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Endemism hot spots, core areas and disjunctions in European Orthoptera

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Abstract. The paper overviews the endemism hot-spots of the European Orthoptera and reveals the paleogeographic processes which have shaped the recent faunal structures of the European Orthoptera fauna. Descriptions of seven endemism centres (the southern Balkan Peninsula and western Asia Minor; the Dinaric Mountains; the Alps; the Appenines; the Carpathian Mountains and the Carpathian Basin; the Iberian Peninsula; the Caucasian Mountains) are given. Significance of these areas is not only mirrored in the richness of endemic Orthoptera species but also in the postglacial expansion processes of the European Orthoptera fauna. The aims of the study were to summarize the literature data and hypotheses of the topic, and to discuss formation and evolution of endemism centres and endemic species of European Orthoptera.

Key words: Orthoptera, endemism, disjunction, hot spot, core area, Europe.

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I. INTRODUCTION

The survey of the areas of endemism (HAROLD & MOOI 1994) belongs to the focal issues of biogeography considering its evolutionary and conservation biological aspects. Generally, those taxa are regarded endemic whose range of distribution is essentially smaller than the geographic unit framing it (GASTON & SPICER 1998). This practical definition also entails the scale dependence. The scale- and time dependence, and also the various attempts for interpretation can explain the introduction of further biogeographical notions (subendemism, holo-endemism, relict-endemism, palaeoendemism, neoendemism, dysharmonic endemism etc). The more precise definition of endemism is still the pre-condition of the effective protection of restricted and often also threatened species (PETERSON & WATSON 1998). Several authors (HALL & MOREAU 1962; TERBORGH & WINTER 1983; BIBBY et al. 1992) unanimously suggest in the definition of area-based endemism that the area of the geographic unit must be restricted to 50 000 km^2 (i.e. ‘spot-like endemism’). It became numerical in the recurring definition, namely the ’relatively small surface of the Earth’. In this paper species are restricted a well-defined geographical unit (considerably smaller than the studied area) were handled as endemic species.

Areas rich in endemic taxa are generally remarkable for their species richness as well. Therefore, they are usually referred to as diversity hot-spots (GASTON & SPICER 1998; MYERS et al. 2000). Several articles deal with the relations between species richness, diversity and the number of endemisms and the classification of their other factors, e.g. long-range/distance climatic stability, and instability (e.g. VARGA 1995, 1996; PETERSON & WATSON 1998; JANSSON 2003; GREEN et al. 2003).

Our aim was to review the Orthoptera fauna of the endemism hot-spots well-known by other aspects in Europe and neighbouring areas in close connection with it. Further goal was to reveal the paleogeographic processes which have shaped the recent faunal structures of the European Orthoptera fauna. Comprehensive critical summary of the literature data and hypotheses was taken, including also the interpretation of several former case studies (e.g. the unexpected appeareance of *Uvarovitettix transsylvanicus* (BAZYLUK et KIS 1960) in Slovenia**,** (see: NADIG 1991), considered as relict endemism of the Fogaras Mts. in Romania). To enlist the whole endemic species of the hot spots is impossible. Chapters contain the most important samples. The nomenclature follows HELLER (2004a) and OTTE et al. (2004). We designated the borders of the study area according to HELLER et al. (1998), however, with some exceptions since in several cases the core areas cannot be limited by artificial geopolitical boundaries.

II. AREAS OF ENDEMISM IN EUROPEAN ORTHOPTERA

The areas rich in endemisms in European Orthoptera mostly fall within the Mediterranean region including the peninsulas but also some larger islands and mountainous habitats like continental islands display a high level of endemism (HAMRICK & HAMRICK 1989; SERGEEV 1998). We describe seven endemism centres whose significance is not only revealed in the richness of endemic Orthoptera species but also in the postglacial expansion processes of the European Orthoptera fauna.

II.1. The southern Balkan Peninsula and western Asia Minor

The distribution of several genera rich in endemic taxa demonstrates the very close faunal connections between the Balkan Peninsula and Asia Minor. Due to this relation this area is considered as the most important core area of European endemic Orthoptera (Fig. 1.).

Eupholidoptera MARAN, 1953 is one of the most important genera with its core area in the southern Balkan Peninsula and western Asia Minor. More than 50 species belongs to *Eupholidoptera* from Corsica to Israel in the Mediterranean region. The peninsular part of Greece and the surrounding islands, and also the southern part of Asia Minor are characterised by a high diversity of the genus. On the island of Crete, for example, 10 endemic *Eupholidoptera* species occur. In many cases the area of the species is confined to the locus classicus only. The typical habitat of the most *Eupholidoptera* species can be classified as typical Mediterranean coastal vegetation types (usually as shrubs). Several species are restricted to a single island of the Aegean Sea. According to ÇIPLAK (2004), the present range of *Eupholidoptera* practically coincides with the area of the Aegean tectonic plate. This plate was isolated from the other continental regions by the Paratethys during the upper Oligocene (25-23 My BP) and also the mid-Miocene (16.8-16 My BP). The ancestor of the genus probably evolved in the latter period since in the late Oligocene a continental connection between the Aegean and the Iranian tectonic plate existed. Nevertheless the genus is absent in Iraq and Iran (ÇIPLAK 2004).

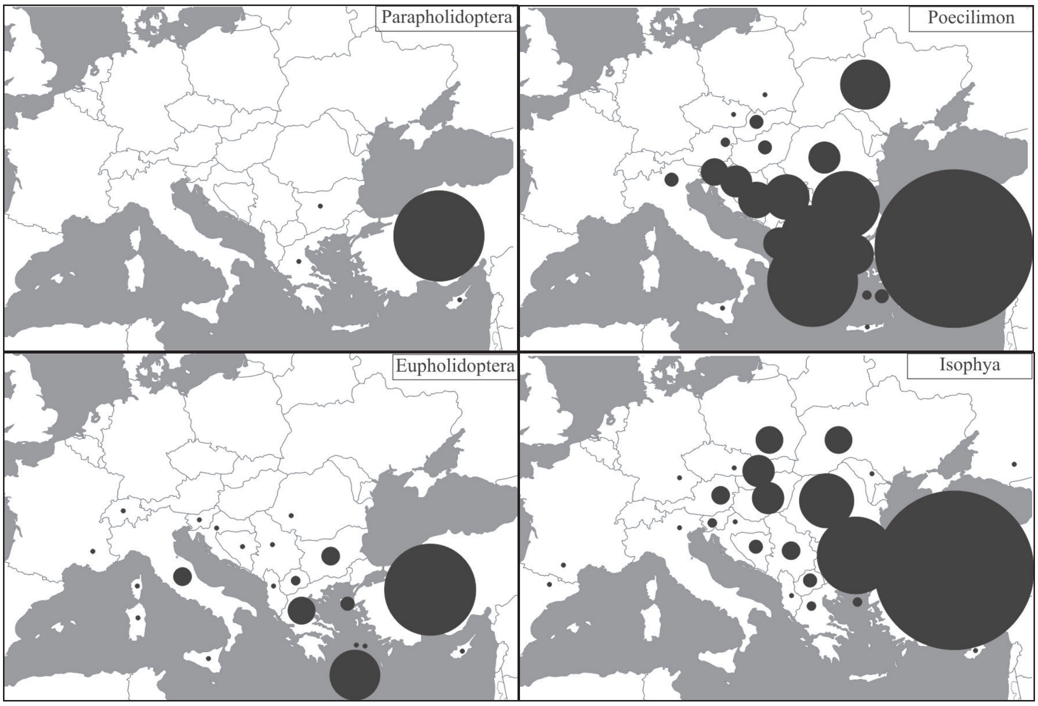

Fig. 1. Species number of some Balkanic and Asia-Minor centered orthopteran genera in Europe and Asia Minor [the size of the symbols is in proportion with the species number (between 1 and 60)].

We find similar palaeo-biogeographical phenomena within two other genera rich in species (and in endemic species) in the same region, namely *Poecilimon* FISCHER, 1853 and *Isophya* BRUNNER v. WATTENWYL, 1878. The majority of the species having a more or less restricted range is concentrated in the area of the Balkan Peninsula and Asia Minor (SEVGILI 2001; ÜNAL 2003). E.g., several endemisms occur in the mountainous areas of Greece, on the islands of the Aegean Sea and also in Anatolia. The genus *Poecilimon* consists of more than 150 described taxa, including subspecies (OTTE et al. 2004). Based on the distribution of *Poecilimon*, ÇIPLAK (2004) hypothesized that the evolution of these species is associated with the vegetation patches of high-mountain habitats, and the glacial, interglacial and postglacial events have formed several isolated populations.

According to the distribution of several other genera, this core area can be subdivided into several sub-units.

II.1.1. The continental regions of the South Balkans (Macedonia, Thrakia, Epiros, Thessalia, central Greece, Peloponnesos)

The range size of endemic species shows a significant variation (WILLEMSE 1984, LEGAKIS & SPYROPOULOU 1998). A considerable part of endemic taxa of the Balkan Peninsula are known only from one mountain or hill (in some cases restricted to the type locality). Such extremely restricted species are e.g. *Pterolepis trilobata* (LA GRECA & MESSINA, 1974) on the Mt. Killini, *Poecilimon klisurensis* WILLEMSE, 1982 in the area of Kastoria, *Poecilimon athos* TILMANS, WILLEMSE F. et L., 1989 on the Athos Mts., *Poecilimon soulion* WILLEMSE L. P. M., 1987 in the Soulion Mts., etc. *Poecilimon pindos* WILLEMSE F. M. H., 1982 is also endemic in the Pindos Mts., but these mountains have an endemic grasshopper genus *Peripodisma* WILLEMSE F. M. H., 1972 as well, represented by the only species *Peripodisma tymphii* WILLEMSE, 1972. *Chorthippus lacustris* LA GRECA, 1976 is the endemic species of the marshy meadows near Lake Joanina. *Metaplastes oertzeni* (BRUNNER VON WATTENWYL, 1891) was described as an endemic species of the Peloponnesos while *Metaplastes ornatus* (RAMME, 1931) occurs in a greater part of Greece, Albania and Macedonia (KALTENBACH 1965; INGRISCH 1981; WILLEMSE 1987; WILLEMSE & TILMANS 1987; TILMANS et al. 1989).

WILLEMSE (1980, 1982) pointed out that probably the same barrier was responsible for the separation of subspecies in case of *Eupholidoptera chabrieri* CHARPENTIER, 1825 (*Eupholidoptera chabrieri schmidti* (FIEBER, 1861) and *Eupholidoptera chabrieri garganica* LA GRECA, 1959), and also of *Poecilimon jonicus* (FIEBER, 1853) (*Poecilimon jonicus jonicus* (FIEBER, 1854) and *Poecilimon jonicus lobulatus* WILLEMSE F. M. H., 1982) in the Pindos Mts.

From *Oropodisma* in Greece, nearly all species are endemic within a restricted mountainous range, which is reflected in the species names: *Oropodisma parnassica* (SCUDDER, 1897), *Oropodisma kyllini* WILLEMSE F. M. H., 1971, *Oropodisma erymanthosi* WILLEMSE F. M. H., 1971, *Oropodisma karavica* LA GRECA & MESSINA, 1976, *Oropodisma taygetosi* WILLEMSE F. M. H., 1972 and *Oropodisma tymphrestosi* WILLEMSE F. M. H., 1972. Only *Oropodisma macedonica* (RAMME, 1951) can be found also in the adjoining areas of Albania and Macedonia with the northernmost occurrence on the Šar-planina.

LA GRECA & MESSINA (1976) suggested the reciprocal stepwise evolution of *Oropodisma* taxa during the Pleistocene supported by the morpho-anatomical differences of the species. 5 species out of the so far described 10 exist on the Pindos Mts. A larger evolutionary distance was observed between the group of closely related species (*Oropodisma macedonica*, *O. karavica*, *O. tymphrestosi* and *O. willemsei* LA GRECA et MESSINA, 1977) and *Oropodisma parnassica*. One species (*O. macedonica*) occurs in Northern Greece but also in Macedonia and Albania, the *karavica–tymphrestosi–willemsei* group is confined to the Pindos Mts. in Central-Greece, while *O. parnassica* is restricted to the relatively remote, southern mountains of the Parnassos. LA GRECA & MESSINA (1976) concluded that *O. parnassica* was separated at the first step. It was followed by the separation of *O. macedonica* and the *O. karavica–tymphrestosi–willemsei* group and the presumed most recent step was the isolation of the three stenochorous species in Central Greece. LA GRECA & MESSINA (1976) also suggested that the evolution of the species in the Pindos system was independent from the species in the Peloponnesos (i.e. *O. chelmosi*, *O. kyllini*, *O. taygetosi* and *O. erymanthosi*).

Oppositely, ‘only’ 58 species (14%) are endemic in the Orthoptera fauna of Bulgaria situated north-east of the main endemism centre of the Balkan Peninsula. The endemic species also belong to Balkanic genera. The majority of endemisms (12 species) was revealed in the area of Pirin Mts. (e.g. *Poecilimon harzi* PESHEV, 1980), Kresna gorge and the Sandanski-Petrich region (11 species, e.g. *Tartarogryllus sandanski* ANDREEVA, 1982, *Isophya andreevae* PESHEV, 1981), the Slavyanka Mts. (10 species, e.g. *Isophya kisi* PESHEV, 1981) and Belasitsa Mts. (9 species, e.g. *Poecilimon mistshenkoi tinkae* PESHEV, 1980). Concerning the habitat requirements, the majority of mountainous taxa are restricted to the high-mountain habitats, while the lowland species are exclusively xerophylous (HUBENOV et al. 1998). Some of these genera contain a high number of endemic species (RAMME 1951; HELLER 2004a), however they show a limited dispersal capacity also into the northern, mountainous part of the Balkan Peninsula (Albania, Macedonia), e.g. *Odontopodisma albanica* RAMME, 1951, *Pholidoptera macedonica* RAMME, 1928, *Poecilimon vodnensis* KARAMAN Z., 1958, *Isophya tosevski* PAVICEVIC 1983, *Myrmecophilus zorae* KARAMAN Z., 1963.

II.1.2. The Archipelago of the Aegean Sea, the Kyklads and mountains of Crete

The range of several endemic species of this region is restricted to only one or some islands. *Poecilimon ikariensis* WILLEMSE F. M. H., 1982 and *Eupholidoptera icariensis* WILLEMSE F. M. H., 1980 are only known from the island of Ikaria. *Eupholidoptera annamariae* NADIG, 1985 (and further nine *Eupholidoptera* species), *Oedipoda venusta* FIEBER, 1853 and *Chorthippus biroi*

(KUTHY, 1907) are endemics of Crete, *Eupholidoptera uvarovi* (KARABAĞ, 1952) of Carpathos, *Pterolepis anatolica* WERNER, 1933 of Cos, *Pterolepis distinguenda* WERNER F., 1934 of Lesvos and *Isophya lemnotica* WERNER, 1932 of Lemnos.

From a paleobiogeographical point of view species restricted to several isolated islands deserve special attention. For example *Pterolepis agiostratica* WERNER, 1937 is endemic on Limnos and A. Efstratios. *Pterolepis insularis* RAMME, 1928 occurs on the islands of Antiparos, Naxos and Serifos, while *Pezotettix lagoi* JANNONE, 1936 is distributed on the partly fairly remote islands of Lefkas, Kalimnos, Cos and Rhodes (WILLEMSE 1980, 1982, 1985).

Some 'continental' species also occur on one or more islands close to the coasts. In the eastern Mediterranean area *Poecilimon brunneri* (FRIVALDSZKY, 1867) can be regarded as a possible evidence of the former link of the peninsula with the islands Limnos, Samothraki and Thasos. The widely distributed eastern Mediterranean *Isophya speciosa* (FRIVALDSZKY, 1867) can also be found on the island of Samothraki. *Poecilimon thessalicus* BRUNNER VON WATTENWYL, 1891, *P. hamatus* BRUNNER VON WATTENWYL, 1878, *P. aegaeus* WERNER F., 1932, *P. sanctipauli* BRUNNER VON WATTENWYL, 1878, *P. propinquus* BRUNNER VON WATTENWYL, 1878 and *Eupholidoptera smyrnensis* BRUNNER VON WATTENWYL, 1882 occur on the peninsula as well as on the islands near the coasts. South-western Anatolia and Rhodes belong to the area of *Saga rhodiensis* SALFI, 1929 (KALTENBACH 1967).

The consequences of the breakdown of the Aegean tectonic plate can be exemplified by the species *Eupholidoptera jacquelinae* TILMANS, 2002. This species is an endemism of the island of Gavdros occurring 40 km to the South of Crete. Gavdros is separated by an 1100 m deep sea barrier and situated on the edge of the tectonic plate. Morphologically *Eupholidoptera jacquelinae* does not belong to the closely related 10 endemic species of Crete but much more to the species living in Kithiria close to the Greek coasts, as well as on western coastal regions and on the islands (Ikaria, Hios, Samos) near to Anatolia (*Eupholidoptera spinigera* (RAMME, 1930), *E. icariensis, Eupholidoptera prasina* BRUNNER VON WATTENWYL, 1882) (TILMANS 2002).

II.1.3. Asia Minor

83% of the Tettigoniinae species is endemic or subendemic (see above several features of the Anatolian Orthoptera fauna). The mountainous character, the extreme differences of elevation, the varied geomorphology and habitats, the role of the area as glacial refuge and also the north-south and east-west faunal migrations have mostly influenced the evolution of the Anatolian Orthoptera fauna, justifying the status of biogeographical subregion (ÇIPLAK 2003, 2004).

Out of the 17 species of *Parapholidoptera* MARAN, 1953, 15 species can be found only in Turkey, and 11 species are endemic. *Parapholidoptera castaneoviridis* (BRUNNER VON WATTENWYL, 1882) occurs on the eastern coast of the Aegean Sea and is considered a typical species of the European part of Turkey, and also of certain Greek islands (e.g. Samothraki) of the Aegean Sea. *Parapholidoptera signata* (BRUNNER VON WATTENWYL, 1861) is a widespread species in the Toros Mts., further it can also be found in Cyprus. Some endemic species (e.g. *P. syriaca* RAMME, 1930; *P. yoruka* ÇIPLAK, 2000; *P. intermixa* KARABAĞ, 1961; *P. karabagi* DEMIRSOY, 1974) occur west of the 'Anatolian-diagonal' from the north of Israel to the Caucasus (ÇIPLAK et al. 1993). The distribution of the genus was strongly influenced by the Pleistocene glaciations (Cryogenic period). The southern mountainous range of Asia Minor was an important barrier for the Balkanic-Anatolian species in that time (ÇIPLAK 2000, 2004).

Number of endemic species less prone to isolation is also high in glacial refuges. Accordingly the genus *Chorthippus* also has several known endemic species in Anatolia (e.g. *Chorthippus bozdaghi* UVAROV, 1934, *Ch. ilkazi* UVAROV, 1934, *Ch. helverseni* MOL, ÇIPLAK & SIRIN, 2003) (MOL et al. 2003).

II.2. The Dinaric Mountains

The fauna of the Dinaric Mts. is closely connected to the southern areas of the Balkan Peninsula. However, this territory will be considered separately, because of the two following reasons: (1) the number of the endemic species is lower than in the above mentioned centres; (2) this region does not belong to the Aegean tectonic plate. The connection of this territory to the Balkanic core area can be demonstrated by some joint endemic species (e.g. *Platycleis orina* BURR, 1899, *Platycleis macedonica* BERLAND & CHOPARD, 1922, *Poecilimon macedonicus* RAMME, 1926, *Pholidoptera stankoi* KARAMAN Z., 1960, *Chorthippus lesinensis* (KRAUSS, 1888)) occurring both in the Dinaric Mts. and in the continental regions of Greece and its archipelago. It can be assumed that the Dinaric Mts. became an endemism centre in a relatively younger phase of the fauna-genesis. During the last glacial phases the Dinaric Mts. served also refuges for some characteristic species.

The typical Balkanic genera (Eupholidoptera, Poecilimon, Isophya) are represented in this region by a low number of endemic species, since the ‘former Yugoslavian’ endemisms are localised rather in Macedonia and not on the major block of the Dinaric Mts. On the other hand, some relict endemic species of cold climatic periods (e.g. the species *Stenobothrus posthumus* RAMME, 1931 and *Podismopsis relicta* RAMME, 1931) occur on high elevations in Montenegro (Hajla Planina). *Metrioptera prenjica* (BURR, 1899) is also considered as a glacial relict. It occurs in Bosnia-Hercegovina on the mountains Prenj and Treskavica, and also on the Maglić Mts. on the border of Bosnia-Herzegovina and Montenegro. It is however has been found in the Julian Alps (Slovenia) recently (BEDJANIC 2005). Similarly, *Metrioptera karnyana* UVAROV, 1921 is also the endemism of Prenj Mts. while *M. hoermanni* (WERNER, 1906) is endemic in Èvrsnica and Maglić. The species richness of other endemic taxa is significant, as well.

Endemisms are frequent in taxa occurring in caves. The cave grasshoppers *Troglophilus brevicauda* CHOPARD, 1934 [Mileševo] and *Troglophilus ovuliformis* KARNY, 1907 [Kotor] (ADAMOVIĆ 1967a; MIKŠIĆ 1973, 1976; US 1967, 1992) are endemic in Serbia and Montenegro.

The relation between two described centres should mention. At the discussion of the South Balkan and Asia Minor centres it was already mentioned that Albania, Macedonia and Bulgaria are considered to be its northern marginal areas. The mountains of Albania can be considered as a transitional area between the two major core areas since the Albanian Alps belong to the Dinaric Mts. endemism centre demonstrated by the Albanian occurrence of the *Pachytrachis frater* (BRUNNER VON WATTENWYL, 1882) typical in the Dinaric Mts. However, the rest of the country mostly displays the features of the southern Balkanic centre at the northern border of the Aegean tectonic plate. Phylogeographic analyses of species distributed from the South Balkans to Italy, as *Eupholidoptera chabrieri* with several subspecies of uncertain taxonomic status (HELLER 2004a) could unravel such enigmatic patterns.

II.3. The Alps

The western and the eastern Alps are both endemism centres, although the number of the endemic species is lower than in the previously mentioned ones. *Anonconotus ligustinus* Galvagni, 2002 is endemic in the Western Ligurian Alps, *Anonconotus alpinus* (YERSIN, 1858) in the Swiss Alps (GALVAGNI 2004). *Chorthippus alticola* RAMME, 1921 is endemic in the area from Trentino (Monta Rosa) to the Karawanken Alps (borderland of Italy, Austria and Slovenia). *Miramella formosanta* (FRUHSTORFER, 1921) is the endemic species of certain Italian and Swiss ranges of the Alps (KÖHLER et al. 1999). *Stenobothrus cotticus* (KRUSEMAN & JEEKEL, 1967) is restricted to the Cottian Alps and to the Pelvoux region (Montgenèvre, Col d’Izoard, see MOSSOT 1999). *Barbitistes vicetinus* GALVAGNI & FONTANA, 1993 is endemic species of Veneto region (North-east Italy) (GALVAGNI & FONTANA 1993). *Ephippiger terrestris terrestris* YERSIN, 1854 is endemic in the Western-Alps (France, Italy, Switzerland) (HELLER 2004; OTTE et al. 2004). *Antaxius pedestris pedestris* (FABRICIUS, 1787) is endemic in the southern slopes of the Alps.

Epipodisma Ramme, 1951 is a monotypic – *Epipodisma pedemontana* (Brunner von Wattenwyl, 1882) – endemic genus of the western Alps on the border of France and Italy. The genus *Chortopodisma* Ramme, 1951 also consists of single described species only, i.e. *Chortopodisma cobellii* (Krauss, 1883) which occurs exclusively in southern Tirol and in the Dolomites. Similarly, *Pseudoprumna baldensis* (Krauss, 1883) is the only known species of the monotypic *Pseudoprumna* Dovnar-Zapolskij, 1932, restricted to the unglaciated refugial massiv of the Monte Baldo which is known as *locus classicus* of endemic taxa from other insect groups, as well. Other, more widely distributed southern Alpine endemics are *Miramella carinthiaca* (Puschnig, 1910) and *Stenobothrus ursulae* Nadig, 1986 from the Alpine areas of Italy, Austria and Slovenia (Nadig 1986, 1987).

II.4. The Appenines

The Appenines have only a single, in the mountains widely distributed endemic species: *Stenobothrus apenninus* Ebner, 1915. Nevertheless, several more restricted endemic species were recorded from the central part of the Appenines: *Metrioptera caprai* Baccetti, 1956, *Podisma goidanichi* Baccetti, 1958, *P. ruffoi* Baccetti, 1971, *P. silvestrii* Salfi, 1935, all species of the endemic genus *Italopodisma* Harz, 1973: *I. acuminata* (La Greca, 1969), *I. baccetti* (La Greca, 1969), *I. costae* (Targioni-Tozzetti, 1881), *I. ebneri* (La Greca, 1954), *I. fiscellana* (La Greca, 1954), *I. lagrecai* (Galvagni, 1973), *I. lucianae* (Baccetti, 1959), *I. samnitica* (La Greca, 1954), *I. trapezoidalis* (La Greca, 1966), furthermore *Italohippus modestus* (Ebner, 1915), *I. albicornis* La Greca, 1948, *I. monticola* (Ebner, 1915) (Figs 2-5). *Ephippiger cavannai* (Targioni-Tozzetti, 1881) is endemic in the area of Calabria–Campania, *Ephippiger ruffoi* Galvagni, 1955 is endemic in the area of Umbria–Marche of the Apennines. The occurrence of *Ephippiger apulus* (Ramme, 1933) is restricted to the Salentina Peninsula.

36,1% of the orthopteran fauna of the high mountainous region of Central Appenines consists of endemic or subendemic species (La Greca & Messina 1982). It can be explained by the strict isolation from other similar habitats of the Appenine peninsula during the last glaciations. The recur-

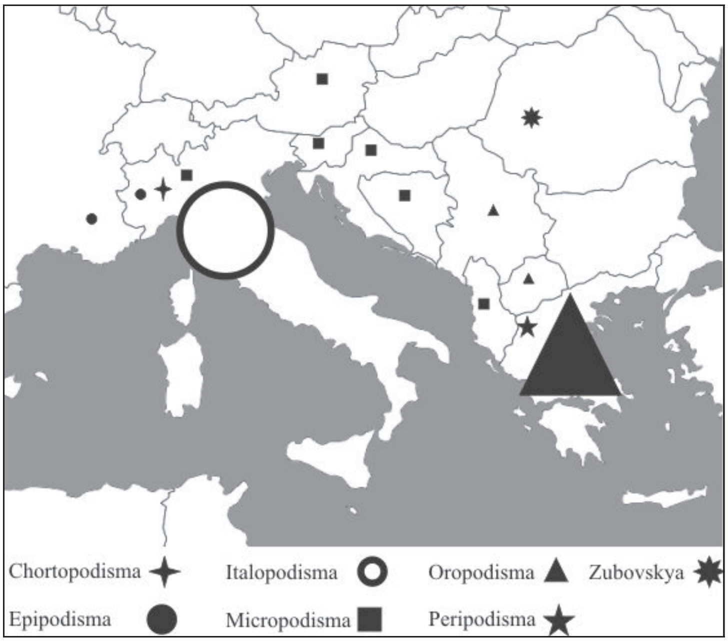

Fig. 2. Number of species of the restricted Podismini genera in the European countries [the size of the symbols is in proportion with the species number (between 1 and 10)].

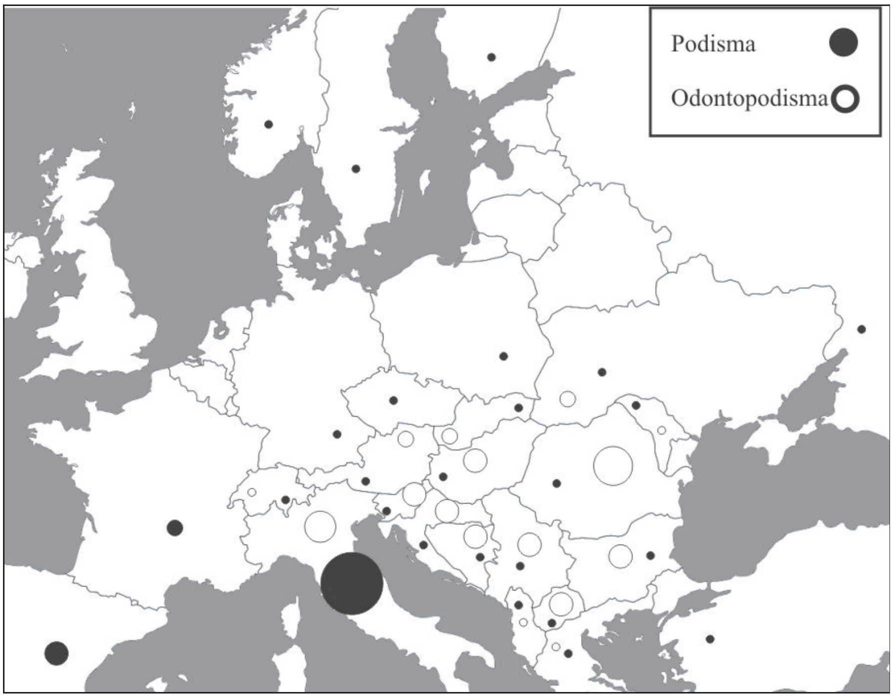

Fig. 3. Number of species of the wide-spread Podismini genera in Europe and Asia Minor I. (*Podisma*, *Odontopodisma*) [the size of the symbols is in proportion with the species number (between 1 and 8)].

Fig. 4. Number of species of the wide-spread Podismini genera in Europe and Asia Minor II. (*Miramella*, *Pezotettix*) [the size of the symbols is in proportion with the species number (between 1 and 3)].

Fig. 5. Number of species of the wide-spread Podismini genera in Europe and Asia Minor III. (*Pseudopodisma*) [the size of the symbols is in proportion with the species number (between 1 and 2)].

rent glaciations – similarly to other mountainous areas – formed a special mountainous fauna characterized by more widely distributed northern species and also by stenochorous relicts in the small, restricted mountaineous regions of the peninsula. The range of several endemisms is restricted to a single mountain. The presence of xerothermic habitats at high levels also stimulated the evolution of endemisms. Thus, the occurrence of xerophylous species is generally situated quite close to habitats of mountainous species.

II.5. The Carpathian Mountains and the Carpathian Basin

The endemic species of this region are mostly restricted to some mountaineous regions of the Carpathians. However, endemic taxa also can be found on lowlands connected with peculiar types of edaphic grasslands (VARGA 1995, 2002). The richest areas in endemisms are the Eastern and Southern Carpathians, and the Szörényi Ore Mts. Endemic species of the region are usually flightless and occur in mountainous habitats, considered partly as relict endemisms. *Zubovskya banatica* KIS, 1965 is the only European species (described from the Mt. Semenic) of a relict-like Eastern Palaearctic genus, occurring in South Siberia, Manchuria and Korea. *Podismopsis transsylvanica* RAMME, 1951 is relict endemism of the Fogaras Mts. *Miramella ebneri* GALVAGNI, 1953 is more widely distributed in the Southern and Eastern Carpathians, but a separated subspecies of it can also be found in south-eastern Poland. Supposedly, more recently isolated taxa are the endemic Orthoptera species of the Cozia Mts.: *Isophya harzi* KIS, 1960 and *Chorthippus acroleucus* (MÜLLER A., 1924) or the widespread *Odontopodisma carpathica* KIS, 1962 occurring in the Fogaras and also in Cozia Mts. *Isophya beybienkoi* MARAN, 1958 was considered (KIS 1960, 1961, 1962, 1965; HARZ 1975; VARGA 1995; ORCI et al. 2001) as endemic species of the Slovakian Karst. All these species are localized endemisms, which have survived at least the last glaciation *in situ*.

The endemism richness of the Southern Carpathians can be explained by its refugial character and mostly, by the isolation from other high-mountains. In addition, the geomorphological variety of the Southern Carpathians results extreme microclimatic differences and occurrences of Alpine, sub-Alpine and Mediterranean taxa (KIS 1961).

The area center of several low mobility species is connected to the Balkan-Asia Minor endemism centre. It is generally supposed that the number of species decreases from its centre of dispersal to the periphery (VARGA 1971; BĂNĂRESCU & BOŞCAIU 1978). The Balkan-Asia Minor endemism centre can also be considered as the dispersal centre of the genus *Isophya* (HELLER et al. 2004). Speciation processes could be also associated with the expansion of the genus. These follow partly from the size (HAMRICK & HAMRICK 1989) and habitat requirements of the populations and they are strongly affected by climatic oscillations and habitat fragmentations. These changes often proceed at the margin of the range, while others can occur in any part of the area where ever barriers are established.

The ancestors of *Isophya* species of the Carpathian Basin, including also the widespread eurytopic species, presumably penetrated from the Balkan-Asia Minor centre into this region following mainly two dispersal routes, from the western part of Balkan Peninsula and from the southeast, along the western Transylvanian (Apuseni) Mts., respectively. These main routes were separated by the arid central Balkanic and Carpathian basin areas and often resulted in the separation of Illyrian-Dacian vicarious pairs of species (VARGA 1964, 2002), as it was demonstrated in the species pair of *Isophya modestior* BRUNNER VON WATTENWYL, 1882 and *Isophya stysi* CEJCHAN, 1957. Former species have expanded from the western Balkanic core area into the southern and central part of Transdanubia, while Transylvania and the eastern part of the Carpathian basin was occupied by the eastern vicariant species (Fig. 6-7).

Isophya camptoxypha (FIEBER, 1853) occurs in humid natural forest clearings (KENYERES & BAUER 2005). It reaches the Carpathians and the Transylvanian Mts. Furthermore it is distributed in the marginal areas of the Eastern Alps and in the adjoining Hungarian areas (Kőszegi Mts., Őrség), and also in the Mecsek Mts. In the Carpathian Basin *Isophya modesta* FRIVALDSZKY, 1867 occurs in the Transylvanian basin and on certain spots of the Northern Middle Range, in northern Serbia (Vojvonina), in the Mecsek and Villányi Mts., and also on the isolated volcanic Somló Hill.

As opposed to the above mentioned, *Isophya costata* (BRUNNER VON WATTENWYL, 1878) is a postglacial relict species (VARGA in RAKONCZAY 1990) with a scattered range in the Carpathian Basin. The origin of this species probably lies in the continental meadow steppes on loess territories south of the Carpathian Basin. Within the Carpathian basin, it can be considered as a relict of the post-glacial steppe period. However, *Isophya costata* shows a fairly broad habitat range from loess meadow steppes to mesophytic hayfields. Moreover, it occurs in low densities also in slightly degraded tall grasslands of similar physiognomy (KENYERES et al. 2004; BAUER & KENYERES 2006).

II.6. The Iberian Peninsula

The Orthoptera fauna of the Iberian Peninsula is very diverse and rich in endemic species. Third of the 300 known species are endemic (OLMO-VIDAL 2006). This fauna basically differs from the fauna of the above mentioned regions. The flightless grasshopper genera of the Balkans and Asia Minor (*Isophya*, *Poecilimon*, *Eupholidoptera* spp.) are absent, except for *Isophya pyrenaea* (SERVILLE, 1839) occurring also in the Pyrenees. On the Iberian Peninsula the bulk of endemic species belongs to completely other, not closely related genera, e.g. several Ephippigeridae as *Pycnogaster algecirensis* BOLIVAR, 1926, *P. inermis* (RAMBUR, 1839), *P. gaditana* BOLIVAR I., 1900, *P. cucullatus* (CHARPENTIER, 1825), *Ephippigerida areolaria* (BOLIVAR, 1877), *E. carinata* (BOLIVAR, 1877), *E. pantingana* (NAVAS, 1904), *E. zapaterii* (BOLIVAR, 1877), *E. paulinoi* (BOLIVAR, 1877) (HERRERA 1982). The core area of these genera is definitely the Iberian Peninsula, but certain species can also be found on other parts of the western Mediterranean area (e.g. Sicily, South France, North Africa).

The number of Iberian endemic species is also high in many other genera, e.g. *Antaxius* BRUNNER VON WATTENWYL, 1882*,* *Uromenus* BOLIVAR, 1878, e.g. *Antaxius hispanicus* BOLIVAR, 1887, *A. florezi* BOLIVAR, 1900, *Uromenus andalusius* (RAMBUR, 1838), *U. perezii* (BOLIVAR, 1877), *U. ortegai* (PANTEL, 1896). Some of them also occur in North Africa and in other parts of the western mediterranean. Endemic Acridid genus for example are *Eumigus* BOLIVAR, I., 1878 with 8 species

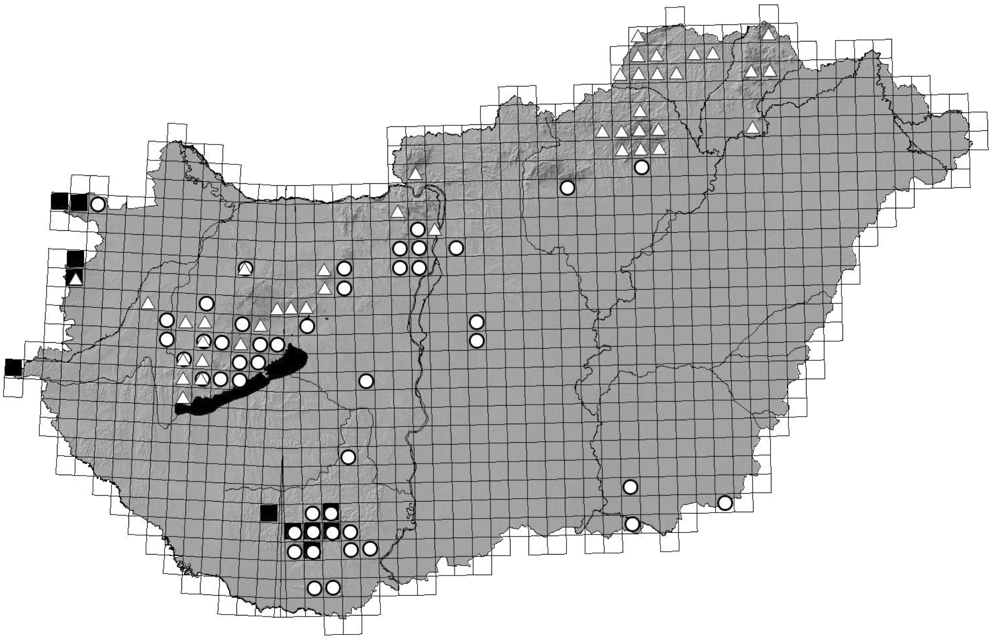

Fig. 6. Distribution of *Isophya costata* (white circle), *Isophya kraussii* (white triangle) and *Isophya camptoxypha* (black square) in Hungary.

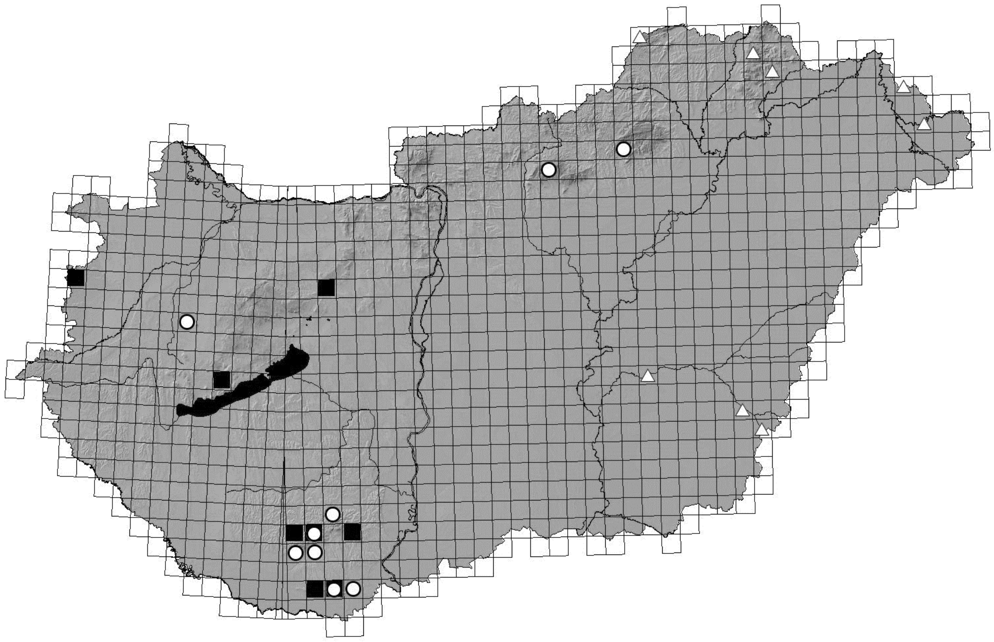

Fig. 7. Distribution of *Isophya modestior* (black square), *Isophya stysi* (white triangle) and *Isophya modesta* (white circle) in Hungary.

and subspecies (PRESA et al. 2007) and *Ocnerodes* BRUNNER VON WATTENWYL, 1882 with 6 species and subspecies. *Kurtharzia nugatoria* (NAVAS, 1909) and *Omocestus burri* UVAROV, 1936 are endemic to Iberia. Many species have more restricted area. E.g. *Dolichopoda linderi*, *Platystolus obvius*, *Petaloptila pyrenaea* and *Steropleurus panteli* are endemic to Catalonia.

The genus *Ctenodecticus* BOLIVAR, 1876 deserves a special emphasis: several endemic species are restricted to small parts of the Iberian Peninsula. The micropterous species of this genus are mostly endemic in some regions of the Iberian Peninsula except for *Ctenodecticus bolivari* TARGIONI-TOZZETTI, 1881 (Tunesia, Algeria, Sardinia, Sicily). *Ctenodecticus masferreri* (BOLÍVAR, 1894) is endemic species of the Catalonian Mts. (Montseny), *C. thymi* OLMO-VIDAL, 1999 is known only from the Montsech Mountain and area of *C. pupulus* BOLIVAR, 1876 is restricted to the Guadarrama Mts. (Segovia). In the middle of the 20th century several strictly restricted species became known from the Betica Mts. in Southern Spain. In 1956 *C. ramburi* MORALES AGACINO, 1956 was published from the region of Jaén. In 1978 further two species (*C. granatensis* PASCUAL, 1978 and *C. major* PASCUAL, 1978) were described from the southern range (Sierra Nevada) of the Betica Mts. The westernmost data of the genus is the presence of *C. lusitanicus* BARRANCO & PASCUAL, 1992 in Portugal: Serra de Estrela (MORALES AGACINO 1956; HARZ 1969; PASCUAL 1978, 1980; HERRERA 1982; GALVAGNI 1989; BARRANCO & PASCUAL 1992; OLMO-VIDAL 1999).

Ctenodecticus species also occur outside of the Iberian Peninsula, in North Africa, Sardinia and Sicily which can be explained by the paleogeographic processes from Oligocene to the mid-Miocene (LA GRECA 1983, 1984). During that time the former Tyrrhenic landmass which originally reached to recent Sardinia in the Tethys Sea, was fragmented into several micro-blocks and then the blocks moved towards the east-southeast. The occurrence of the flightless *Ctenodecticus* species on some western Mediterranean islands can be explained by these processes. This theory is further supported by the distribution of other taxa (e.g. ground-beetles) (Fig. 8.). The newer researches confirmed that the geodynamic development and the rapid paleobiological changes during in Oligocene triggered a mainly endemic evolution of the flora and fauna (STEININGER & WESSELY 2000).

The Iberian Peninsula also has some endemic species from more widely distributed genera, e.g. *Platycleis iberica* ZEUNER, 1941, *Pterolepis lusitanica* (BOLIVAR, 1900), *Dociostaurus hispanicus* BOLIVAR, 1898. Its endemic Catantopinae species e.g. *Podisma cantabricae* MORALES AGACINO, 1950, *P. carpetana* (BOLIVAR, 1898), *Cophopodisma pyrenaea* (FISCHER, 1853) also show different biogeographical connections. *Cophopodisma* DOVNAR-ZAPOLSKIJ, 1932 is a typical, oligotypic genus of the Pyrenées. Besides the more widespread *C. pyrenaea* (FISCHER, 1853), *C. ibera* is only known from a single location (Gavarnie) in the Eastern Pyrenées (ZEUNER 1941; HARZ 1969; HERRERA 1982).

II.7. The Caucasian Mountains

This mountain range has relatively few endemic bushcricket species. Near to the Black Sea coast occurs *Isophya pylnovi* MIRAM, 1938 and in the Trialeti Mts. *I. transcaucasica* RAMME, 1930. Further endemic species are *Parapholidoptera noxia* (RAMME, 1930) and *Montana decticiformis* SHCHELKANOVTSEV, 1914.

Most endemic grasshoppers of the Caucasus belong to the tribe *Podismini* (Catantopinae), as *Micropodisma koenigi* BURR, 1913, *M. svanetica* DOVNAR-ZAPOLSKY, 1932, *Podisma teberdina* RAMME, 1951, *P. uvarovi* RAMME, 1926. *Pachypodisma* DOVNAR-ZAPOLSKY, 1932 is an endemic genus of this region with only two species: *P. lezgina* (UVAROV, 1917) and *P. crassa* MISHCHENKO, 1950. *Chorthippus fallax elbrusianus* BEY-BIENKO, 1941 is a high-mountain subspecies of a widely distributed genus.

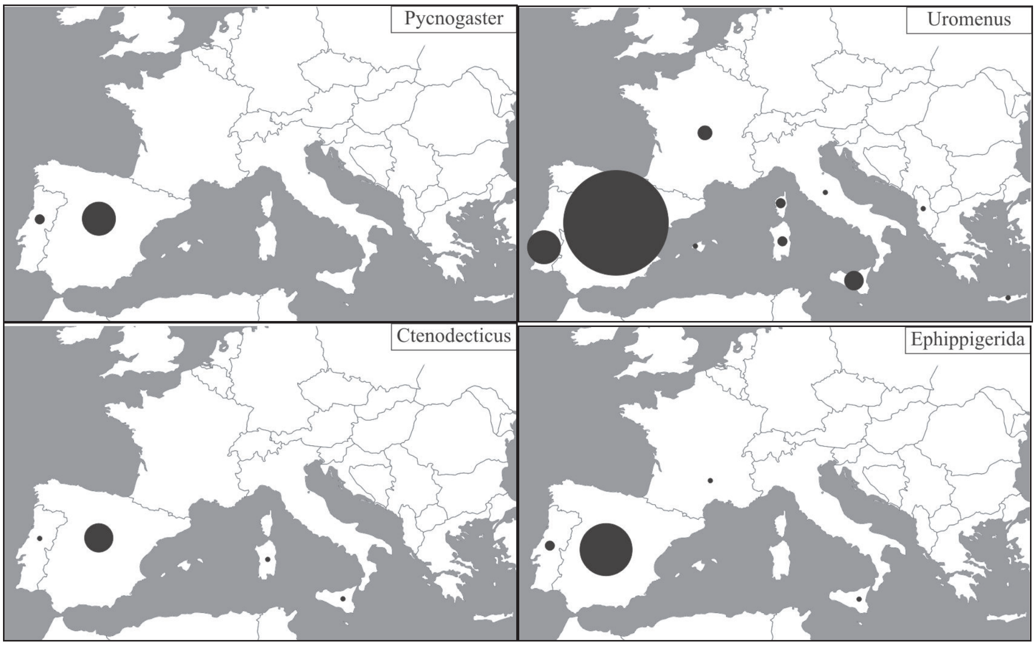

Fig. 8. Number of species of some Iberian centred orthopteran genera in the European countries [the size of the symbols is in proportion with the species number (between 1 and 22)].

III. DISCUSSION: FORMATION AND EVOLUTION OF ENDEMISM CENTRES AND ENDEMIC SPECIES OF EUROPEAN ORTHOPTERA

III. 1. The centre Southern Balkans – Asia Minor

Based on the above mentioned it can be suggested that the basic morphological, genetic and taxonomic differentiation of the European orthopteran fauna can be explained with the processes in the period of mid-Miocene. Supposedly, this was also the main period in the evolution of the endemic genera of south-eastern Europe (incl. Asia Minor). *Isophya, Poecilimon* and *Eupholidoptera* species are almost absent from the western part of the Mediterranean region which is oppositely characterised by some genera (e.g. *Ctenodecticus, Pycnogaster, Ephippigerida*) which have occupied the western Mediterraneum and partly also North Africa by adaptive radiation.

It was demonstrated (HEWITT 1996, 1999, 2000, 2001, 2004a-b; TABERLET et al. 1998; SCHMITT 2007) that during the glacial periods the climatically favourable parts of the Mediterranean region served as refugia of the xero- and thermophilous species. On the other hand, the more cool-humid habitats were populated mainly by continental ('Angarian') and boreal species which also penetrated into the periglacial areas. During the glacial periods the thermophilous elements were repeatedly restricted into the refugia of the Mediterranean peninsulas while the continental steppic and tundral species have expanded onto the huge Holarctic 'mammouth steppe' area. The famous palaeontological site of Starunia clearly demonstrates the fossil Orthoptera assembly of this last glacial period (ZEUNER 1954; HOLDHAUS 1954). Opposite processes took place during the interglacial periods with northward expansion and colonisation of the thermophilous elements from the southern refugia (Iberian, Appenin and Balkan Peninsulas) while the northern and continental species were restricted northwards or into the high mountains (SCHMITT 2007).

From the characteristic genera of the South Balkan-Asia Minor centre, *Eupholidoptera* is related to the coastal scrubby vegetation type (especially macchia), therefore it could hardly penetrate northwards of the eu-Mediterranean climatic belt. Oppositely, *Poecilimon* species mostly occupy steppic or tall forb habitats, thus they were not restricted to Mediterranean habitats. The ranges of *Isophya* species were probably strongly differentiated during the last glacial phases and in inter- and postglacial periods they could have had fairly 'individual' re-colonisation patterns. These processes are mirrored by several examples of isolated species and subspecies on peripheric areas. The following *Isophya* species are rather similar morphologically and also concerning their habitat requirements, nevertheless their areas are isolated on different scale. They were probably derived from a single ancestral species by area fragmentation and geographical isolation. Acoustic studies have demonstrated that *Isophya pyrenaea* is restricted to the Pyrenées and mountains of France (INGRISCH 1991). The eastern central European (Germany, Austria, Poland, the Czech Republic, Hungary, Slovakia and Slovenia) *Isophya kraussii* (BRUNNER VON WATTENWYL, 1878) occurs in Hungary in mountains and hilly areas mainly on forest clearings and forest fringes with dense vegetation (BAUER & KENYERES 2006). The morphologically very similar *Isophya altaica* BEI-BIENKO, 1926 (~*pyrenaea altaica*) is an endemic species of the Altai Mts. (SERGEEV 1986, 1993). As taxonomically more problematic species (NAGY 2003) can be enumerated: *Isophya brevicauda* RAMME, 1931 (Austria, Croatia, Slovenia), *Isophya obtusa* BRUNNER VON WATTENWYL, 1882 (Bulgaria, Serbia, Bosnia-Herzegovina [?] and Montenegro), *Isophya pienensis* MARAN, 1954 (Poland, Romania, Slovakia, Ukraine). Unfortunately, some species are quite poorly known, as *Isophya iraca* MAŘAN, 1977 (MAŘAN 1977). Molecular phylogenetic analyses of the whole genus could answer most of the open questions.

Most *Isophya* species occurring in the Dinaric Mts. are also distributed in other parts of the Balkan Peninsula, since their dispersal was apparently not impeded by barriers. Endemic species became isolated with greater chance in the Southern and Eastern Carpathians, e.g. the Dacian elements as *Isophya harzi* and *I. stysi.* The role of the Illyrian-Dacian subdivision can be studied also in other taxa, e.g. in the geographical and subspecific subdivision of *Pholidoptera littoralis* (FIEBER, 1853). The separation of three subspecies seems to be justified: *Pholidoptera littoralis insubrica* NADIG, 1961 occurs in the Italian part of the West Alps, *Pholidoptera littoralis littoralis* (FIEBER, 1853) occurs in the southern ranges of the Eastern Alps and of the northern areas of the Dinaric Mts. (Istria, Velebit) and *Pholidoptera littoralis similis* Brunner von Wattenwyl, 1861 occurs in Romania and Hungary (NADIG 1961; NAGY et al. 2000). These subspecies have obviously associated with the three refugia during the last glacial maximum.

In chapter II.5 it was mentioned that *Isophya costata* probably dispersed northwards from the southern lowland areas of the Carpathian Basin where it could survive the last glacial maximum, isolated from other related steppic species of *Isophya*. BAUER & KENYERES (2006) supposed that *I. modesta,* similarly to *I. costata,* whose occurrences characteristic of plains and hilly areas and the forest steppe zones of mountains, is also a species of steppe grasslands rich in dicotyledonous plant species (KIS 1960; RÁCZ 1998). Following the diminishing of its major habitat, however, *I. modesta* could not colonize secondary hayfields [but sometimes can be found in abandoned vineyards (personal communication of Gergely Szövényi)]. The phylogenetic connection between the above supposed species-pair have been confirmed by genetic analyses (ORCI et al. 2007) recently. ORCI & HELLER (2004) stated that *I. rossica* (earlier mentioned as an endemism of Kursk and Eastern Ukraine (BEI-BIENKO 1954)) is a subspecies of *I. modesta*. Further examples of similar allopatric, partly peripheric isolates of steppic species are as follows. The range of *Isophya rectipennis* BRUNNER VON WATTENWYL, 1878 includes the western coast of Asia Minor, the islands near to the coast, the European part of Turkey, the ranges of Rhodope, the lowlands between the Stara Planina Mts. and the Black Sea, the pre-Carpathian Romanian lowland and parts of Bosnia-Herzegovina (KIS 1977). The endemic species of the East Romanian lowland is *Isophya dobrogensis* KIS, 1994 recorded in the Island of Popina along the Danube (KIS 1994). *Isophya zubowskii* BEY-BIENKO, 1954 can be found in the foreland of the East Carpathians and in Muntenia, Moldova and also in southern

Ukraine (Krim, Podolian table-land) (KIS 1960, 1979). *Isophya stepposa* BEI-BIENKO, 1954 occurs from the area of Kursk, Voronezh to the Don River (BEI-BIENKO, 1954). *Isophya taurica* BRUNNER VON WATTENWYL, 1878, is endemic species of the Crymean Peninsula.

Endemisms associated with lowland areas can also be found in other taxa. In the region of the Danube's and River Sava's fork around Beograd *Metrioptera amplipennis* (BRUNNER VON WATTENWYL, 1882) occurs on the alluvial flatland with hygrophytic marshy vegetation. *Zeuneriana marmorata* is also a lowland species in northeastern Italy and Slovenia (KLEUKERS et al. 1997; GOMBOC & SEGULA 2005).

III. 2. Refugia of the thermophilous and psychrophilous species as endemism and dispersal centres

Significant refugia of thermophilous and psychrophilous species existed in different parts of the Mediterranean region during the glaciations. The significant relations between requirements of thermophilous species and formation of endemism centres are known from earlier periods as well. In Late Miocene the Messinian crisis produced extreme aridity in the Mediterranean. In early Pliocene Mediterranean was dominated by arid-semiarid vegetation (SUC et al. 1995). Many taxa adapted to aridity in that time. The arid areas became important refugia during glaciations, because in more humid and temperate areas usually less endemisms occur (VERDÚ & GALANTE 2002; ERONEN & ROOK 2004).

Due to the isolation during the glacial phases, a significant differentiation could be established even in mobile species, as it was recently shown in *Chorthippus parallelus* (ZETTERSTEDT, 1821) (HEWITT 1996, 2003, 2004a-b; COOPER et al. 1995). Following the isolation period, hybrid belts were formed along the 'sutures' of the area as consequences of dispersal from the different refuges. Similar cases are known also in other species groups. *Chorthippus brunneus* (THUNBERG, 1815) and *Ch. biguttulus* (LINNAEUS, 1758) are considered sympatric, sibling species, which are able to hybridize, their offsprings have intermediate features both morphologically and acoustically (RAGGE 1976). The same is true for *Chorthippus brunneus* and *Ch. bornhalmi* in northeastern Italy (KLEUKERS et al. 2004). However, they can co-occur with a minimal chance of hybridisation as a consequence of different sexual signals. The species group *Ch. dorsatus* (ZETTERSTEDT, 1821), *Ch. dichrous* (EVERSMANN, 1859) and *Ch. loratus* (FISCHER DE WALDHEIM, 1846) can also be mentioned as examples of sympatric sibling species characterized by markedly different acoustic signals (STUMPNER & HELVERSEN 1994).

Allopatric sibling taxa of *Chorthippus biguttulus* were described from the Mediterranean peninsulas which are morphologically very similar, but clearly separated by acoustic signals. These were considered subspecies by some authors (HARZ 1975; RAGGE et al. 1990; SCHMIDT 1990): *Ch. rubratibialis* SCHMIDT, 1978 is endemic in the Appenines, *Ch. jacobsi* HARZ, 1975 and *Ch. yersini* HARZ, 1975 are typical for the Iberian Peninsula (however, latter species was also found in Sicily as a consequence of paleogeographic connections) and *Ch. crassiceps* (RAMME, 1926) was described from the Balkan Peninsula.

Similar phenomena can be observed in *Euchorthippus* TARBINSKY, 1926 species as well. *E. albolineatus siculus* RAMME, 1927 in Sicily, *E. angustulus* RAMME, 1931 on the Balearic Islands, *E. madeirae* UVAROV, 1935 on Madeira, *E. chopardi* DESCAMPS, 1968 on the Iberian Peninsula and on the Mediterranean coast of France, *E. sardous* NADIG, 1934 on Sardinia, *E. elegantulus* ZEUNER, 1940 in the Loire's delta, and on the islands of Jersey, Guernsey, and Alderney are strictly localised allopatric sibling species (RAGGE 1997; ORCI et al. 2002).

The above mentioned species have not completely lost the ability of hybridisation as a result of the relatively young isolation which probably took place during the last glacial phases of the Pleistocene. During the maximum of the last glacial (Weichsel, about 18 000 y BP) large part of Central Europe was covered by tundra and cold-steppe vegetation in which only few Orthoptera species could survive. At present these species show an endemic or disjunct, alpine or arctic-alpine distribution. The bulk of the species was restricted to the southern peninsula of the continent and partly, also in the refuges of the continental areas. During this period a significant regression of the Mediterranean Sea took place with formation of a Transadriatic connection and also Sicily was linked to the Apennine Peninsula. Nevertheless the Gibraltar Strait already existed. Presumably the evolution of the European *Euchorthippus* species took place from more southern centres simultaneously with the climatic warming up. *E. elegantulus* expanded from the Iberian Centre. *E. declivus* (BRISOUT DE BARNEVILLE, 1849) is characterized by an Italian centre and occurs also in France, in the Iberian Peninsula and in Eastern Europe. *Euchorthippus pulvinatus* (FISCHER DE WALDHEIM, 1846) could survive the glaciation on the Balkans (RAGGE 1997; ORCI et al. 2002).

WILLEMSE (1973) revised the European species of the genus *Paracaloptenus* BOLIVAR I., 1876 with Mediterranean xeromontane distribution. The species of this genus are associated with xeric, short-grass swards. Recently, we distinguish three species and three subspecies. *Paracaloptenus caloptenoides caloptenoides* (BRUNNER VON WATTENWYL, 1861) is the most widespread. It occurs in Austria (mostly extinct!), Hungary, and nearly on the whole Balkan Peninsula (except for the Peloponnesos Peninsula), as far as the Bosporus. *P. caloptenoides brunneri* (STÅL, 1876) occurs in the western part of Asia Minor (in Turkey at the southern coastal parts of the Marmara Sea, in the region of Bursa). The occurrence of *P. caloptenoides moreanus* WILLEMSE F. M. H., 1973 is restricted to the Peloponnesos Peninsula. According to WILLEMSE (1973) *Paracaloptenus cristatus* WILLEMSE F. M. H., 1973 occurs in similar habitats, but rather localized on Istria (Učka – Mt. Maggiore) and the southernmost ranges of the Dinaric Mts (Mostar, Livno, Nevesinje, Senj). *Paracaloptenus bolivari* UVAROV, 1942 occurs in the Pyrenées with a disjunct range from the others.

The mountains of the only partly glaciated Southern Alps, Carpathians and northern Balkans had a different refugial character. They have provided colonization and radiation opportunities for the continental ('Siberian') species (VARGA 1975). SERGEEV (1998) considered that the South European mountains are significant areas of diversity in endemic species of the Melanoplinae grasshoppers (see also the occurrence of *Zubovskya banatica*). In this respect these mountains approach the East Asian centres in their importance.

Some species with disjunct ranges are considered glacial relicts as the more widespread *Gomphocerus sibiricus* (LINNAEUS, 1767) [= *Aeropus sibiricus*] and *Aeropedellus variegatus* (FISCHER VON WALDHEIM, 1846). They are typical cold-continental steppic species with isolated occurrences in mountaineous regions of the Pyrenées, the Alps, the Appennines and the Balkan Peninsula (LA GRECA & MESSINA 1982; WILLEMSE 1984; VOISIN 1987; HERRERA 1987).

Metrioptera saussuriana (FREY-GESSNER, 1872) is a local species in cool-humid habitats of the western Alps of France, Italy and Switzerland (DREUX 1962), but it was also found on similar habitats of other French Mts. (VOISIN 1981) and in the Pyrenées as well (HARZ 1969; HERRERA 1982). In the Appennines, however, the endemic *Metrioptera caprai* exists.

The endemic *Italopodisma* species of the Central Apennines provide a good example for a relatively rapid speciation of continental species. The Apennines were only partly glaciated during the last glacial maximum, and it was characterized by habitats with milder climatic conditions. These habitat patches were populated by cold-adapted continental species which were increasingly fragmented and isolated from the northern populations during the deglaciation. Rapid evolutionary differentiation could proceed in several isolated populations with low individual numbers leading to formation of many endemisms (LA GRECA 1984). Similar phenomena were observed in the populations of *Podisma pedestris* penetrating to the Apennines during the last two ice ages. Subsequently, they have differentiated in different scales on subspecies and/or species level (LA GRECA & MESSINA 1982; HELLER et al. 1998). According to LA GRECA & MESSINA (1979) the endemic, psychrophilous Orthoptera of the high mountain habitats in Greece are also considered autochtonous since the Pliocene. They have originated from Angarian genera which survived the Pleistocene glaciations in several small, isolated refugia.

III. 3. The endemisms of the islands in the Mediterranean Sea

The speciation of endemic Orthoptera of the Mediterranean islands has some peculiar characters in relation to the palaeogeographical events of the younger Tertiary and Quaternary epochs. Several endemisms occur in the islands, e.g. Sicily: *Odontura arcuata* MESSINA, 1981, *Pamphagus marmoratus* BURMEISTER, 1838; Sardinia: *Odontura calaritana* A. COSTA, 1883, *Uromenus annae* (TARGIONI-TOZZETTI, 1881), *Pamphagus sardeus* (HERRICH-SCHAEFFER, 1840), *Antaxius maculipedes* INGRISCH, 1983; Corsica: *Uromenus chopardi* EBNER, 1938; Mallorca: *Uromenus balearicus* (BOLIVAR, 1884); Formentera: *Euchorthippus angustulus*; Cyprus: *Isophya mavromoustakisi* UVAROV, 1936. Similar examples are known from Crete and the archipelago of the Aegean Sea (HERRERA 1982; LA GRECA 1983; INGRISCH 1983).

Oppositely, the dispersal and subsequent isolation could also proceed during the phases of glacial regressions of the Mediterranean Sea. For example the distribution of *Pterolepis bucchicii* (HERMAN, 1874) demonstrates the former connection of the islands Hvar, Brač and Korčula. *Pterolepis thyrrhenica* LA GRECA, 1952 occurs in the islands of Ponza and Elba, further examples of endemic species are mentioned in the chapter II.4. MASSA et al. (2001) stated that the isolation proceeded in *Pterolepis thyrrhenica* in several waves. Sea level fluctuations exceeding 100 m were the 'pacemakers' of isolation and differentiation in this species. It became isolated at the first phase from the peninsular populations, and subsequently also the populations of Ponza et Elba became isolated. However, this latter isolation proved to be rather young for further specific differentiation.

In other cases, however, we have to assume isolations due to the breakdown of former continental plates in connection with much older, Tertiary palaeogeographical changes. The fact that the endemic *Eupholidoptera jacquelinae* in the island of Gavdros is morphologically close to the species occurring in Cithiria, and also on the western coast of Anatolia including its coastal islands (Icaria, His, Samos), can be interpreted as a consequence of the breakdown and fragmentation of an earlier continental plate (TILMANS 2002). The tectonic movements during Oligocene and mid-Miocene played a significant role in the evolution of the Orthoptera species in the islands occurring on the western part of the Mediterranean Sea. The disintegration of the Tyrrhenic subarea does not only explain the pattern of distribution in *Ctenodecticus* species, but also the current sporadic occurrence of the genus *Uromenus* (LA GRECA 1983, 1984; STEININGER & WESSELY 2000).

Of course, the last phase of the faunal history of the Mediterranean islands was strongly influenced by human populations. Therefore, vegetation is mainly secondary, and also the events of species introductions cannot be excluded from the formation of the Orthoptera fauna of these islands.

III. 4. Geographic, eocological, acoustic and reproductive isolation

The acoustic differences in Orthoptera are much more significant factors of speciation than the morphological characters (HELLER 2004b; NISCHK & OTTE 2000). However the expressed acoustic differences are not always accompanied by reproductive isolation. RAGGE (1997) considers therefore that these changes are relatively young and presumably connected to the younger Pleistocene isolations.

We can assume that fragmented populations of flightless Orthoptera are demographically and also genetically nearly closed with minimal chances to recolonize new habitats. Several genetic differences were found among geographically separated populations of the wide-spread, flightless *Isophya kraussii* (PECSENYE et al. 2003). RITCHIE et al. (2001) could find significant differences in the mitochondrial DNA of two large population groups of *Ephippiger ephippiger* which makes it reasonable to separate them on subspecies level. The mapping of the occurrences, however, strongly suggests that there is a hybridization zone, which would provide a continuous gene flow. The genetic differences of the two populations could be originated during the time of isolation in separate glacial refuges. In *E. ephippiger*, however, beside the widespread *E. ephippiger ephippiger* (FIEBIG, 1784) further subspecies were described (ADAMOVIC 1967b; HELLER 1988) on morphological and acoustic basis from southeastern Europe, e.g. *E. e. balcanicus* ANDREEVA, 1985 (Bulgaria), *E. e.*

harzi ADAMOVIC, 1973 (Bosnia-Herzegovina: Troglav), *E. e. tamaninii* GALVAGNI, 1956 (Italy) and *E. e. usi* ADAMOVIC, 1973 (Serbia and Montenegro: Miroè). The genetic analysis of these taxa would be rather timely.

Relatively significant differences in the acoustic signals could also be revealed in the populations of more mobile species (STUMPNER & HELVERSEN 1994). Studies of the acoustic signals show difference on species level in connection with taxa morphologically considered as subspecies. It was also observed that the acoustic differentiation alone was insufficient for the complete reproductive isolation. It means that these taxa represent an intermediate stage of the formation of biological species (according to DOBZHANSKY 1951; MAYR 1963) by pre-mating isolation evolved in allopatric situation which could be re-inforced by additional differentiation due to the reduced gene-flow by subsequent sympatry (character displacement). The change of the mating signal, just as every hereditary feature, is considered to be the result of random mutation, underwent the effects of selection pressure and/or genetic drift. While the change of the acoustic isolation can appear relatively rapidly in small, isolated populations, the morphologic evolution usually takes place rather conservatively (MARTÍNEZ WELLS & HENRY 1998). The speciation which is initiated in the phase of spatial separation can re-inforced by sexual selection or by adaptation to different niches as well (MAYR 1942; MAYNARD SMITH & SZATHMÁRY 1997).

It is a basic question if the reproductive isolation caused by acoustic signals will be followed by a morphological change. The acoustic and the genital-morphological characters and also the viability of hybrid offspring probably evolve rather independently. However, it can be supposed that these characters are subjected to sexual selection which can act against the hybridisation. In addition, the former differentiation can be conserved by the genetic drift mostly in small, demographically and genetically closed populations. If meanwhile isolation disappears, e.g. by postglacial colonisation processes, further genotypical and phenotypical differentiation will mainly depend on the effectivity of acoustic pre-isolation and the viability of hybrids. Nevertheless there are only few case studies (COOPER et al. 1995) that cover the analyses of sound signals, of other genetic markers and also the extent and consequences of hybridization.

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