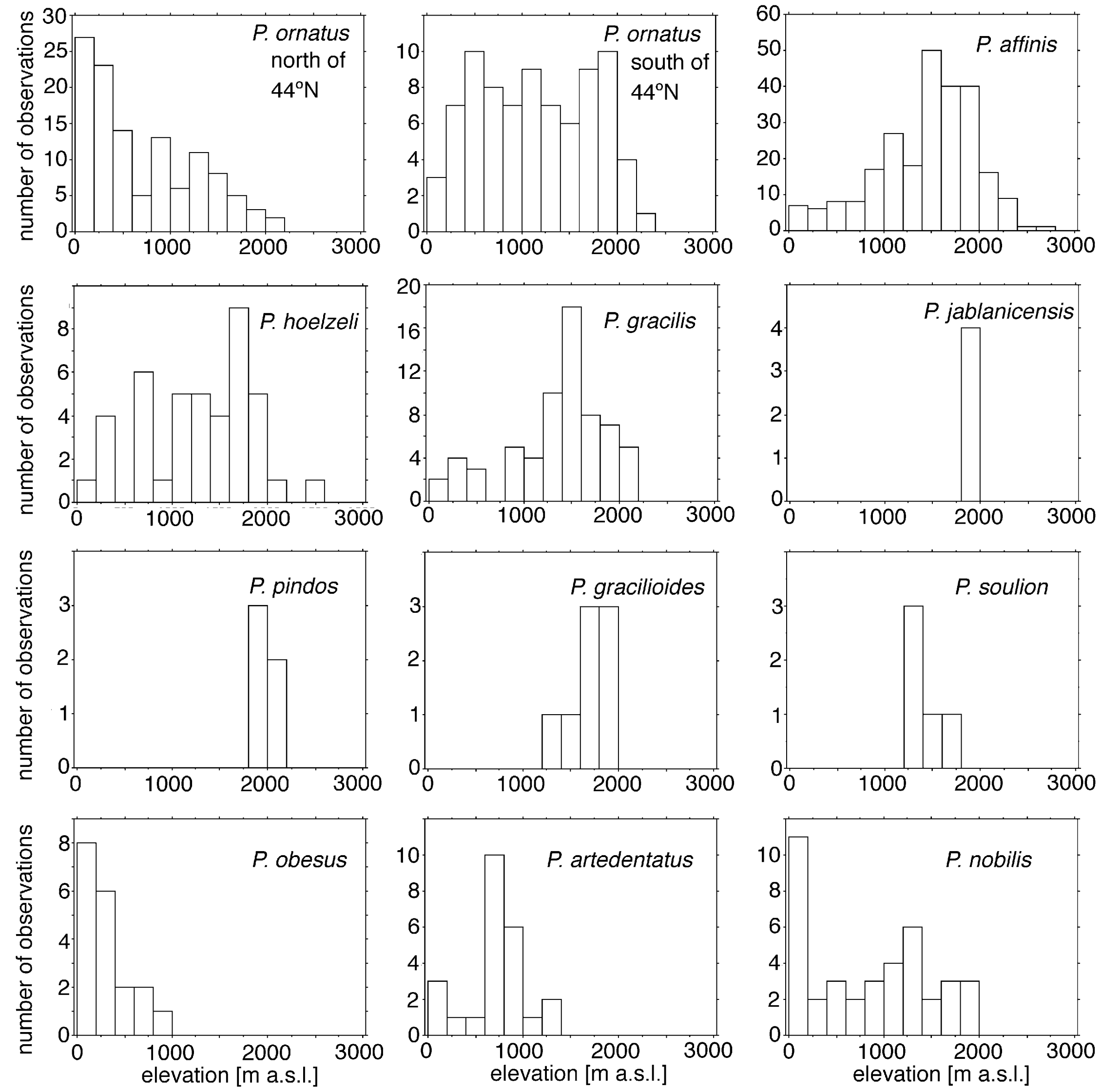

Fig. 16. Altitudinal distribution of the species in the *P. ornatus* group.

Poeclimon holtzi Werner, 1902 (116, 2 Figs), type locality Greece, Kambos. Synonym of *P. nobilis* after Werner (1933).

This species' general appearance is shown in Fig. 1H, cercus shape in Fig. 2N and song in Fig. 7G.

Distribution (Figs 12, 13, Appendix). *Poecilimon nobilis* is restricted to the Peloponnesos, where it is found from sea level up to 2000 m a.s.l. The locality "Athens", mentioned by Brunner von Wattenwyl (1878) as one of the type localities, is considered to be doubtful.

Poecilimon soulion L. Willemse, 1987

Poecilimon soulion L. Willemse, 1987 (173–177, Figs 1–8, 10, 14, 17); Heller, 1988 (51, Abb. 121–D, F); Willemse & Heller, 1992 (303, Fig. 11).

This species' cercus shape is shown in Fig. 2S1, S2.

Bioacoustics. The male's calling song (Figs 7H, I, 14B) consists of single syllables, usually repeated irregularly. The song of a topotypical male (Figs 7H, 14B) recorded at 20°C at 10:30 h when it was sunny and at 29°C at 18:30 h was similar (possibly the body temperature of the animal at 20°C was higher as it was lit by the sun). At 20°C the syllable duration was 466–617 ms (mean 531 ± 43, n = 18) and the syllable period 4.4–15.5 s (mean 7.9 ± 3.4, n = 17). At 29°C the syllables lasted 331–407 ms (mean 368 ± 33, n = 5), the syllable period 6.3–9.8 s (mean 7.8 ± 1.5, n = 4). In the song of the male from Central Greece (Fig. 7I) the mean syllable duration was 546 ms and mean syllable period 16.4 s (n = 4/3; T = 26.5°C).

The syllable consists of three parts. The first part consists of about 30 to 80 irregularly arranged low amplitude impulses with an impulse period of 1–3 to 15 ms. The second part follows without interruption and has 5–10 high-amplitude impulses, produced at longer intervals of 15–60 ms. After a silent interval of 30–70 ms the second part is followed by the third part, consisting of 15–30 densely arranged impulses with an impulse period of 2–4 ms (measurements mostly on the topotypical male). The peak of the frequency spectrum (male from Central Greece) occurs at about 30 kHz (Fig. 15).

Distribution (Figs 12, 13, Appendix). This species does not only occur on the mountains of Soulion and Tomaros in

Western Continental Greece, but also in Central Greece, always at altitudes of between 1200 to 1900 m a.s.l. The specimen from Central Greece clearly differs in pronotum, cerci (Fig. 2S2) and song (Fig. 7I) from *P. gracilioides*, the main range of which is closer than that of the typical *P. soulion*.

Poecilimon gracilioides Willemse & Heller, 1992

Poecilimon gracilioides Willemse & Heller, 1992 (303–305, Figs 1–5, 12, 24, 30), type locality Greece, Arta, Tsoumerka Mt., S of Theodoriana, 1400–1800 m.

This species' general appearance is shown in Fig. 1I, cercus shape in Fig. 2G1, G2 and song in Fig. 7J.

Distribution (Figs 12, 13, Appendix). This species has a restricted range occurring on a few summits in Western Continental Greece, in particular the Tsoumerka, Chatzi, Avgo, Karava, Voutsinaki and Kakardhitsa Mts, between 1350 and 1850 m a.s.l.

Composition of the *Poecilimon ornatus* group and recognition of the taxa

The group includes 14 valid taxa, 2 of which are doubtful (32 described forms), belonging to 11 species: *P. ornatus, P. affinis affinis, P. affinis komareki*, two taxa with doubtful status: *P. affinis serbicus* and *P. affinis hajlensis, P. hoelzeli, P. artedentatus, P. obesus, P. nobilis, P. pindos, P. soulion, P. gracilioides, P. gracilis* and *P. jablanicensis*. Recognition of the relevant taxa, i.e., excluding *P. affinis serbicus* and *P. affinis hajlensis*, is given in Table 2.

DISCUSSION

Phylogeny of the *Poecilimon ornatus* group and affinities between its taxa

Variation within the group, especially the autapomorphies of *P. jablanicensis*, which are convergent with those of other species within the genus, makes the definition of the main characteristics of this group difficult. However, the plesio-/apomorphic state of some features of the species makes it possible infer some intragroup relationships.

I. Basal taxon. *Poecilimon gracilis* appears to be morphologically and bioacoustically the most primitive species in the *P. ornatus* group, indicating its connection with other species of the genus (cf. Heller, 1984) and thus is basal to the other taxa and a sister taxon to the hypothetical ancestor of this group. This view is supported by molecular data (Ullrich et al., 2010), where in a tree based on mt-DNA sequences (see Ullrich et al., 2010: Fig. 3B) *P. gracilis* also occupies the most basal position. However, its position in this tree is statistically not well supported as it is the same as that of the other basal species of this branch, which do not seem to belong to the *P. ornatus* group for biogeographical and morphological reasons. The shape of the pronotum and body size of *P. gracilis* are similar to those of two taxa with unclear positions, *P. thoracicus* (Fieber, 1853) and *P. schmidtii* (Fieber, 1853). However, the song structure of *P. gracilis* differs from these species in having much longer syllables, temporarily separated in the first and longer part of detached impulses, followed by a second louder and shorter part of more frequent impulses. This type of song is produced by species in one of the main stems of the group, although the transition from bipartite to compact syllable consisting of many impulses appears to have evolved independently at least three times within this group.

II. Southern stem. Two complexes are included here. *P. gracilioides* and *P. soulion* form the first complex, well supported by both mt- and nucleolar-DNA-data (Ullrich et al., 2010). They are morphologically similar to *P. gracilis* and distributed south of its range. In their song, there is an additional part of frequent and low-amplitude impulses, which tripartitions the song. The second complex, also well supported by mt-DNA-data (Ullrich et al., 2010), *P. nobilis, P. obesus* and *P. artedentatus*, occupy the southernmost range of the group, occurring in Southern Continental Greece, including the Peloponnesos. These species are morphologically similar, but *P. artedentatus* has a song consisting of compact syllables, similar to that of *P. affinis*, *P. hoelzeli, P. pindos* and *P. jablanicensis*.

III. Northern stem. Four sibling species form this stem: *P. pindos, P. hoelzeli, P. affinis* and *P. ornatus*. While the stem itself is well supported by mt-DNA-data, the relationships within it are not well resolved and the molecular data are partly contradictory (Ullrich et al., 2010). Although morphologically *P. pindos* shows some similarity with the smaller representatives in the southern stem, generally the species in this stem have much more pronounced apomorphies. These include cerci with pointed tips, but lacking a detached tooth and a song consisting of compact syllables made up of many impulses. Additionally, this species is characterized by a large body size and a low-frequency song. In *P. ornatus* the syllables are secondarily shortened, which is associated with morphological specialization of the stridulatory row (see under this species).

This stem is probably of relatively recent origin and connected historically with that of the Balkan mountain ranges. *P. affinis* and *P. ornatus* have the widest distribution within this group. Both species do not occur further south than Northwestern Greece (northernmost part of the Pindos range) but spread far northwards through the central and western parts of the Balkan Peninsula up to the Southeastern Alps (*P. ornatus*) and the Northeastern Carpathians (*P. affinis*). *P. hoelzeli* and *P. pindos* have much more restricted ranges in the mountains of Northern Greece and neighbouring territories.

IV. Species *Poecilimon jablanicensis*. Morphologically *P. jablanicensis* is closest to *P. gracilis*. Due to many autapomorphies (small auditory spiracle, squamipterous females, continuous syllables, arranged in fast sequences, low-frequency song) it is considered separately. However, this species occurs parapatrically with *P. gracilis* and may have evolved by rapid speciation after recent separation from the latter or from a gracilis-like ancestor of both species.

On the basis of morphological and behavioural characteristics, the following phylogenetic relationships within the group are suggested: [(*P. gracilis*, *P. jablanicensis*), ((*P. gracilioides, P. soulion*), (*P. nobilis,* (*P. obesus, P. artedentatus*))), (((*P. pindos, P. hoelzeli*), *P. affinis*), *P. ornatus*)].

The characteristics of the group may be summarized as follows:

1. Metazona of pronotum with a tendency to be raised and broad. This character is differently exhibited in the taxa (see Table 2) and may even depend on climatic conditions and population-size (Karaman, 1974) (see below).
2. Metazona of pronotum elongated. This character is found in other species groups, e.g. the *Poecilimon heroicus* group, but is not present in the basal taxon *P. gracilis*.
3. Auditory spiracle large and wide open. This character is found in many groups of the genus; as an autapomorphy within the group in *P. jablanicensis* the spiracle is smaller.
4. Massive cerci with a single detached tooth or pointed tip (also found in other species groups of *Poecilimon*).
5. Song consisting of single syllables with a duration usually between 100 and 1000 ms, with the exception of *P. ornatus*, where secondarily the first part of the syllable is reduced and the latter distinctly shorter than 100 ms.
6. Spines on ventral edge of hind femora: present in all large species including *P. soulion*, but tend to be lost or fewer in number in *P. gracilis* (only one spine in some populations: some specimens lack spines (Heller, 1984)), *P. jablanicensis* (does not posses spines) and *P. graciliodes* (occasionally there is one spine on both or one of the femora).

Biogeography and ecology of the *Poecilimon ornatus* group

The present-day distribution of species of the *Poecilimon ornatus* group has an interesting “patchy” pattern in the Balkans, which is a result of para- or allopatric speciation and, in some taxa, numerous subsequent vertical and horizontal shifts in range.

This group probably originated in the Southern Balkans, where most species with primitive morphological and bioacoustic characters occur. Spreading to the North was realized by two groups: *P. gracilis* and *P. ornatus/affinis*. *P. gracilis* and *P. ornatus* took mainly a western route, occurring often sympatrically and even syntopically (compare Figs 10 and 12 with Figs 11 and 13). The most western point reached by *P. ornatus* is Trentino in Italy. *P. affinis* spread towards the east reaching as far as Kanev in the Ukraine. However, in the south *P. gracilis* occurs sympatrically not only with *P. ornatus*, but more often with *P. affinis*, indicating spread by different paths. In fact, the only reliable co-occurrences of *P. gracilis* and *P. ornatus* are in the north-western part of their ranges in Slovenia and Southern Austria, and the southern slope of the Jakupica Mountains in Central Macedonia (see Figs 10, 11, 12, 13). It is difficult to hypothesize about the spread of *P. ornatus* and *P. affinis* because the distribution records for *P. ornatus/affinis* North of Macedonia and Bulgaria up to Slovenia are unreliable. However, their distribution in the southern part of the range (Fig. 11) indicates that the dispersal of these species followed a complex pattern but that probably after allopatric speciation the ranges overlapped. Interestingly, ranges of mountains are mostly occupied by one of these species, with only very few exceptions (e.g. Bulgaria: Northern Pirin Mts). Future detailed studies in less well studied areas like Albania are likely to prove very informative.

Most other taxa seem to have retained an endemic state, failing to expand their original range to any great extent. Generally, there are very few localities known with syntopic occurrence of two species of the group (except of *P. gracilis* with *P. ornatus* or *P. affinis*): *P. affinis* and *P. hoelzeli* in the mountains of Pieria and Olympus in Greece (Willemse, 1985; F. Willemse, in litt.); *P. affinis* and *P. pindos* on Mavrovouni Mt. N of Metsovon, Ioannina, Greece (Willemse, 1982 as *P. ornatus* and *P. pindos*; cf. Willemse, 1985); *P. affinis* and *P. jablanicensis* in the (pseudo-) subalpine belt on Jablanica Mt. (Albanian-Macedonian border), Macedonia (pers. observations); *P. ornatus* and *P. hoelzeli* in the pseudosubalpine meadows along the ridge of the Belassitsa Mountain (Bulgarian-Greek border), Bulgaria (pers. observations); *P. ornatus* and *P. obesus* near Kouklii, Ioannina, Greece (pers. observations); *P. ornatus* and *P. gracilioides* on Tsoumerka Mountain, Arta, Greece (pers. observations); *P. nobilis* and *P. artedentatus* on Mikinai, Argolis, Greece (leg. E. Blümm) and Langadia, Arkadhia, Greece (leg. B. Grzywacz).

The distibutions of these species seem to indicate competitive exclusion, either because of their behaviour or ecology. It is difficult to argue for both. Their calling songs should differ enough to allow the coexistence of at least some species combinations, although the females of *P. ornatus* are quite unselective (Heller et al., 1997). In terms of ecology, there are no obvious differences between the species. However, three groups, generally differing in their habitat- and/or altitude preferences (Fig. 16), can be distinguished.

First group includes the widely distributed species *P. affinis*, *P. ornatus* and *P. gracilis*. *P. hoelzeli*, though having a comparatively restricted distribution, may also be included in this group. These species have a preference for high altitudes (as do some other less widespread species), but *P. ornatus* has a less restricted distribution than the other three, occurring in the lowlands (Slovenia) and from about 300–500 m in Bulgaria and Macedonia up to 2400–2450 m in the Pirin Mts (see Fig. 16). In the North, *P. ornatus*, *P. affinis* and *P. gracilis* seem to prefer lower altitudes than in the South. For example, *P. affinis* in Ukraine is found in low hills and in Romania it is most common between 900 and 1000 m (Kis, 1962). In the South it is commonly found between 1000 and 2000 m, and up to 2400–2450 m in the southernmost areas. *P. gracilis* is sometimes found at low altitudes in the North, while in the South it usually inhabits the beech forest-belt, reaching up to 2250 m. *P. hoelzeli* is found usually in the subalpine belt but ranges from 100–200 up to 2400–2450 m.

A common feature of all four species is the high morphological variability (see under each species). Karaman (1974) argues that microclimate and population density are important factors connected with the morphology. At high altitudes the specimens are darker in colour, smaller (except sometimes the tegmina, which are the same size and thus the ratio of the size of body to tegmina changes) and have a steeply upcurved pronotum. This is especially true of the populations of *P. affinis* and *P. hoelzeli* at the upper limit of their distributions, while such a tendency is less obvious in *P. gracilis*. A similar tendency is observed at high population densities, both at high and low altitudes. A striking example is the high density populations of *P. ornatus* at low altitudes in Macedonia and Bulgaria, where the aggregations of nymphs resemble the swarms recorded in other Barbitistinae species (e.g. *Isophya speciosa, Polysarcus denticauda*) (Kis & Privescu, 1966; Hartley, 1986). These animals are almost completely dark coloured (see Fig. 1K).

The second group includes some species with restricted distributions in an area south of the range of the first group. The species are *P. pindos, P. soulion, P. gracilioides* and *P. jablanicensis*. These are intermediate between the first and the third group in occurring mostly in the mountain/subalpine belt between 1500 and 2100 m. *P. soulion* is closer to the third group in occurring at altitudes down to 1200 m. These species show little variation in morphology and poor dispersal ability, possibly because they are adapted to a comparatively constant microclimate.

The third group includes the three southern species, *P. nobilis, P. artedentatus* and *P. obesus*. *P. nobilis* occurs up to 2000 m without any obvious altitude preference, with a peak occurence at 0–200 m. This peak could be an effect of the accessibility of the localities and relative size of the area, with the result that lowland populations are much more frequently sampled. *P. artedentatus* seems to be a colline species occuring mainly between 500–1000 m. *P. obesus* is active early in the season and has a strong preference for lowlands.

It is interesting to consider the distribution of these three groups during the ice ages. During the Pliocene-Pleistocene the alternating warming and cooling periods resulted in changes in the altitudinal distribution of the climatic and vegetation belts. For example, in the Rila Mountains (Bulgaria), the treeline limit changed from 2300 m about 6700–6500 BP to 1100–1300 m in the coolest periods about 18000 BP (e.g. Tonkov & Marinova, 2005). The *Poecilimon* species, which are mostly tolerant of moderate temperatures and connected with mesophyte vegetation and humid microclimates, could have shifted their ranges towards lower altitudes in the cool periods. The problem would have been finding appropriate humid habitats, since glacial maxima are connected with a lowering of athmospheric humidity and increase in the distribution of xeric grass communities. Though the lower temperatures would have allowed cold-climate adapted species to populate lowlands, mesophile animals would not have been able to colonize the xerophytic grassy habitats. Thus, the species may have been isolated in small populations in areas with the appropriate microclimate. The temperature maxima during the interglacials caused animals to move to higher altitudes (alternative to local extinction) and thus the cold adapted species may have been isolated in the so called “sky islands” (Knowles, 2000, 2001). Therefore, both cooling and warming periods may have promoted speciation within this group.

Bioacoustics of the *Poecilimon ornatus* group

Based on morphological (Heller, 1984; present paper) and molecular (Ullrich et al., 2010) data it is suggested that the basal taxon of this group is similar to *P. gracilis*. Thus, the ancestral song may have had a structure similar to that of *P. gracilis* and its closest relatives. At least, no other type of song has more plesiomorphic characters. This song is quite specialized, consisting of single long syllables, temporarily separated into two parts (bipartite song) (see above). Similar syllables and stridulatory movements are also recorded e.g. in the *P. sanctipauli* group (Heller & Sevgili, 2005). This type of song (**Type I**) is present also in *P. obesus* and *P. nobilis*, while in the other species the syllable has undergone evolution in two directions resulting in three other types of song. It is, however, not clear whether the similar song pattern in *P. obesus* and *P. nobilis* represents the ancestral state or is a result of convergence. In all these species the closing movement begins quite slowly and changes abruptly at the end but there are no obvious modifications of the stridulatory file (Heller, 1988).

Type II. By a minor modification the song becomes tripartite. This may have occured simply by retaining the movement pattern of *P. gracilis* and using a larger part of the file or additionally by increasing the speed of the beginning of the stridulatory movement and slowing down the closing movement of the tegmina. This type of song is characteristic of *P. soulion* and *P. gracilioides*. Both species have a stridulatory file with an abrupt change in tooth size (see Willemse, 1987; Willemse & Heller, 1992).

Type III. The characteristic of this type of song is that the first and second parts of the type I-syllable merge, which is achieved by a transition from an interrupted to uninterrupted stridulatory movement (closing) of the tegmina. As a result, a compact syllable consisting of a crescendo of many impulses developed. Interestingly this type of song has obviously developed independently three times: in *P. artedentatus* in the Southern stem; in *P. pindos/hoelzeli/affinis* in the Northern stem and in *P. jablanicensis*. Except for *P. pindos*, all these species have quite high numbers of stridulatory teeth. An initial stage of type III is observed in *P. artedentatus* where the transition from the first to the second part of the syllable is very sharp and sometimes even marked by a few sparse impulses (see Fig. 7E). This type of song is typical of species in the Northern stem (except for *P. ornatus*), where the syllable is quite compact but both parts are easily recognizable.

P. jablanicensis is an exception as it probably evolved directly from *P. gracilis* (see below). Though it morphologically clearly resembles the latter, the song of *P. jablanicensis* is more highly differentiated within type III in having a smooth transition from low- to high-amplitude impulses. In additon, the high-amplitude part is much longer than in all the other species in the group, probably because it is not the trigger for the timing of the acoustical response of the female. Its similarities to *P. gracilis* in "non-acoustical" morphology and restricted range, parapatric to that of *P. gracilis*, are thought to be a consequence of a comparatively rapid speciation of *P. jablanicensis*. Heller et al. (2008) observed that the morphological evolution, especially that of the male genital structures, typically occurs faster than the evolution of song characters. In contrast, the speciation of *P. jablanicensis* involved unusually fast changes in both the song and the "acoustical" morphology as a consequence of the change in the communication system.

Type IV. *P. ornatus* shows another stage in the differentiation. Being clearly a representative of the Northern stem, its song evolved by reducing the low-amplitude first part of the type III-syllable. This is achieved both physiologically by shortening the closing stridulatory movement and morphologically by developing a fold in the distal part of the stridulatory row. This species is also characterised by very poor specific song recognition by the female (Heller et al., 1997).

Of special interest is the repeated "compactization" of the syllables in the male calling song, which occurs three times within this species group (see above). It may be connected with the advantages of louder and far reaching signals, since in the neuronal system close impulses may increase the loudness if they fall within the female integration time. Still, this phenomenon cannot be easily explained and may have a different cause in each case. Nevertheless, it is interesting to discuss the specializations in the song of *P. jablanicensis*, the most peculiar species in the *P. ornatus* group.

Poecilimon jablanicensis probably evolved on a restricted range of mountain summits from an isolated population of *P. gracilis* or a *gracilis*-like ancestral form. This could be inferred by its resemblance to the latter and the autapomorphies within this group. These are a result of specialization, involving the secondary development of a unidirectional acoustic communication system.

This is the only known example within the *P. ornatus* group where females lost the ability to answer males. The loss of bidirectional communication may be connected with the need to produce an easily recognizable and traceable call. This is achieved by using long sequences of frequently repeated simple syllables, with high intensity and low frequency maximum, a phenomenon recorded for other *Poecilimon* species with a unidirectional communication system (Heller & Lehmann, 2004; Heller et al., 2006). The lower frequency maximum of the song is typically connected with a larger body size. *P. jablanicensis* is the smallest species within the group with song frequencies ranging from 15 to at least 24 kHz and a frequency peak at about 21–22 kHz, thus the frequency properties of the song are similar to those of the much bigger *P. nobilis, P. artedentatus* and *P. ornatus* (cf. Heller, 1984, 1988). The song of the related *P. gracilis* (comparatively small species) has a much higher frequency range (carrier frequency in the range 24–36 kHz after Heller, 1988; see also Fig. 15). Interestingly, another representative of the group with moderate body size, *P. pindos*, has a quite low frequency range (12–24 kHz) with the maximum at about 15 kHz. In both *P. jablanicensis* and *P. pindos* the lowering of the song frequency is achieved by increase in the size of the tegmina and widening and uplifting of the metazona on the pronotum.

The low frequency sounds spread over a greater distance than high frequency sounds. Heller et al. (2006) proposed two hypotheses to account for the development of a low-frequency song – an adaptation to inhabiting dense vegetation or sexual selection. Occurring in a habitat with dense but not high vegetation, *P. jablanicensis* would not need a low-frequency song. However, having evolved in a mountain environment with frequent winds and an unstable microclimate could have led to the need for a reliable and fast mechanism of finding a partner under such conditions.

Interestingly, *P. jablanicensis* also has reduced auditory spiracles and they are exclusively and without exception found in all species of *Poecilimon* with unidirectional communication. This reduction (together with the fact that the females do not respond acoustically) must thus have ocurred at least three times independently within *Poecilimon*. The reasons for this reduction and its association with a change in female behaviour are still unclear. Here, the reduced auditory spiracle is assumed to be a result of the need to protect it against physical factors that affect hearing ability, such as wind, but this is not obvious in the other cases. Due to the clear phylogenetic relationships with other species, *P. jablanicensis* seems to be a very suitable species for studying other factors that may have influenced this change, like predation pressure, operational sex ratio, population density or duration of the mating season. For some of these factors there is data for closely related species (Heller & Helversen, 1991; Heller, 1992).

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APPENDIX ONLINE:

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