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Dispersal, vicariance and refuges in the Anatolian Pimeliinae (Coleoptera, Tenebrionidae): remarks on some biogeographical tenets[1]

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To every complex problem, there is a simple solution, and it is usually wrong.
H.L. Mencken

Key words: Turkey, Tenebrionidae Pimeliinae, phylogeny, ecology, zoogeography.

SUMMARY

A brief overview of the family Tenebrionidae is presented, and general biogeographical patterns are discussed with emphasis on the subfamily Pimeliinae. The influence of historical and current ecological effects on patterns of biogeographical distributions of this subfamily in the Anatolian peninsula is examined by different standpoints. The Anatolian pimeliine fauna includes at least 78 species. Endemics account for a large proportion (26.92%) of the whole fauna. The majority of the non endemic species show distribution ranges referable to the East Mediterranean, Turanian and South West Asiatic chorotypes. The North African component is very little and the Anatolian pimeliine fauna seems to be scarcely related to West Mediterranean areas. By contrast, many species have Syro-Anatolian and Irano-Anatolian distributions. In particular, the East Anatolian chains seem to have a filtering effect on some eastern Pimeliini. The coastal plains of the west and south are eminently suitable for species adapted to Mediterranean conditions, accounting for the high percentage of East Mediterranean elements (24.36% of the whole pimeliine fauna). Species from North Eurasia and Caucasus should find no barriers to colonization of the northeastern part of the Anatolian peninsula. However, post-Pleistocene increasing aridification could have favored desert-adapted Middle Eastern species. Dispersal routes involving the Anatolian peninsula have presumably been available since the Miocene, providing sufficient time for penetration of parts of the region and subsequent vicariant events, but lack of phylogenetic reconstruction makes difficult to state it. Present distributions may also reflect Pleistocene climatic changes. Lowering of temperatures during the Pleistocene glaciations may have contracted some species into relict distributions and some refugial areas could be recognized.

1. INTRODUCTION

The fauna of the Anatolian peninsula occupies an important biogeographical position at the junction of Europe and Asia. The area is also the northern frontier for several tropical and eremic species. The zoogeography of a number of groups

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within this fauna has been discussed at some length in various papers (*e.g.*, Bytinski-Salz, 1953; Kosswig, 1955, 1972; Basoglu and Ozeti, 1973; Baran, 1976; Banarescu, 1977; Basoglu and Baran, 1977, 1980; De Freina, 1979; Hacker, 1990; Daszak and Cawthraw, 1991; Hesselbarth et al., 1995; Cook, 1997; and references therein).

As with Tenebrionidae, no recent papers are available. The tenebrionid fauna of Anatolia probably includes more than 200 known species (cf. Koch, 1948), but both the exact distribution and taxonomic status of many of these are uncertain.

The aim of this paper is to study the geographical distribution of the Anatolian species of Pimeliinae (the largest tenebrionid subfamily) from a historical standpoint.

Historical biogeography attempts to explain geographical distributions of taxa in terms of their history rather than exclusively in terms of their current ecology. Thus, historical biogeography aims to study general patterns of area relationships as shown by congruence among present animal or plant distributions, palaeogeography, palaeoecology and phylogeny. These patterns of area relationships can be translated into vicariant and dispersal events that are correlated distinctly with former historical scenarios. In fact, it is stipulated that large-scale historical events have affected entire biotas, resulting in similar distribution patterns among different biotic elements. In the present study, all available data on Tenebrionidae Pimeliinae (= Tentyriinae of authors) from the Anatolian peninsula are summarized and the distribution patterns analyzed with relation to different much debated general hypotheses of historical biogeography.

2. THE FAMILY TENEBRIONIDAE: AN OVERVIEW WITH SPECIAL REFERENCE TO THE SUBFAMILY PIMELIINAE

2.1. Systematics and phylogeny of Tenebrionidae

The family Tenebrionidae is one of the largest of Coleoptera, comprising about 18,000 known species. Adult tenebrionids exhibit a superficial diversity of form possibly exceeding that of any other family of beetles and some are often wrongly identified as they closely resemble members of other families (*e.g.*, Carabidae, Passalidae, Scarabaeidae, Chrysomelidae, Curculionidae). Brachyptery and aptery are common, and characterize almost all members of certain large taxa like Pimeliinae and Adeliini. Larvae are more uniform and easily recognizable superficially (although they also include some highly specialized forms), but relatively few tenebrionid larvae have been characterized in terms of the important taxonomic structures (large reviews of larval morphology are reported by Lawrence and Spilman, 1996).

Some Tenebrionidae are stored products pests, and others may do considerable damage to roots or seedlings of crops in arid and semi-arid areas; finally, few species are hosts for parasitic Acanthocephala and Nematoda and have medical or veterinary importance (Butler, 1949; Golvan, 1969; Watt, 1974). However, relatively few Tenebrionidae are of great economic importance.

Perhaps because of its scarce economic importance the family has attracted less attention than other large coleopteran families. Most systematic work has been at the specific, generic or tribal levels, while few have attempted to improve the higher classification within the family. Among the large families of Coleoptera, Tenebrionidae has proved particularly difficult for specialists to partition into phylogenetically meaningful higher categories. Since Watt (1974), in addition to adult morphology, characters of larvae have been used in reconstructing phylogenetic relationships among Tenebrionidae (*e.g.*, Doyen and Lawrence, 1979; Doyen and Tshinkel, 1982; Doyen, 1993). However, the overall results derive mainly from adult characters (*e.g.*, abdominal defensive glands, ovopositor, tentorium, structure of the labrum-epipharynx, wing venation, metendosternite). Larvae are relatively simple in structure, compared to the adults, and present relatively few features that can be used by taxonomists. Watt (1974) viewed simplicity and uniformity as an advantage for phylogenetic analysis; however, simplicity of structures makes convergence evolution (*i.e.*, homoplasy) more difficult to detect, while adult characters are more robust indicators of cladistic relationships (Doyen and Tshinkel, 1982).

Relationships between Tenebrionidae and other Tenebrionoidea are unclear. The family Tenebrionidae is not closely related to any other family, and has had a long, independent evolutionary history (Watt, 1974).

Cladistic analyses have emphasized phylogenetic relationships among Tenebrionidae and some groups formerly regarded as distinct families (*e.g.*, Alleculidae, Lagriidae, Nilionidae, Cossyphodidae, and Rhysopaussidae), agreeing that all should be included in a single family. By contrast, Zopheridae, previously included in Tenebrionidae, are now regarded as an other family. Also, several genera previously included in Colydiidae are now placed in Tenebrionidae and other ten families, while the remainder of the Colydiidae genera are regarded as a subfamily (Colydiinae) of the family Zopheridae, with the exclusion of the tribe Pycnomerini, which is included in Zopheridae but not in the subfamily Colydiinae (cf. Slipinski and Lawrence, 1997). According to Doyen and Tshinkel (1982), Tenebrionidae consist of two main groups, the lagrioid branch and the tenebrionid branch. The tenebrionid branch consists of three main subdivisions: the tenebrionine lineage (including Alleculini), the coelometopine lineage and the diaperine lineage. The lagrioid branch is less clearly defined. Three clades (the lagriine lineage, the belopine lineage and the pimeliine = tenetyrine lineage) could tentatively be referred to this branch, but their cladistic relationships are unclear. The pimeliine lineage (including Pimeliini, Zolodinini and Tentyriini) represents the largest group of Tenebrionidae in number of species. As might be expected for such a large group, the pimeliines are extremely diversified, and the proper position of the pimeliine lineage is unclear, since it shares derived characters with both the lagrioid and the tenebrionid branches. Zolodinini may be the sister group of Tentyriini+Pimeliini. The larvae of Zolodinini do not differ significantly from primitive members of the tenebrionid branch, supporting thus a tenebrionid origin for the pimeliine lineage. Alternatively, Zolodinini could represent a specialized derivative of some Tenebrionid group, perhaps related to Cyphaleini, with only convergent similarities to Pimeliinae. A recent cladistic analysis of Pimeliinae (Doyen, 1993) showed basic difficulties in regarding Zolodinini as a pimeliine clade (see below).

Due to these unclear cladistic relationships among Tenebrionidae, Doyen and Tshinkel (1982) refrained from presenting a formal reclassification of the tenebrionid tribes. Therefore, despite this recent attention and critical re-examination of taxa and characters, from a nomenclatorial point of view the tribal classification of Tenebrionidae is still essentially that of Gebien (1937; 1938-44).

Also, in contrast to their high cladogenesis and adaptive radiation, Tenebrionidae seem to be a conservative coleopteran lineage from the karyological point of view. Data on the evolution of chromosomes and genome size have been summarized and discussed by Juan and Petipierre (1991) and Petipierre et al. (1991). As a rule, Tenebrionidae exhibit a reduced range of variation in the chromosome numbers ($n = 7$-19) and they show a very striking modal value at $n = 10$, in agreement with the suggested most primitive number of Polyphaga. Also, both the two main subfamilies (Pimeliinae and Tenebrioninae) have $2n = 20$ as their modal chromosome number; only Akidini ($2n = 16$), Pimeliini ($2n = 18$ principally), and Blaptini (mostly with numbers higher than 30 and having multiple sex chromosomes), deviate from the modal value. In the subfamily Pimeliinae, there is a trend towards decreases in chromosome number from $2n = 20$ to $2n = 18$ in species of *Adesmia*, *Glabrasida*, *Zophosis* and *Pimelia* probably produced by fusion of one pair of autosomes. By contrast, in the subfamily Tenebrioninae, there is a trend towards increases of chromosome number up to a maximum of $2n = 26$ (excluding *Blaps*), which can be explained by centric fission with or without shifts in the sex-chromosome system. Nevertheless, the identity of chromosome number does not mean karyological resemblance: in fact, a detailed analysis of seven tenebrionids with 20 chromosomes showed differences in arm number, whole bivalent area at metaphase I, total complement length and amount of C-banded heterochromatin. The conservative genome evolution of Tenebrionidae is however confirmed also by low variations in the nDNA amount. Based on microdensitometric measures of DNA amount of Feulgen-stained spermatids of about fifty species, Tenebrionidae show a clearly modal value (0.2-0.3 pg) with a reduced range of variation (0.18-0.86 pg). However, the average genome size of Pimeliinae is lower than in Tenebrioninae, suggesting a more advanced phylogenetic position of the former.

The first known fossil assigned to the family with high probability is a beetle from the Middle Eocene Brown Coal of Geiseltal, Germany, which also represents the first known fossil of the superfamily Tenebrionoidea (Watt, 1974). According to Watt (1974), this fossil is close to Pimeliinae Epitragini, a group regarded by Watt as a primitive lineage being fully winged and often having distinctly striate elytra. By contrast, Doyen's (1993) reconstruction showed a probably more derived position of this tribe. The superfamily Tenebrionoidea probably originated in the Jurassic, and the family Tenebrionidae may have arisen not long afterwards, and most probably before the separation of the New Zealand from Australia in the Mid Cretaceous (Watt, 1974).

2.2. General ecology and biogeography of Tenebrionidae

Tenebrionids (both adults and larvae) are primarily saprophagous, feeding on a variety of dead plant and animal matter, including humus, leaf litter, decaying trees, wind-blown detritus, carrion, and dung. However, some tenebrionids are predators or semipredators feeding on other insects, while a number of geophilous larvae feed on living plant roots, stems or seedlings. Termitophily is known in the Rhysopaussini and in *Pseudeba*, and mirmecophily occurs in *Tribolium*. Various *Tribolium* are also known to inhabit the nests of wild bees (Lawrence and Spilman, 1991). Some Eleodini and helaeine species (*Pterohelaeus* and *Brises*) have invaded caves and feed probably on bat guano, while some Opatrini and species of *Tenebrio*, *Alphitobius* and *Palembus* have been recorded from bird nests (Lawrence and Spilman, 1991). Butler's (1949) review of tenebrionid biology should be read for additional information on life history and feeding habits.

Most adult Tenebrionidae have defensive glands located near the abdominal apex and sometimes on the prothorax (see Dettner, 1987 for references). However, adult tenebrionids, notably those without defensive glands, are attacked by a number of vertebrates, such as skunks, foxes, rodents, bats, coyotes, hedgehogs, pole-cats, turtles, lizards, geckos, toads, white storks, owls, kestrels, and swallows (*e.g.*, Gridelli, 1937; Eisner and Meinwald, 1966; Lovari, 1975; Slobodchikoff, 1978; Holm and Scholtz, 1980; Hernández et al., 1991; Ayal and Merkl, 1994; Hacini and Doumandji, 1998; Fattorini et al., 1999a; and references therein), becoming sometimes an important food resource for predators in arid environments (*e.g.*, Holm and Scholtz, 1980; Ayal and Merkl, 1994). In some species, intraspecific predation plays an important role in population structure and dynamics (Polis, 1981). Various Gregarinia (Ormières, 1967) and Cestoidea (*e.g.*, Jolivet, 1998) are tenebrionid parasites.

The majority of adult Tenebrionidae are more or less heavily scelorotized, dark in color, and active at night on the ground or on the surfaces of logs or tree trunks.

In various tenebrionid groups (Phrenapatini, some Lagriinae Pycnocerini, some Opatrini, Trachyscelini, Ulomini), the adults are adapted for burrowing into substrates, occupying the same habitats as their larvae. In others (*e.g.*, Cyphaleini, Cnodalonini, Strongyliini, most Lagriinae and Alleculinae), the adults are relatively soft-bodied, brightly colored and diurnal.

Alleculinae occur in open and forest areas, including both species whose larvae live in litter and soil, and species feeding on decaying wood invaded by fungi. Adults feed generally on pollen and nectar (especially of umbelliferous flowers), but some species lead a nocturnal life feeding on rotten wood (Burakowski, 1993). The pectinate claws of the adults are regarded as an adaptation which assists walking on foliage (Watt, 1974). Alleculinae have a worldwide distribution, and their occurrence on certain islands suggests an extraordinary dispersal power. The genus *Lobetis* contains the only tenebrionids occurring naturally on the Hawaiian islands (Watt, 1974).

Lagriinae occur in both woodlands and isolated forest clearings, on the edges of deciduous and mixed tree stands, in logging places and along the forest sections. Larvae are found among leaf litter, in rotten wood, or under the bark of dead trees, feeding on the dead leaves lying on the ground and on the bark of fallen twigs. Adults live under bark and logs, on the ground, on flowers, on the foliage and branches of trees, bushes, perennial plants and grasses (Watt, 1974; Burakowski, 1993).

As a whole, tenebrionids can be divided into two groups according to major habitat of their larvae (cf. Lawrence and Spilman, 1991; and references therein): i) xylophilous species, which occur in rotten wood and associated cambium and subcortical spaces, and ii) geophilous species, which occur in the soil and leaf litter.

Xylophilous tenebrionids feed generally on rotten wood, but a number of taxa (*e.g.*, Diaperiini, Bolithophagini and species of Alphitobiini, Triboliini and Hypophloeini) feed on fungi, algae, lichens and mosses. Some xylophilous species (*e.g.*, various Hypophloeini, *Lyphia*, species of *Tribolium* and *Palorus*) are predators or semipredators, while few predaceous species are known among geophilous Tenebrionidae.

The geophilous Tenebrionidae include the assemblage of tribes (Tentyriini, Asidini, Pimeliini, etc.) forming the subfamily Pimeliinae, the Goniaderini, most Adeliini and Lagriini, Phaleriini, most Helaeini and Nyctozoilini, Scaurini, Blaptini and Eleodini, Opatrini, Trachyscelini, Crypticini, Apocryphini, some Alleculini and some Helopini. Some geophilous tenebrionids are restricted to littoral regions (*e.g.*, Phaleriini, Trachyscelini, and some Opatrini), where they occur in the soil beneath dune plants or in sea weed, carrion, or other organic debris. Others (*e.g.*, some Stenosini, Cossypohodini and Opatrini) have become associated with ants, and some arid land species are highly specialized in the use of ant-nest debris as an important source of food during the hot seasons (Sánchez-

Piñero and Gómez, 1995). Many geophilous tenebrionids occur in the steppes and deserts, where larvae mature in the soil, feeding on plant roots or decaying organic material. In fact, Tenebrionids are a conspicuous element of most arid and semiarid environments, and many species inhabiting these habitats exhibit a number of morphological, physiological and behavioral adaptations, like subelytral cavity, sand-walking and sand-swimming modifications, wax bloom covering the integument to minimize water loss, drinking of fog water, active uptake of atmospheric water, use of metabolic water, high specialized osmoregulation processes, etc. (*e.g.*, Nicolson, 1990; Santos, 1994; and references therein). Pimeliinae are the most important geophilous tenebrionid group in arid and semiarid regions (Watt, 1974). Adult Pimeliinae are frequently diurnal, taking shelter only during the hottest part of the day. Their larvae live in soil, feeding usually on dead plant debris, although some species feed on living roots or seeds. In the more specialized Pimeliinae and a few "Blapimorpha" adapted to arid conditions, adults (more resistant to desiccation than larvae), oviposit in a damp substrate (normally after rain), and the larval development is very rapid to make the best use of ephemeral moisture (Watt, 1974).

All these ecological characteristics make Tenebrionidae a very useful taxon for studies of ecological biogeography in different habitats, including researches on habitat distribution and segregation (*e.g.*, Aldryhim et al., 1992; Ayal and Merkl, 1994; Colombini et al., 1994; Fallaci et al., 1997; Faragalla, 1999; and references therein), morphological variation along altitudinal and latitudinal gradients (*e.g.*, Doyen and Rogers, 1984; Krasnov et al., 1996), vertical distribution (*e.g.*, Rickard, 1971), diversity patterns (*e.g.*, Santos, 1994) and community structure (*e.g.*, Stapp, 1997; Krasnov and Shenbrot, 1998; Vilenkin and Chikatunov, 1998; and references therein).

Tenebrionidae are also excellent subjects for testing historical hypotheses at every spatial scale (*e.g.*, Juan et al., 1995, 1996; Endrödy-Younga, 1996; Epps et al., 1998). According to vicariance biogeographers, present distribution patterns are more dependent on the subdivision of ancestral biotas in response to changing geography than dispersal abilities. However, an understanding of a group's vagility is a prerequisite for any biogeography study because species with higher dispersal ability are obviously less affected by vicariance events (*e.g.*, Noonan, 1988: 377, 381). Most Tenebrionidae are characterized by aptery. The vagility of apterous beetles is greatly reduced by their inability to fly, making these animals excellent materials to test vicariance hypotheses. Some apterous tenebrionids such as Zophosini and most Adesmiini are capable of swift movement on the ground, rapidly covering large distances. However, Tenebrionidae, notably geophilous ones, are generally sedentary animals of very slow mobility, active and passive, unable to readily disperse, as shown by their very high degree of endemism (*e.g.*, Endrödy-Younga, 1988, 1996).

The family Tenebrionidae occurs in all major zoogeographical regions. However, Tenebrionidae are strongly represented in tropical and subtropical regions and in both hot and cold deserts, but are not numerous in damp, cool-temperate climates; for instance, within Europe, 281 species (including Alleculinae and Lagriinae) are known from Italy (Gardini, 1995), while only 27 species are definitely established in the British Isles and the majority are confined to southern England (Watt, 1974). Many species occur much further north in continental Europe, where the summers are more reliable than in Britain: for example, *Scaphidema metallicum* (Fabricius, 1792) and 10 other species occur north of the Arctic Circle in Sweden (Watt, 1974). In the Southern Hemisphere, a single species occurs on Campbell Island (52°30'S) and several occur slightly further south (to 55°S) on Tierra del Fuego (Watt, 1974).

As a whole, the Mediterranean region, harboring more than 2,500 species (cf. Gebien, 1937; 1938-43), is one of the most diverse areas.

According to Watt (1974), the most primitive Tenebrionidae occur in Australia, New Zealand and the Old World tropics (including Malagasy), while the Palaearctic and Nearctic regions are not rich in primitive forms.

2.3. Systematics and biogeography of Pimeliinae

According to Watt (1974), Pimeliinae (plus Zolodininae) could be the sister group of all other Tenebrionidae. However, cladistic analyses (Doyen, 1993) and karyological evidences (see above) suggest a more advanced phylogenetic position for Pimeliinae. The almost complete absence of Pimeliinae from the Australian region also suggests that they are younger than most of the other major lineages (Doyen, 1993).

Pimeliinae (Zolodininae excepted) are most diverse in the Ethiopian Region, where they may have originated (Watt, 1974). There are endemic tribes in each of the main arid areas of the world. As a rule, Pimeliinae are strongly represented in the arid parts of the Palaearctic, Nearctic, Neotropical and Ethiopian regions (including Malagasy), but they are rare in the Oriental region (Doyen et al., 1989). Zolodininae were considered a distinct subfamily of Tenebrionidae by Watt (1974). According to Watt (1974), Zolodininae and Pimeliinae are vicariant groups, in that Zolodininae are confined to Australia and New Zealand, whereas Pimeliinae occur in all except these regions. In contrast to Watt's assumptions, Doyen and Tschinkel (1982) reduced Zolodininae to a tribe of Pimeliinae. However, more recently Doyen (1993) provided a detailed cladistic reconstruction of the relationships among Pimeliinae, showing basic difficulties in regarding Zolodinini as a sister group of Pimeliinae or a pimeliine lineage. Thus, the phylogenetic position of this key group is uncertain.

According to Doyen (1993), Pimeliinae are an actually monophyletic group including a number of major clades (cnemeplatiine, stenosine, pimeliine, eurymetopine, tenetyriine and asidine clades) and various genera and tribes of uncertain position.

The biogeography and phylogeny of Pimeliinae (especially that of Pimeliini) was the object of a large number of papers by Kwieton (*e.g.*, 1976, 1977a, 1977b, 1977c, 1978a, 1978b, 1978c, 1980a, 1980b, 1981a, 1981b, 1981c, 1982a, 1982b, 1983, 1986a, 1987). However, these works are founded on unclearly elucidated phylogenetic (but not properly cladistic) assumptions, mainly based on Skopin's papers on larval morphology (*e.g.*, Kwieton, 1977c) or derived from Kwieton's unpublished D. Phil. thesis (Kwieton, 1981a).

As to Pimeliini, biogeographical patterns of taxonomic diversity can be depicted on the basis of a number of papers, especially those published by Gridelli (1933, 1937, 1939, 1953, 1954), Koch (1935, 1948), Normand (1936), Gebien (1937), Español (1943), Kaszab (1957, 1960b, 1961b, 1974, 1982) Kocher (1958), Pierre (1964a, 1964b, 1974), Kühnelt (1965), Skopin (1973), Ardoin (1978), Grimm (1981, 1991), Kwieton (1976, 1977a, 1977b, 1977c, 1978a, 1978b, 1978c, 1980a, 1981a, 1981b, 1982a, 1982b, 1986b, 1987), Oromí (1982), Viñolas (1994). As a whole, Pimeliini include approximately 450 species, about 400 of which are placed into the genus *Pimelia*.

I calculated the number of genera of Pimeliini known through the world, as well as the number of species and subspecies of the genus *Pimelia*. Based on these numbers, different classes of taxonomic diversity were established as shown in Figs 1-2. Due to their aptery, populations of Pimeliini are frequently characterized by high isolation, resulting in a number of different but clearly related taxa. These facts led some authors to regard such populations as true species, while other students reduced them to subspecies. Lacking recent taxonomic revisions for many taxa, I have provisionally counted both species and subspecies. Values of taxonomic diversity reported for each region were calculated according to the literature cited above. Although I have scored a large amount of other literature on Pimeliini, no attempt has been made to state full synonymies or the true systematic value of each genus, species and subspecies presently known. However, as Pimeliini were studied by a great number of entomologists since the past century, I think that the values of taxonomic diversity are accurate enough.

Boundaries between different regions of taxonomic diversity are, except those faunistically very well known and harboring few species (*e.g.*, France, Italy, Spain), approximations of somewhat wider areas where numbers of genera, or of species and subspecies, shown notable change.

On the whole, the highest number of presently recognized genera of Pimeliini resides in the Turanian area (Fig. 1), while the greatest diversity of the genus *Pimelia* is in Northern Africa (Fig. 2). However, the high number of taxa (species and subspecies) of the genus *Pimelia* recorded from Libya could reflect both a high but composite diversity, due to the cooccurrence, in Libya, of two different faunal components (a western component, related to the Moroccan fauna, and an eastern component, related to the Egyptian fauna), and a higher level of faunistic knowledge compared to other near regions.

3. THE ANATOLIAN PIMELIINAE

3.1. Checklist of Anatolian Pimeliinae

There are few papers dealing with Anatolian Tenebrionidae. The checklist given in Appendix 1 is mainly based on Gebien's catalogue (1937) and a number of papers by Kaszab (1938, 1939, 1960a, 1961a, 1968). Papers by Bytinski-Salz (1956), Pierre (1964), Skopin (1973), Ardoin (1978), Grimm (1981, 1991), and Leo and Fattorini (2000) provided other data. All literature records were critically revised and the updated information is corrected for errors, changes in nomenclature, new distribution records and other pertinent information.

For each species, both the chorotype and the distribution type (when it is a very small part of the chorotype range) are reported (see below for definitions of chorotypes and distribution types). These general distributions are mainly based on data published by Gebien (1937; 1938-43), Gridelli (1937, 1939, 1954), Koch (1935, 1948), Kocher (1958), Kühnelt (1965), Kaszab (1982), Schawaller (1982), and Penrith (1983. 1984). Other sources were specimens preserved in the collections of Museo di Zoologia, Università di Roma "La Sapienza" (Rome).

For critical taxa, some information is also presented that includes taxonomic problems, nomenclatorial changes and bibliographic sources.

I have omitted subspecies in the checklist, but their taxonomy is discussed in the annotations. Also, great problems exist in the species-level classification on some groups, notably *Pimelia* (cf. Leo and Fattorini, 2000), which require exhaustive comparative studies to resolve. Therefore I have avoided premature taxonomic changes. I have refrained from including species probably occurring in Anatolia but presently not recorded, except for few instances. Such records are listed as "?" (not absolutely certain) and discussed in the annotations.

The checklist given in Appendix 1 is also an attempt to modernize the suprageneric classification of the Anatolian Tenebrionidae. The arrangement of tribes in the checklist grossly approximates Doyen's (1993) cladistic reconstruction. Of course, a one-dimensional listing requires much compression and distortion of phylogenetic relationships, and this checklist cannot be contrived as cladistic arrangement. Due to their uncertain cladistic relationships, genera and species are listed alphabetically for each tribe.

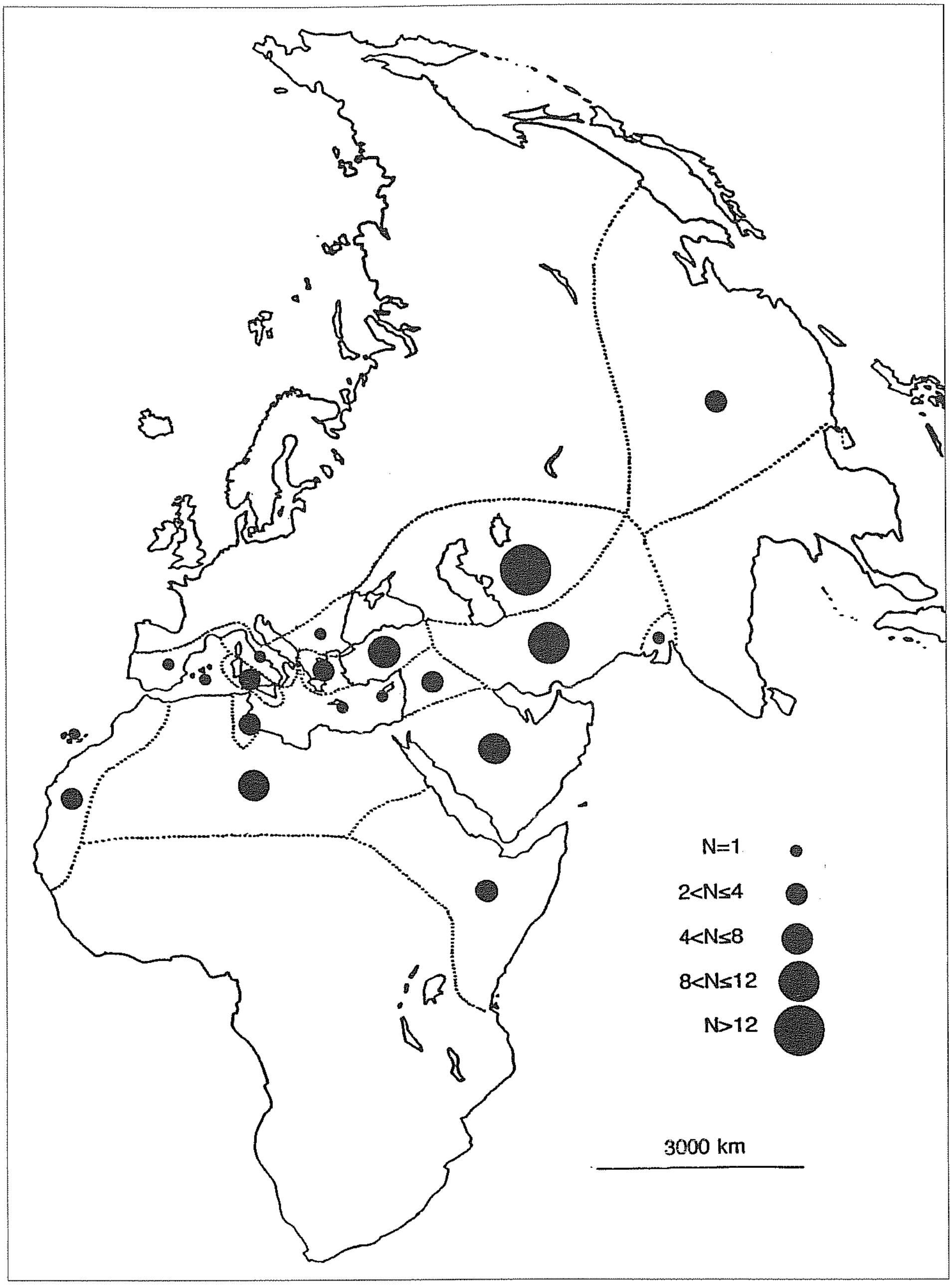

Fig. 1 - Map showing patterns of taxonomic diversity of the tribe Pimeliini at the genus level. Numbers of genera (N) known from each area were arranged in five classes of richness.

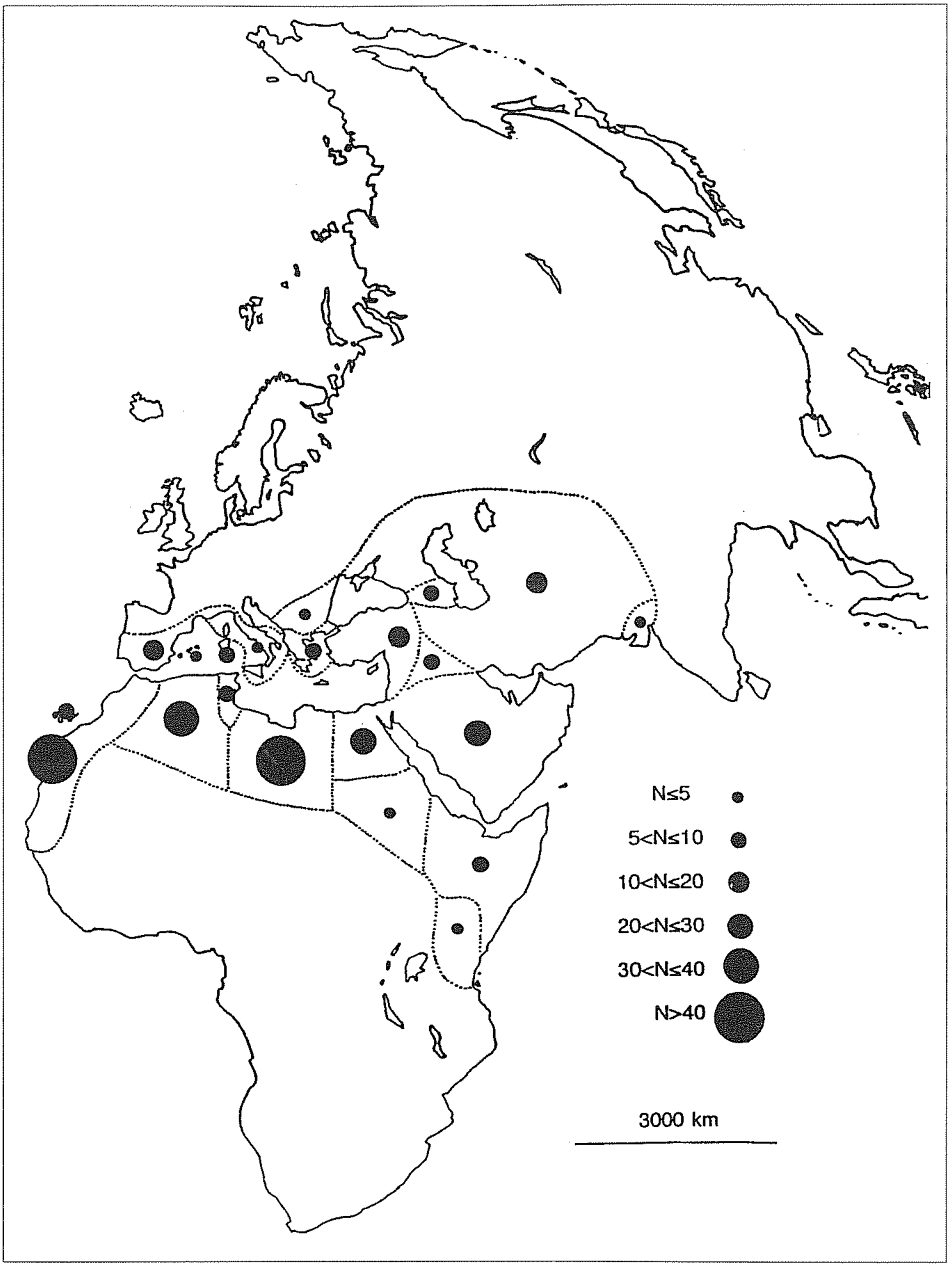

Fig. 2 - Map showing patterns of taxonomic diversity (species and subspecies) of the genus *Pimelia*. Numbers of species and subspecies (N) known from each area were arranged in six classes of richness.

3.2. Defining chorological categories for Anatolian Pimeliinae

At least 78 species of Pimeliinae inhabit the Anatolian peninsula with certainty. Such figure is provisional, because of lack of faunal knowledge and still unresolved taxonomic problems, especially for Pimeliini. In fact, many pimeliine species, presently known from Syria, could be found also in Anatolia.

In descriptive biogeography, identification of chorotypes (*i.e.*, common distribution patterns referable to previously established models) is a largely used approach to state the relative importance of different biogeographical components.

Chorotype study is a classical tenet of Italian biogeographers. In the past, general chorotypes proposed by La Greca (1964) for the Italian area, but obviously also applied to near countries, were largely used. Recently, Vigna Taglianti et al. (1993, 1999) proposed a revised classification of general chorotypes included in the West Palaearctic area. I followed the chorotype classification established by Vigna Taglianti et al. (1999) instead of La Greca's one. Indeed, these new chorotypes are generally wider, and therefore more suitable for large-scale studies, than La Greca's ones. Likewise I refrained from using chorological categories established by Wagner (1995) for the Anatolian butterflies because too detailed, including 20 major categories in turn divided into 102 minor types.

The chorotypes proposed by Vigna Taglianti et al. (1999) are based only on distribution patterns, without palaeogeographical or ecological assumptions. In fact, some biogeographers use distribution types (including general chorotypes) based on ecological, palaeoecological and palaeogeographical assumptions (cf. Vigna Taglianti et al., 1993, 1999). However, identification of distribution types should be an attempt to state merely descriptive categories without regarding to the origin of the distributions: in fact, distribution types based on current ecological or historical assumptions vary in relation to the studied taxon and it is impossible to use such models to compare distribution patterns of different animal groups. Also, such distribution types are subjective, because based on *a priori* assumptions that could be wrong or difficult to prove. By contrast, distribution types based only on distribution patterns, without regarding to ecological and historical factors, are objective and can be applied to every animal group.

Based on their distributions, Pimeliinae inhabiting Anatolia can be arranged in a number of general chorotypes (Appendix 1, Fig. 3). According to Vigna Taglianti et al. (1999), due to their restricted ranges, endemic species should be referred to general chorotypes on the basis of the distributions of their relatives. However, there is a lack of information on the phylogenetic relationships of most Pimeliinae endemic to Anatolia. This fact forced me to count endemics as a

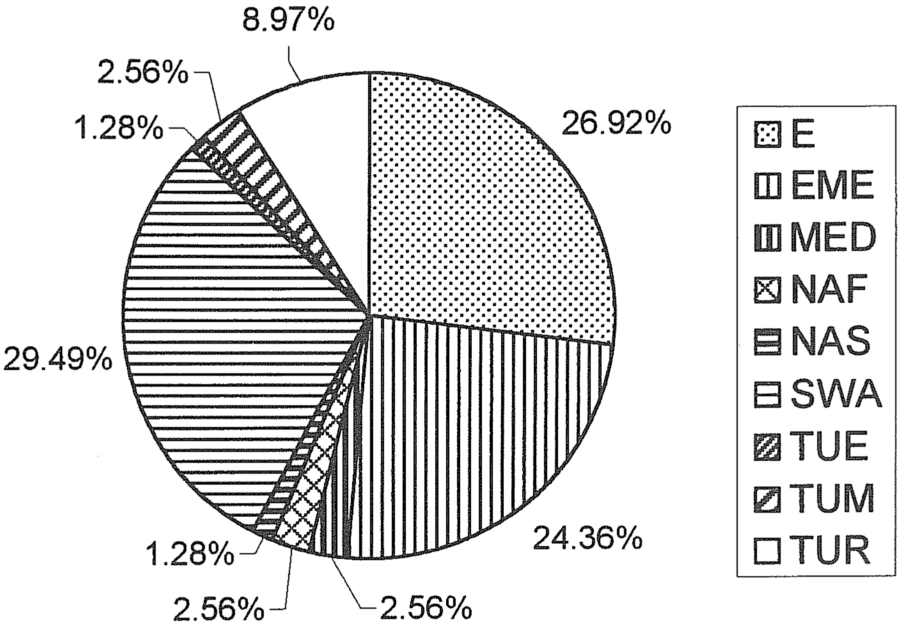

Fig. 3 - Percentage of chorotypes found in the tenebrionids of the Anatolian peninsula. Codes as in Appendix I. Species not recorded with certainty from Anatolia are omitted. A total of 78 species were considered.

distinct chorotype. Only for the endemic species belonging to the tribe Pimeliini a possible chorotype based on the distribution of their relatives is reported (cf. Leo and Fattorini, 2000). To avoid confusion, these species were obviously counted as endemics in the following chorological analyses, but their hypothesized chorotypes were used in studying the distribution patterns of the tribe Pimeliini within Turkey (see below).

Endemic species are about 27% of the whole Pimeliinae fauna. The SWA elements are the most abundant (29% of the whole fauna), followed by the EME ones (24%). Interestingly, "Turanian" elements (including TUE, TUM and TUR) are scarcely represented (13%). NAF, NAS and MED elements are very scarce chorological components.

Although SWA and EME are the most abundant elements, no SWA and EME species show a distribution range almost entirely involving the areas covered by these chorotypes. On the contrary, all the SWA and EME species show more restricted distributions.

In his masterwork on the tenebrionids of Crete, Koch (1948) recorded many species with distributions we could refer to the EME or SWA chorotypes, and proposed for these elements a number of restricted distribution types grouped into some major categories. However, Koch's types are of scarce utility because sometimes too restricted. Also, Koch's types of distribution are based on speculative assumptions on the origin of the included species. For example, some species occurring in Greek and on the Anatolian coasts were grouped by Koch in the "Trans-Aegean" type of the "Anatolian" major category, but there are no clear evidences that these species originated in the Anatolian plate.

I think that, for an in-depth zoogeographical treatment, the EME and the SWA chorotypes could be usefully divided into four different distribution types which can be exemplified as shown in Figs 4-7. Indeed, the EME species show an Aegean distribution (68% of EME) or a Ponto-Mediterranean distribution (26% of EME), while the SWA species show a more properly Syro-Anatolian distribution (57% of SWA) or an Irano-Anatolian distribution (43% of SWA). Finally, all the TUR elements are actually restricted to the Ponto-Caspian area, showing a Ponto-Caspian distribution (Fig. 8).

The distribution types I used have to regard as a practical tool to describe distribution patterns of some Anatolian tenebrionids. Therefore, these chorological categories are not exhaustive: they could be compared to distribution models of other animal groups, but obviously other animals could have distributions not referable to these types.

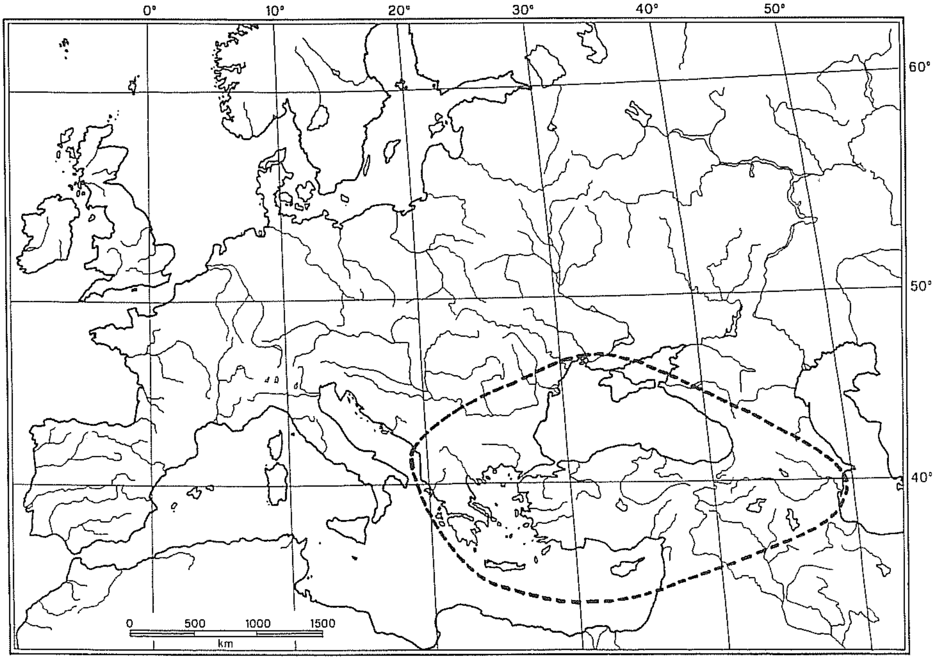

Fig. 4 - Distribution pattern of Ponto-Mediterranean tenebrionid species.

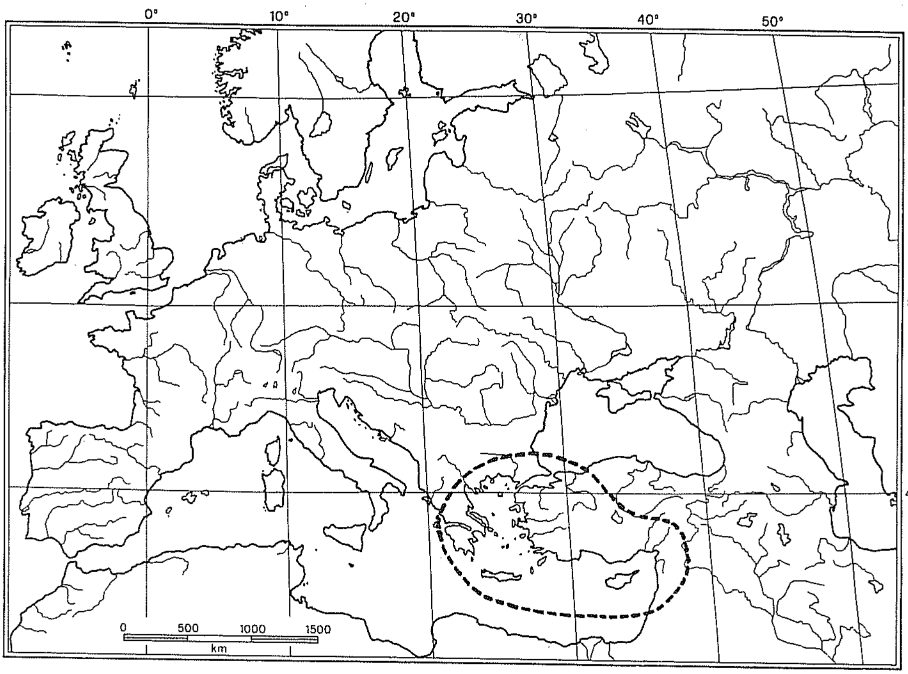

Fig. 5 - Distribution pattern of Aegean tenebrionid species.

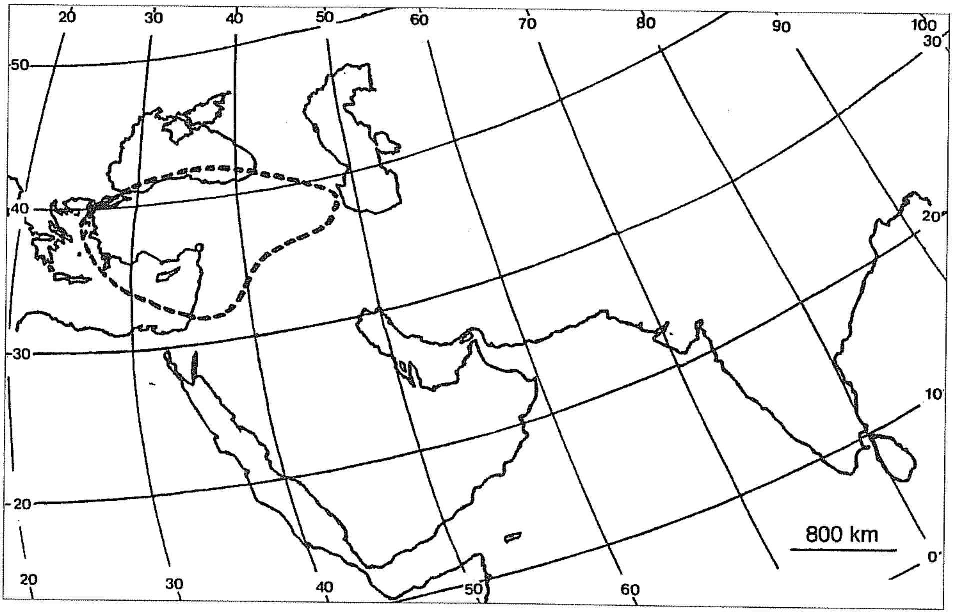

Fig. 6 - Distribution pattern of Syro-Anatolian tenebrionid species.

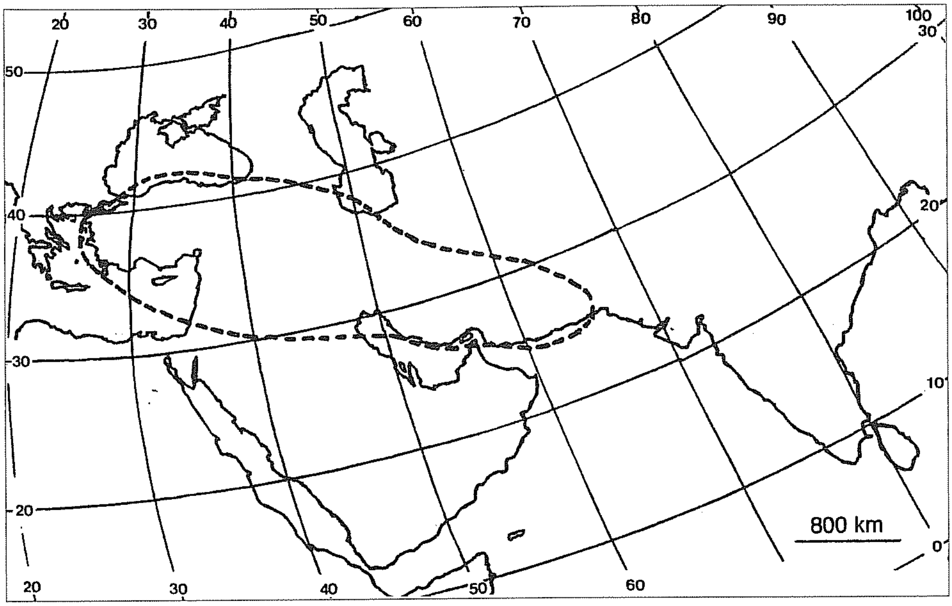

Fig. 7 - Distribution pattern of Irano-Anatolian tenebrionid species.

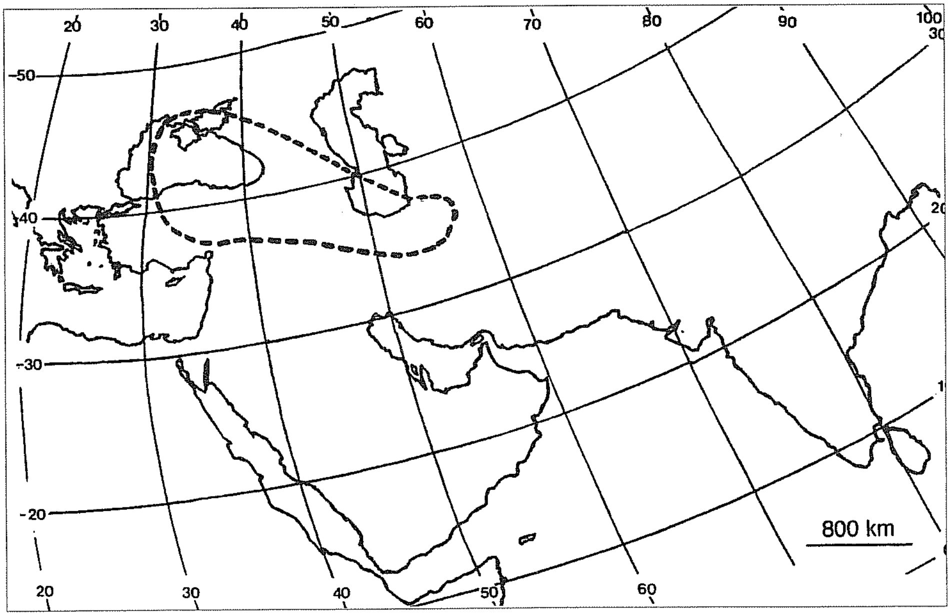

Fig. 8 - Distribution pattern of Ponto-Caspian tenebrionid species.

3.3. Distribution patterns within the Anatolian peninsula

A typical target of descriptive biogeography is to identify faunal similarity or discontinuities among areas. The distribution of the tribe Pimeliini within Turkey is sufficiently known to explore faunal affinities among regions. For this analysis I used the natural regions reported by Cook (1997) (Fig. 9). The occurrence of each taxon in each division is given in Tab. I. Due to the regional approach, in this analysis I have distinguished in the *P. subglobosa*-group three populations morphologically well characterized and referable to the following taxa: "*testudo*" Kraatz (Central Anatolia), "*polita*" Solier (West Anatolia) and "*euboica*" Boieldieu (West Anatolia). A possible new taxon, strictly related to *P. subglobosa*-group, was also included. As no species was recorded from the region 6, this region was omitted.

I compared pimeliine faunal similarity among regions by cluster analysis and multidimensional scaling using STATISTICA (4.5) software. Two cluster analyses were performed using different amalgamation rules. For a first cluster analysis, a joining (tree clustering) method was used with Ward's method as amalgamation rule and Euclidean Distance measure between groups. Another cluster analysis was performed using Complete Linkage and Euclidean Distances measure. Ward's methods is regarded as the clustering method with the best overall performance by Fraire (1994: 90), while the Complete linkage is suggested for qualitative data by Fabbris (1997: 334). A multidimensional scaling based on a matrix of Euclidean Distance measure was performed using two and three dimensions.

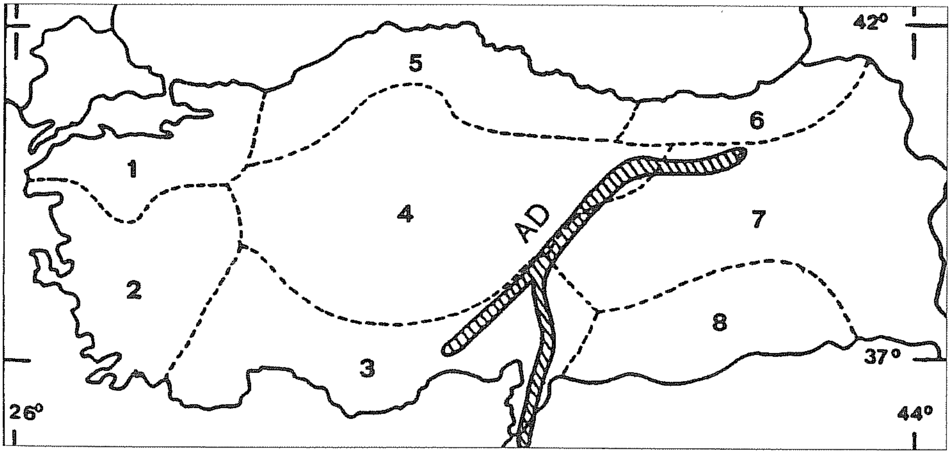

Fig. 9 - Map showing the Anatolian Diagonal (AD) and the subdivisions of regions used in this study. 1. Marmara, including European Turkey, 2. Aegean, 3. Mediterranean, 4. Central Anatolia, 5. West and Central Black Sea, 6. Eastern Black Sea, 7. Eastern Anatolia, 8. Southeast Anatolia.

Tab. I - Regional distribution of the Anatolian Pimeliini. Subdivisions of regions as in Fig. 9: 1. Marmara, including European Turkey, 2. Aegean, 3. Mediterranean, 4. Central Anatolia, 5. West and Central Black Sea, 6. Eastern Black Sea, 7. Eastern Anatolia, 8. Southeast Anatolia.

	1	2	3	4	5	6	7	8
Graecopachys quadricollis (Brullé, 1832)	0	1	1	1	0	0	0	0
Pachyscelis musiva (Ménétriés, 1832)	0	0	0	0	0	0	1	0
Pachyscelis villosa (Drapiez, 1820)	1	1	1	1	0	0	0	0
Pimelia akbesiana Fairmaire, 1884	1*	1	1	1	0	0	0	0
Pimelia bajula Klug, 1830	0	0	1	0	0	0	0	1
Pimelia dubia Faldermann, 1837	0	0	0	0	0	0	1	0
Pimelia timarchoides Ménétriés, 1832	0	0	0	1	1	0	0	0
Pimelia repleta Reitter, 1915	0	0	0	0	0	0	1	0
Pimelia robusta Kraatz, 1865	0	0	0	0	1	0	1	1
Pimelia subglobosa Pallas, 1781 group: **P.** cf. **euboica** Boieldieu, 1865	1	1	0	0	0	0	0	0
Pimelia subglobosa group: **P.** cf. **polita** Solier, 1836	1	1	0	0	0	0	0	0
Pimelia subglobosa group: **P.** cf. **testudo** Kraatz, 1865	1	1	1	1	1	0	0	0
Pimelia subglobosa group: Malatya population	0	0	0	0	0	0	1	0
Pimelia werneri (Ganglbauer, 1905)	0	0	0	1	0	0	1	0
Sternoplax nicomedia (Reitter, 1908)	0	0	0	0	1	0	0	0
Trachyderma philistina Reiche and Saulcy, 1857	0	0	1	0	0	0	1	0
Trachyderma setosa (Fischer, 1832)	0	0	0	0	0	0	1	0

As a rule (Figs 10-11), regions 1 and 2 clustered at low distance. The region 3 clustered with 4. The groups 1-2 and 3-4 were included in the same cluster. By contrast, 5 and 8 were grouped in a well separated cluster. Using Ward's method, 7 clustered with 5+8, while the Complete linkage separated 7 from all the other regions. As a whole, cluster analysis showed a clear faunal breakdown between North-Eastern and West-Central Anatolia. Multidimensional scaling (Figs. 12-13) gave similar results, also confirming the separate position of 7 from the remaining regions. Comparing distributions of Turkish Pimeliini (cf. Leo and Fattorini, 2000) with their chorotypes, we can see that eastern areas are mainly characterized by species that have "Irano-Turanian" distributions (*i.e.*, Turanian and Turanian Mediterranean species, or South West Asiatic species with Irano-Anatolian distribution) or by endemic species that, according to their phylogenetic relationships, can be referred to such distributions.

The occurrence in Anatolia of species with "Irano-Turanian" distribution is well known in several animal groups as a result of Pleistocene and present climatic conditions. Eig (1931-32, cited after Fishelson, 1987) was the first to analyze and compare the phytogeographical and climatic divisions of the Middle East and to establish borders for the following ecological provinces: the Eurosiberian province, the Mediterranean province, the Saharo-Sindian province, the Irano-Turanian province and the Sudano-Deccanian (Ethiopian) province. In the Anatolian peninsula, the Mediterranean, the Eurosiberian, and the Irano-Turanian provinces occur.

In fact, on the north side of the Anatolian peninsula there is heavy rainfall, sometimes throughout the year, which supports lush forests (Eurosiberian province). By contrast, to the west and south the climate is Mediterranean, with

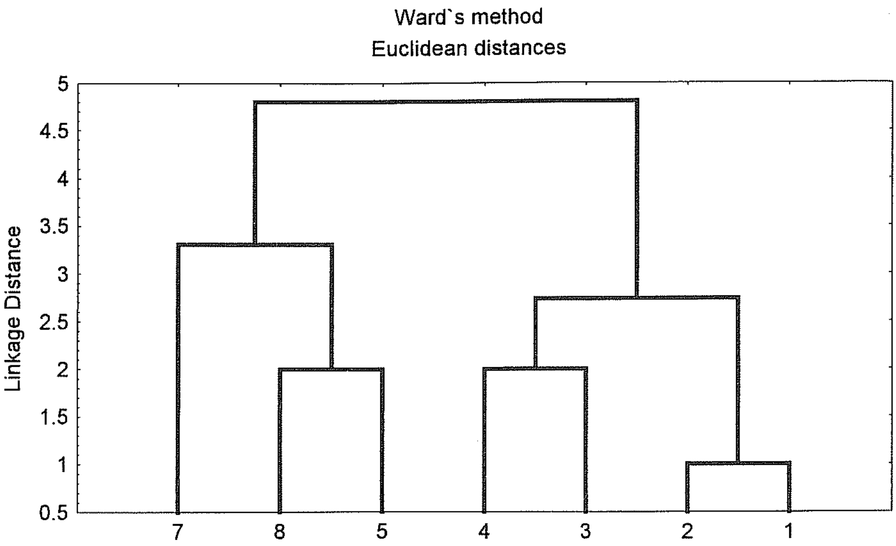

Fig. 10 - Cluster analysis of Anatolian regions using presence/absence data of Tab. I. Linkage rule: Ward's method. Distance: Euclidean distance.

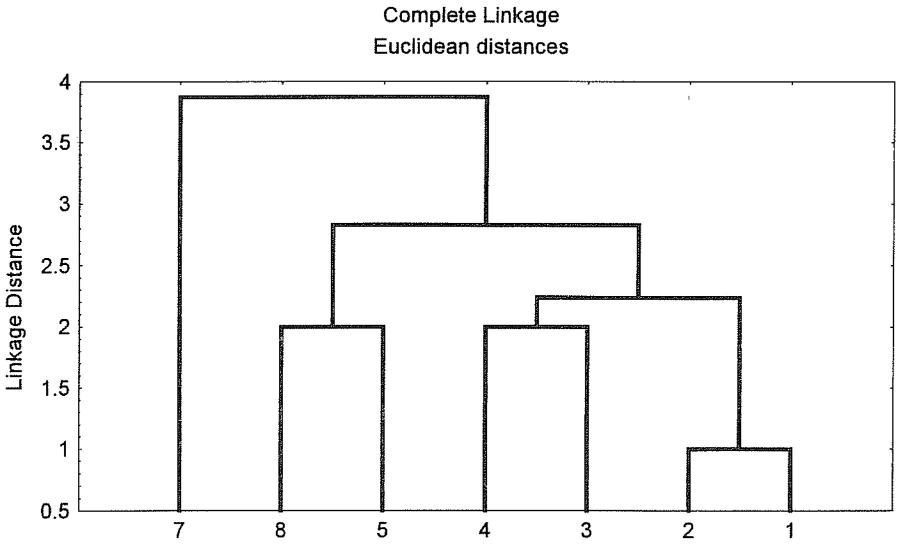

Fig. 11 - Cluster analysis of Anatolian regions using presence/absence data of Tab. I. Linkage rule: Complete linkage. Distance: Euclidean distance.

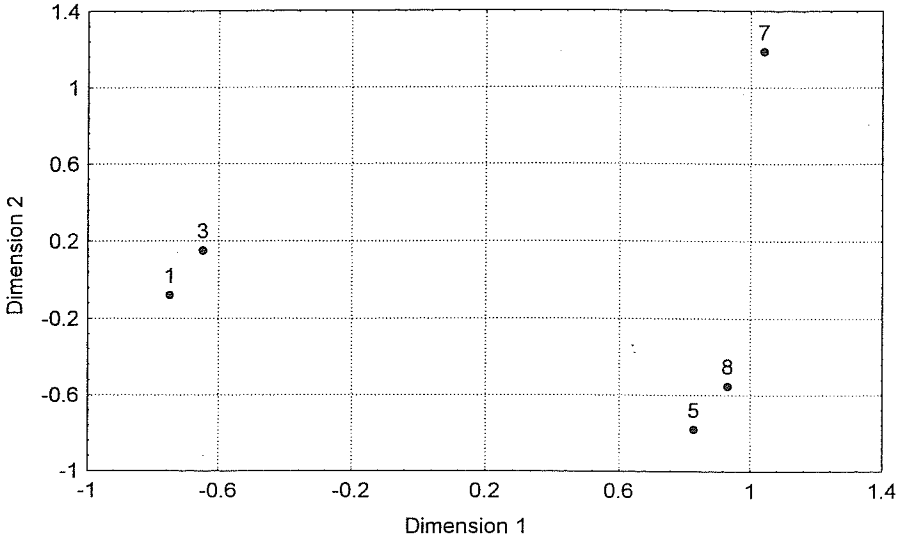

Fig. 12 - Multidimensional scaling of faunal similarity (Euclidean distance) among Anatolian regions. 2 Dimensions, Gutman-Linoges method. Last iteration computed: 185, best iteration: 100. D-star: Raw stress = 0.00124, D-hot: Raw stress = 0.00060. Alienation = 0.00503, Stress = 0.00349.

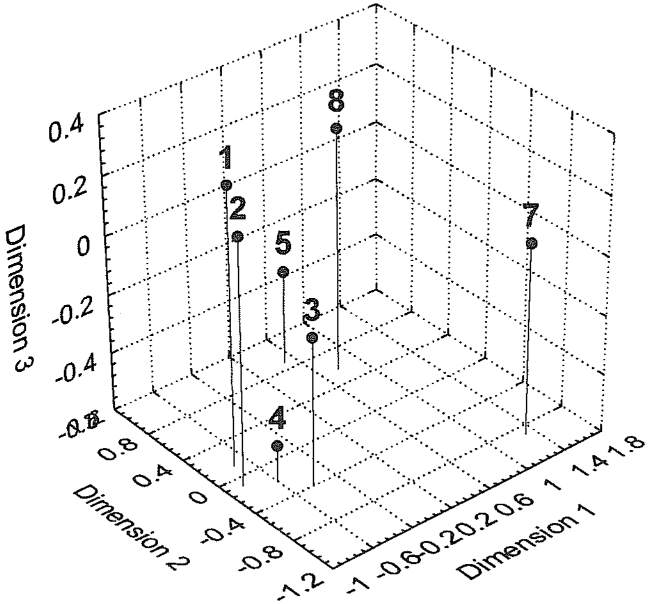

Fig. 13 - Multidimensional scaling of faunal similarity (Euclidean distance) among Anatolian regions. 3 Dimensions, Gutman-Linoges method. Last iteration computed: 259, best iteration: 100. D-star: Raw stress = 0.00068, D-hot: Raw stress = 0.00002. Alienation = 0.00118, Stress = 0.00067.

cool damp winters and hot, dry summers, but with damper and more extreme conditions taking over as the ground rises inland. Finally, conditions in the Central plateau can be severe, with very hot arid summers and icy winters.

Cluster analysis largely fits these subdivisions. However, Central Anatolia (region 4) clustered with "Mediterranean areas" (1, 2, 3). This is probably due to the transition character of its fauna, which includes both Irano-Turanian and Mediterranean elements (Leo and Fattorini, 2000).

Also, presently East Mediterranean species occurring in Central Anatolia could be Irano-Turanian elements in origin. For example, the subgenus *Camphonota*, which has a mainly East Mediterranean distribution with a Turanian penetration towards east, includes in Anatolia both species distributed in the Irano-Turanian province and species occurring in the Mediterranean province.

On the other hand, post-Pleistocene aridification, by climatic changes and human occupation (Butzer, 1978; Erinç, 1978), could have played an important role in determining present distribution of Irano-Turanian elements in Central Anatolia. According to Kosswig (1972), the large majority of pretended "Irano-Turanian" species are, in fact, elements secondarily adapted to a life in regions merely steppified by men, while true elements of an eremic fauna (Irano-Turanian or Saharo-Sindian) are late invaders in Anatolia, prevalently restricted to its eastern part.

3.4. The eastern Anatolian mountains as a filter

Unfortunately, the vertical distribution of Anatolian Pimeliinae is very poorly known. However, some detailed data concerning the vertical distribution of the tribe Pimeliini are available (Leo and Fattorini, 2000). On the basis of these data, we can see (Figs 14-16) that: (i) *P. villosa* and *P. bajula* are generally distributed from about 50 to about 1000 m; (ii) *P. subglobosa*-group and *P. akbesiana* are generally distributed from about 500 to about 1500-2000 m; (iii) *P. timarchoides* is apparently distributed from about 1100 to about 2000 m; (iv) *P. dubia* (1900-2000 m) and *P. musiva* (2200-2300 m) are distributed about 2000 m. As a whole, species which can be related to the East Mediterranean chorotype or to the Irano-Anatolian distribution type of the South West Asiatic chorotype, such as *P. villosa*, *P. subglobosa*-group, *P. akbesiana*, *P. timarchoides* and *P. bajula*, show a vertical distribution principally ranging between 50 and 2000 m, while *P. dubia* (a Turanian species) and *P. musiva* (a South West Asiatic species with a north Irano-Anatolian distribution) have a vertical distribution restricted to high altitude areas (about 2000 m). Interestingly, among the species generally distributed under 2000 m, *P. akbesiana*, *P. timarchoides* and *P. subglobosa*-group, which are referred to the East Mediterranean chorotype but which could be derived from an Irano-Turanian ancestor (cf. Leo and Fattorini, 2000), show the highest distribution range.

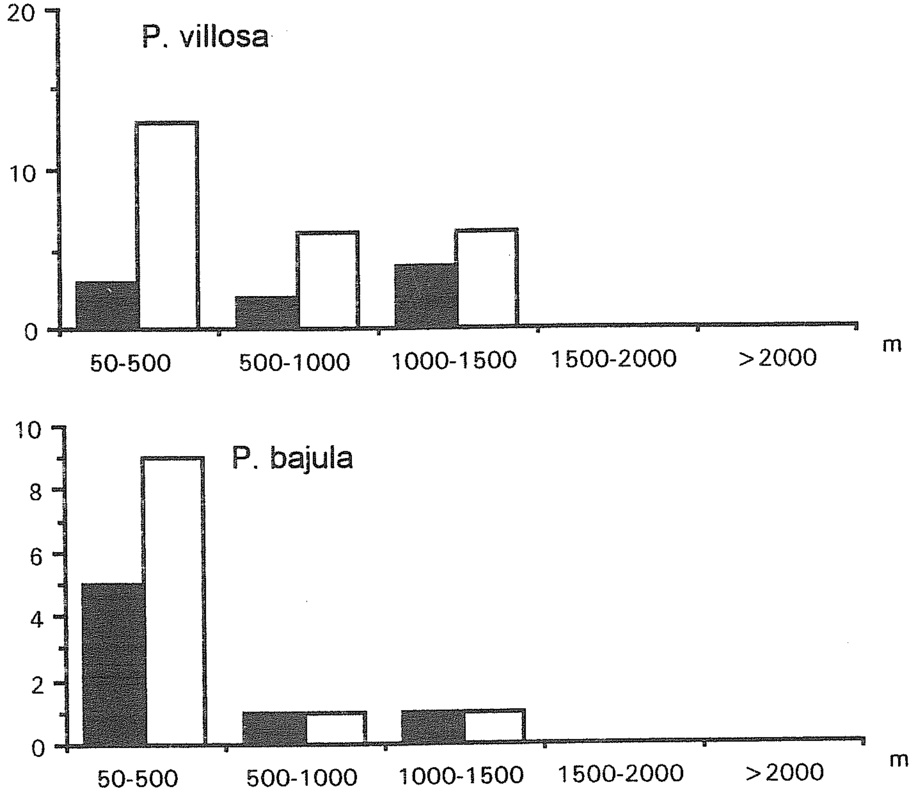

Fig. 14 - Vertical distribution of *Pachyscelis villosa* and *Pimelia bajula*. Data are based only on specimens examined by Leo and Fattorini (2000). Data concerning specimens bearing labels with too large altitude range specified were omitted. Black: numbers of stations; white: number of specimens.

These data suggest an important role, in past and probably also present times, of the high altitude areas as a biogeographical filter (*i.e.*, a barrier that selectively limits the intergradation between biota), connecting the easternmost and the Central Anatolian areas with the Irano-Turanian region on one side, and separating them from the Mediterranean areas on the other. Indeed, the Irano-Turanian influence seems to be greatest in Eastern Anatolia, where high altitude mountains predominate, while the Mediterranean influence is greatest in the south and west Anatolian chains. The Central plateau shows a transitional character, allowing the overlap of Turanian and Mediterranean elements.

From a more general point of view, there is a congruence among vertical distribution, distribution in biogeographical provinces and general chorotypes. As a whole, species referable to the East Mediterranean chorotype or to the southern part of the Irano-Anatolian distribution type of the SW Asiatic chorotype

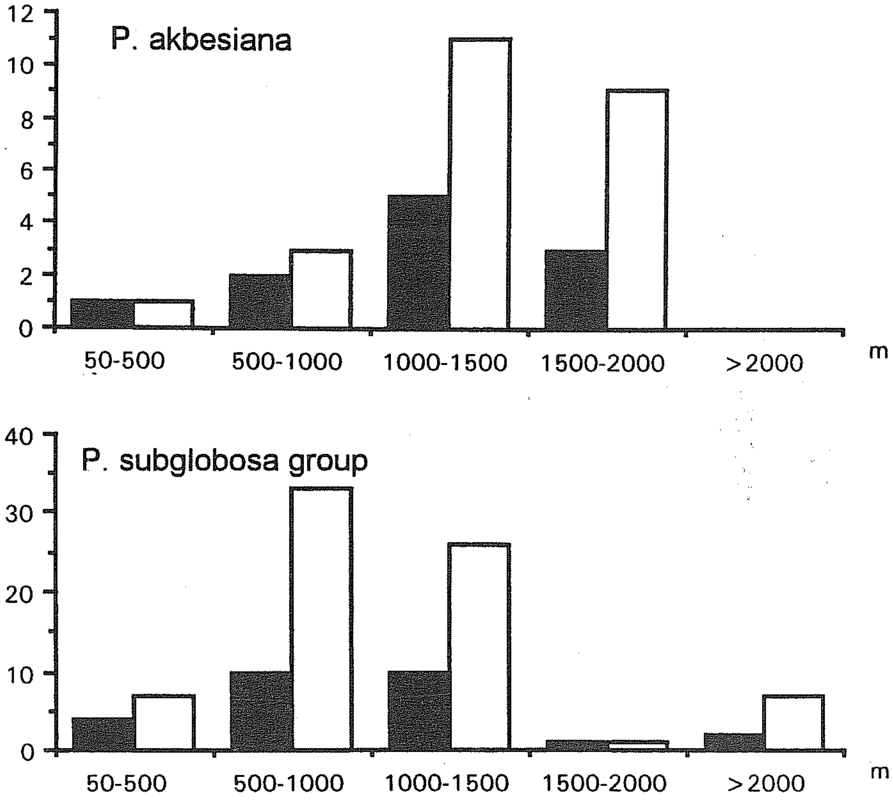

Fig. 15 - Vertical distribution of *Pimelia akbesiana* and *P. subglobosa*-group. Data are based only on specimens examined by Leo and Fattorini (2000). Data concerning specimens bearing labels with too large altitude range specified were omitted. Black: numbers of stations; white: number of specimens.

(such as *P. villosa*, *P. subglobosa*-group, *P. akbesiana*, *P. timarchoides*, and *P. bajula*) are mainly distributed within the Mediterranean province under 2000 m, while "Irano-Turanian" species (such as *P. dubia* and *P. musiva*), are distributed in the Irano-Turanian province about 2000 m and more. This congruence supports the idea that the east Anatolian mountain areas are a filter, which connects the east Anatolian fauna with the Irano-Turanian fauna, while the Central Anatolian plateau seems to have a transitional character between an Irano-Turanian and a more typical Mediterranean fauna.

Interestingly, some endemics are known from both the eastern mountains (*e.g.*, *S. nicomedia*, *P. robusta* and *P. repleta*) and the Central plateau (*P. akbesiana*, *P. timarchoides*, and *P. werneri*). In fact, as filters are basically areas where species range boundaries interfere, endemics should be rare (Por, 1987). However, the action of the Anatolian filter, which probably was functioning from Pleistocene, was likely

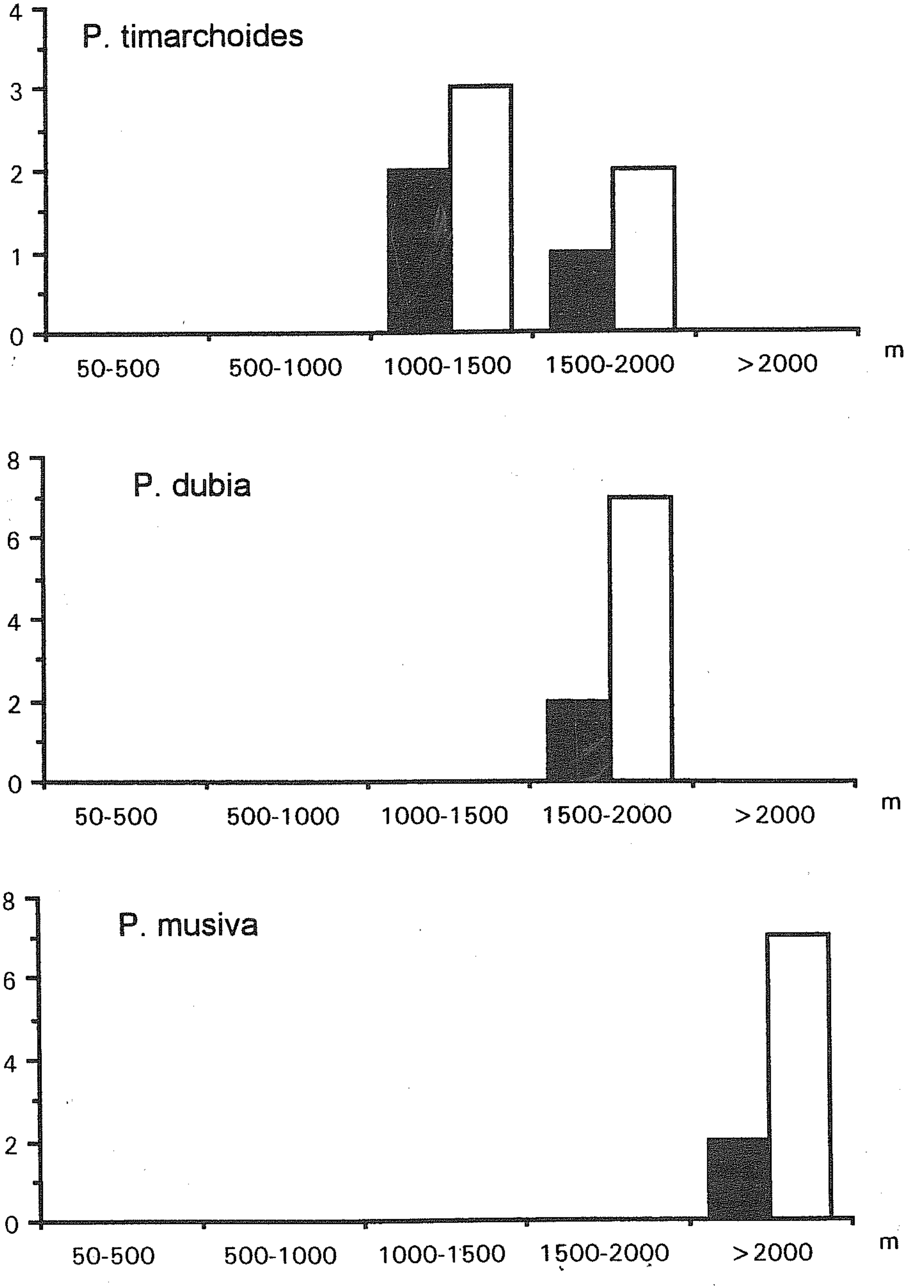

Fig. 16 - Vertical distribution of *Pimelia timarchoides*, *P. dubia* and *Pachyscelis musiva*. Data are based only on specimens examined by Leo and Fattorini (2000). Data concerning specimens bearing labels with too large altitude range specified were omitted. Black: numbers of stations; white: number of specimens.

periodically modified in accordance with climatic changes (cf. Brice, 1978; Wolfart, 1987; Wagener, 1995 for references on Pleistocene climatic changes). In fact, traces of past glaciations are widespread in the east of the region and the movement of floral belts was likely extensive during Pleistocene (*e.g.*, Erinç, 1978; Cook, 1997). The environmental conditions of Anatolia in the Ice Age were presumably characterized by a cold and dry climate with steppe and tundra, while in the Early Holocene the climate was warmer and moister, with colonization of forests; finally, an increasing Holocene aridification was caused by climatic changes and human disturbance (Butzer, 1978). Probably, the penetrability of this filter was periodically modified during the Pleistocene, and some species could have been isolated within the filter area, because some biotopes could have played a role of refuges in glacial phases. Thus, ancestral populations of Irano-Turanian elements which have reached (at different times) this area, could have been divided into various populations during glacial phases. However, phylogenetic studies are needed to test such models.

3.5. Dispersal in Anatolian Pimeliini

According to dispersal theories, all species have a center of origin from which they disperse to assume their present distribution, even if disjunct. In this sense, the word "dispersal" refers to a process of extension of range across a barrier. Since Darwin, the center-of-origin-dispersal model became the ruling theory in historical biogeography, and various biogeographers proposed different criteria to identify centers of origin (see Brown and Gibson, 1983 for a brief review). According to some authors, centers of origin are where new, evolutionarily more successful forms arose and eventually supplanted the original ones, forcing them to peripheral habitats. Thus, the center of origin is where the derived forms reside. However, not necessarily older taxa are forced to extend their range. In contrast, some authors claimed that an ancestral population remains at or near the point of origin and derived forms extend outwards. According to this criterion, the center of origin is where the primitive forms live today. However, primitive forms often survive in isolated regions, also located far from their original ranges (relict distributions). Therefore, primitive forms, even if not forced to extent their range, could have current distributions very different from the original ones. Based on diversity, some authors claimed that the center of origin should be located where the greatest number of taxa of a given group resides, because the number of species is greater where speciation occurred from most time. However, this is invalid if the majority of forms inhabits a region of secondary radiation, and some authors claimed that the center of origin contains only few taxa. Finally, both panbiogeographers and some vicariance biogeographers (*e.g.*, Croizat et al., 1974) warmly deny the concept of center of origin because its recognition is a very difficult (and sometimes insoluble) problem. However, difficulty in recognition does not mean inconsistency. In fact, "if evolution takes place, it is unlikely that any new taxon will appear at the same time over the whole of the range of its ancestor [...]. Instead, it will appear in one area, to the environment of which it is particularly adapted, and spread from there as and when further evolutionary, environmental or plate-tectonic change permits" (Cox, 1998: 821).

On the other hand, vicariance biogeographers warmly criticized dispersal models. According to the theory of the vicariance biogeography, the distributions of taxonomic groups are determined by a splitting in the range of previously widespread taxon (a process named "vicariance"). Of course, to become widespread in the first place, a species must extent its range from the center of origin. The question is if species achieve widespread distributions only in the absence of barriers, resulting in disjunct distributions when this continuous range is divided by vicariance events, or if they are able to across barriers, resulting in disjunct distributions without vicariance. Dispersal biogeographers allow that dispersal (in the sense reported above) takes place in many cases. By contrast, vicariance biogeographers allow that some dispersal across barriers does occur, but feel that it is a relatively rare biogeographical process. Therefore, vicariance seems to be opposite to dispersal. In actuality, either explanation might be correct for different groups or for different biogeographical events of a given group (*e.g.*, Noonan, 1979).

As to Pimeliinae, the center of origin of the tribe Pimeliini, and especially that of the genus *Pimelia*, was the subject of a number of papers by Kwieton.

Initially, Kwieton (1977a: 4, 5) postulated that the genus *Pimelia* arose in a region between Lybia and Mesopotamia. Afterwards, Kwieton (1977c: 581) placed the center of origin of the genus *Pimelia* within a "Sumerian-Iranian" region. Finally, Kwieton (1981a: 4) decided that the whole tribe Pimeliini arose in the Iranian region and extended its range according to four routes: (i) Turanian and Central Asia; (ii) India; (iii) Anatolia and Aegean area; (iv) Mesopotamia, Arabia, Egypt; Mediterranean; Sahel; East Africa. According to Kwieton (1986), nearly all the genera of Pimeliini inhabiting Anatolia reached this area from Iran. The genus *Graecopachys* is regarded by Kwieton (1978, 1986) as a Mediterranean element in origin, which however has its relative (the genus *Afghanopachys* Kwieton, 1978) in Afghanistan.

According to Kwieton (1978), the most primitive groups related to the genus *Pimelia* (*i.e.*, the "pachysceloide" groups) were forced to extend their range from their center of origin as a result of the competition with more advanced taxa, *i.e.*, the species of the genus *Pimelia*, which also arose in the Iranian area and then extended their distribution. If I have correctly interpreted Kwieton's ideas, the most primitive "pachysceloide" lines are restricted to peripheral areas, while the most primitive *Pimelia* species are in the center of origin.

However, these hypotheses are based on unclearly elucidated phylogenetic and biogeographical assumptions; in fact, there is no data to support that the "pachysceloide" lineage is the sister group of the genus *Pimelia*, and no distribution model can be claimed to state that Pimeliini actually arose in the Iranian area.

If the center of origin of a taxon should be identified as the area that harbors the maximum diversity at the genus level (cf. La Greca, 1996), the center of Pimeliini should be identified in the Turanian area. Interestingly, the genera inhabiting Iran and Central Asia also occur in the Turanian area. Thus, at the genus level, all these areas could be grouped, and the center of origin of Pimeliini could be placed within this large Palaearctic area. Therefore, at least some genera could have reached the Anatolian peninsula from a Turanian (or Central Asiatic) area. If we assume that the center of origin of a genus is the area with highest diversity, the genus *Pimelia* should have reached Anatolia from some African area via Arabia. However, all these hypotheses are merely speculative, because phylogenetic relationships among Pimeliini are unknown.

To be quite honest, we must admit that (even though a center of origin existed and it could be recognized) because of lack of information on the Pimeliini phylogeny we are unable to postulate any hypothetical center for Pimeliini. Likewise, we are unable to postulate a center of origin of the genus *Pimelia*, as well as its Anatolian colonization routes.

3.6. Vicariance in Anatolian Pimeliinae

Vicariance biogeography and panbiogeography are often confused: in fact, they are based on very different methodological and theoretical standpoints. The panbiogeography approach was proposed by Léon Croizat (1958) as an empirical way in contrast to the *a priori* center-of-origin theory of the biogeography classical school. According to Croizat (1982), panbiogeography is a method, not a theory. However, as the panbiogeography method lies on some theoretical assumptions and leads to theoretical consequences, it is difficult to separate methodological and theoretical aspects.

Connecting by lines (individual tracks) the distributions of hundreds of plant and animal species, Croizat found that species with quite different dispersal properties and colonizing abilities had the same pattern of geographical distribution (see Croizat, 1982 and Croizat et al., 1974 for other references). He termed these shared geographical distributions generalized or standard tracks. According to Croizat, standard tracks are the present distributions of a set of ancestral distributions which were modified by fragmentation processes. Recognition of general tracks is the true method to formulate biogeographical hypotheses, while classical biogeographers use a priori hypotheses to explain individual cases (see Zunino and Zullini, 1995 for a review of techniques used to trace tracks). Because fragmentation processes, presently known as vicariance, play an important role in panbiogeography, vicariance biogeography and panbiogeography were confused.

At the beginning, Croizat himself (Croizat et al., 1974) collaborated with vicariance biogeographers, but later he disagreed with them (Croizat, 1982). In fact, many methodological and theoretical differences can be recognized between Croizat's panbiogeography and vicariance biogeography.

Croizat rejected dispersal as possible mechanism under any circumstance, while both vicariance biogeographers and most of those who employ the generalized track techniques accept that dispersal may also take place. However, some radical panbiogeographers still seem to be extremely reluctant to accept dispersal (cf. Cox, 1998 for references and criticism). Croizat and his followers avoid any discussion of centers of origin and they refer to this disparagingly as "Darwinian concept". At the beginning, also some vicariance biogeographers rejected this concept (cf. Croizat et al., 1974), but most biogeographers today accept its reality.

Even after Wegener's theory became widely accepted, Croizat for a long time refused to accept that theory, preferring other mechanisms (cf. Cox, 1998). In contrast, vicariance biogeographers commonly refer to Wegener's continental drift. Also, Croizat did not use ancient climatic changes as a possible explanation of disjunct patterns of distribution, while according to the vicariance biogeographers climatic changes could have played an important role in vicariance events.

Vicariance biogeography is a biogeographical theory based strictly on the phylogenetic reconstruction of sister taxa, while panbiogeography is a method based on the identification of generalized tracks. As vicariance biogeography is based on vicariant sister groups, the development of numerical cladistic approaches gave a vigorous impulse to vicariance biogeographers (see Hovenkamp, 1997; Biondi, 1998 for references). Notice that Croizat (1982) despised cladistics.

As to Pimeliini, the cladistic reconstruction proposed by Doyen (1993) grouped this tribe with Platyopini. Pimeliini and Platyopini share all essential features, but the phylogenetic relationships between these two groups are unclear. According to Doyen (1993: 495), a more broadly based comparison of pimeliine genera might show that the Platyopini comprise the primitive sister to other Pimeliini, even if the present data suggest that Platyopini are relatively derived.

Platyopini are mostly distributed in the Turanian region, but various species inhabit other areas and their general distribution largely overlaps that of Pimeliini. Therefore, based on present distributions, no vicariance models seem to be related to their phylogeny.

As far as the Anatolian Pimeliini are concerned, no genera inhabiting the Anatolian peninsula show a disjunct distribution; likewise, except for endemics, Anatolia harbors only species that occur also in the neighboring countries. Therefore, no vicariance models seem to be involved. In fact, from a vicariance standpoint, "widespread taxa are uninformative since they could be the result of species not having responded to vicariance events or could be due to various combination of dispersal" (Noonan, 1988: 367), even if widespread taxa could be used in some cladistically founded biogeographical analyses (cf. Hovenkamp, 1997; Biondi, 1988 and references therein). Of course, vicariance models could be proposed for endemic Pimeliini that have their relatives in other areas, but lack of phylogenetic analyses makes very difficult to relate biogeographical patterns with vicariance events. More in general, because of lack of information on the phylogeny of the pimeliine tribes, it is impossible to identify with certainty any vicariance events in the Anatolian Pimeliinae. The following examples may be cited (palaeogeografic configurations follow Oosterbroek and Arntzen, 1992).

According to Kwieton (1980b), the genus *Afghanopachys*, which inhabits Afghanistan, is the sister group of the genus *Graecopachys*. If this reconstruction is true, one may relate this present distribution to a vicariance event: separation of west Asia Minor and Balkan areas from East Asia Minor (17-13 MYBP). However, lack of reliable phylogenetic reconstruction makes difficult to prove such model. According to Schawaller (1987), *Akis elongata* should be related to *A. bacarozzo* (Shrank, 1786) and *A. subterranea* Solier, 1836, but no cladistical analyses were provided by this author. If *Akis elongata* is the sister species of *A. bacarozzo* and/or *A. subterranea* (both restricted to West Mediterranean areas), the distribution ranges of these species could be explained by vicariant events. In particular, *A. bacarozzo* is distributed in Southern France, Corsica, Sardinia, the Balearic Islands, and Northern and Central Italy, while *A. subterranea* occurs in Sicily and Southern Italy. These distributions suggest that *A. bacarozzo* originated before the disjunction of the Balearic Islands and the Sardo-Corsian microplate, between Upper Oligocene and Lower Miocene (about 23 MYBP). In this case, the vicariance between West Mediterranean (*bacarozzo+subterranea*) and East Mediterranean (*elongata*) taxa could be correlated with the final structuring of the Alps and the Neo-Pyrenees (about 10 MYBP). However, such distribution ranges could be reached also during the Messinian salinity crisis and lack of cladrograms thwarts any vicariance approach to these transmediterranean disjunct distributions.

At the species level, interesting vicariant distributions can be observed in tenebrionid species distributed in Anatolia and in the south Aegean arch of islands. Representative of these distributions are, among others, *Stenosis cretica, Erodius orientalis* and *Tentyria rotundata.*

S. cretica includes two subspecies: the typical form is endemic to Crete, while ssp. *shusteri* is known from Anatolia. *E. orientalis* includes a number of subspecies: the nominal form is distributed in Attica, Peloponnese and on Tinos; ssp. *oblongus* in Anatolia, on Anatolian islands, on the Sporades and Crete; ssp. *brevicostatus* on the Cyclades, the Dodecanese islands and Crete; ssp. *boyeri* is endemic to Crete. Finally, *T. rodundata* includes many subspecies grouped by Koch (1948) into two Rassenkreis: the *rotundata* Rassenkreis (ssp. *rotundata*, endemic to Greece; ssp. *orbicollis* Solier, 1835, distributed in Greece and on the Northern Cyclades; ssp.

jonica Koch, 1948, endemic to Ionian islands, and ssp. *sulcatipennis* Shuster, 1936, distributed on the Southern Cyclades), and the *angulata* Rassenkreis (ssp. *angulata* Brullé, 1832, distributed in the Balkan peninsula and on Thasos; ssp. *paganettii* Shuster, 1915, endemic to Crete; ssp. *mittrei* Solier, 1835, distributed on the Sporades and Anatolian islands; ssp. *winkleri* Koch, 1936, ssp. *daghestris* Koch, 1948, and ssp. *convexipennis* Koch, 1948, distributed in Anatolia).

From a panbiogeographical standpoint, the vicariant distributions of *S. cretica cretica* and *S. cretica shusteri*, the distribution of *E. orientalis oblongus* and that of *T. rotundata mittrei* and its relatives, could be regarded as individual tracks joining Anatolia, the Sporades and Crete. These coincident individual tracks suggest the occurrence of a generalized track joining all these areas. In fact, a number of papers have dealt with the function of the South Aegean arch of islands as stepping stones for the colonization of the islands themselves and for adjacent continental regions of Peloponnese and Asia Minor. It has been suggested that fauna and flora of Crete come mainly from the Asia Minor via Rhodes and Karpathos, and some authors concluded that the land connection with Asia Minor was interrupted much later than that with Peloponnese (cf. Malicky, 1985 for a brief review and contrasting opinions). In fact, a generalized track joining Crete, the Sporades and Asia Minor could be due to both ancient (Miocene) land connections and recent dispersal. However, recent dispersal is unlikely, these species being apterous. Likewise, Pleistocene land connections should be excluded, because Crete was never connected with continental areas after Miocene, and palaeogeographical studies (*e.g.*, Dermitzakis, 1990) show that during the Pliocene Crete was mostly submerged and in the Pleistocene it was an island. Therefore, Cretean endemics should be of Messinian (Miocene) origin. The low morphological distance between vicariant tenebrionid taxa suggests a more recent isolation for these populations, but it is obviously possible an ancient (Miocene) isolation without morphological divergence.

3.7. Dispersal, vicariance and the so-called "Anatolian diagonal"

According to Davis (1971), the Anatolian peninsula is divided into two parts with different floral compositions by a mountain range, named the "Anatolian Diagonal", which extends from the regions of Bayburt and the province of Erzurum in the northeast towards the provinces of Kayseri and Kahramanmaras (Anti-Taurus) in the southwest. Here it divides and one branch continues further southwest towards Bulgar Dagh in the Cilician Taurus. The other runs more southwards through the province Hatay in the direction of the Lebanon mountains. The area east and southeast of this biological break belongs to the Irano-Turanian phytogeographical region. West and northwest of the "Diagonal", the Xero-Euxine and Mediterranean regions prevail.

Interestingly, cluster analysis of the Anatolian regions based on Pimeliini (Figs 9-10) showed a faunal breakdown between west and east Anatolia roughly consistent with the "Diagonal".

Comparing distribution patterns of Pimeliini with the so called "Anatolian Diagonal", some observations can be made.

Most of the Anatolian Pimeliini have been apparently affected by this biogeographical break. Several species have the main part of their ranges west or east of this "Diagonal". *P. villosa*, *G. quadricollis*, *P. subglobosa*-group, *P. timarchoides*, *P. akbesiana*, and *P. werneri* are West Anatolian species, while *T. setosa*, *P. musiva*, *P. repleta*, and *P. dubia* are East Anatolian species. Only few species (namely *P. bajula*, *P. robusta* and partly *T. philistina*) are distributed on both sides of the "Diagonal". As the "Diagonal" is an old event, these distribution patterns suggest different possible biogeographical scenarios. First, the subgenus *Camphonota* is divided into an eastern species (*P. repleta*) and a group of western species (*P. subglobosa*-group, *P. timarchoides*, and *P. akbesiana*), as a possible result of a vicariance event. Likewise, in the genus *Pachyscelis*, we can find an East Mediterranean species with Aegean distribution (*P. villosa*), restricted to western areas, and a South West Asiatic species with Irano-Anatolian distribution (*P. musiva*) restricted to eastern areas. However, we are unable to state if they are vicariant taxa, or if they dispersed in Anatolia from different ways after the origin of the "Diagonal". Finally, the distributions of *T. philistina*, *P. robusta* and *P. bajula* suggest a dispersion after the origin of the "Diagonal". As to *P. bajula*, this is an element the south Anatolian distribution of which could be related to its general distribution in the Middle East. As to *T. philistina*, its distribution in Anatolia reaches the "Diagonal" from west, but there are too few records to state a general pattern. Finally, the distribustion of *P. robusta* encompasses the Diagonal northward, without crossing it.

3.8. Refuges

The glacial refuge hypothesis is a classical tenet of historical biogeography. As to the Eurasiatic areas, Pleistocene climatic changes have been claimed to explain any type of distribution as a result of dispersal and vicariance events. Refuges can be defined as areas into which populations retreat during periods of unfavorable climates. Populations isolated into refuges, becoming allopatric, may speciate. However, the effects of climate on different animals vary from one group to another. A climate that causes one group to retreat into refuges may simultaneously result in another dispersing out from past refuges: the retreat of populations into refuges is a form of vicariance, while their extension into a broad geographical distribution (also across barriers) is a form of dispersal. During the Ice Ages, some species could have survived only in areas with suitable climatic conditions: thus, northern species were forced to extent southward and southern species were favored in expanding northward, while less vagile species become extinct or were isolated into refugial areas. According to the scholars of the refugial center hypothesis, a number of present distributions are largely dependent on the effects of the Ice Ages. In particular, as the Ice Ages molded entire biotas, an analysis of the distribution pattern of various species could lead to the recognition of last-glacial refugial centers.

For the Anatolian butterflies, Wagener (1995) recognized a great number (10 areas) of possible Pleistocene refuges. On the other hand, Naumann (1987) recognized three main refugial centers for the genus *Zygaeana* (Lepidoptera, Zygaeanidae) within the Anatolian area: Syro-Anatolian, Ponto-Caspian and Iranian. Interestingly, a great number of Pimeliinae show Syro-Anatolian, Ponto-Caspaian and Irano-Anatolian distributions, as defined above. Naumann recognized also a Ponto-Mediterranean subrefuge, and the Anatolian Pimeliinae with Turanian chorotype have actually a Ponto-Mediterranean distribution.

The congruence of distribution areas in species belonging to different taxa suggests the actual occurrence of shared nuclei of distribution. This congruence leads to the assumption that all these species have been greatly influenced by the last glaciation and that in this phase they have been restricted to some refugial centers. However, due to the environmental changes that occurred in the Near East after the Ice Ages (Butzer, 1978; Erinç, 1978), one may also stipulate that these distributions could have been affected by post-Pleistocene events.

In fact, all the areas regarded as refuges are substantially characterized at present by an ecological uniformity. Therefore, it could be not surprising that they harbor species with similar distribution patterns. On the other hand, distributive congruence among taxa with presumably different ecology supports the hypothesis that they share a common history.

However, this congruence could be actually due to different causes. For example, the same area could be inhabited by both heat-loving species, which reached their present restricted distribution as a result of a glacial reduction of their former widespread distribution, and cold-loving species, which reached their present restricted distribution as a result of post-glacial reduction of a Pleistocene more widespread distribution. Thus, the same "refuge" could be a "glacial" refuge for some species, but also an "interglacial" refuge for others.

More information on the ecology and distribution of the various pimeliine species inhabiting the Anatolian peninsula may provide useful data to assess how Ice Age events can have affected their present distributions.

4. CONCLUSIONS

A combination of historical (palaeogeographical and palaeoecological) and contemporary ecological factors seem to have affected the different distribution patterns of Anatolian Pimeliinae, resulting in the present chorological spectrum.

A number of species show distribution patterns referable to "Turanian" chorotypes (TUR, TUE and TEM), in accordance to the occurrence of an Irano-Turanian province in the Anatolian peninsula. The coastal plains of the west and south are eminently suitable for species adapted to Mediterranean conditions. In fact, species with distributions referable to the EME component account for a large proportion of the whole fauna. These distributions are presumably related to a habitat selection towards Mediterranean environments. Among Pimeliini (whose distribution patterns within Anatolia are well known), some species show distribution ranges clearly restricted to the west and south coastal plains, while others seem to be related to the Turanian province. Also, the "Irano-Turanian" species seem to be linked to high altitude areas, suggesting a possible filtering effect of the eastern chains.

Many Anatolian pimeliines occur also in Greece and on various Aegean islands (EME elements with Aegean distribution). The lowering of sea level in the Pleistocene could have played an important role for these elements, allowing a faunal continuity between Greece and Anatolia (Fattorini et al., 1998, 1999b, 2000). Most of these species are apterous and are represented by different subspecies in Anatolia and in the Aegean area (see Appendix 1, and some cases discussed above). These facts make less probable an ancient isolation after Messinian land connections or a recent dispersal by stepping stones (see Fattorini et al., 2000). The lack of Pleistocene connections between Crete and continents, suggests however that the tenebrionid fauna of this island (in particular endemic taxa) could be of Messinian origin.

Pleistocene and post-Pleistocene climatic changes probably affected present distribution patterns of the Anatolian fauna. The geographic range of species distributed from the Turanian area to the Anatolian peninsula (especially the easternmost areas) seems to be congruent with the idea of a Ponto-Caspian refuge, but present ecological conditions or aridification processes (cf. Kosswig, 1972) could be claimed to explain such distribution patterns. In fact, species from north Eurasia should find no barriers to colonization of the north-eastern parts of the Anatolian peninsula. However, it is difficult to state if species with such distribution patterns are actually north elements, which arrived in Anatolian from northern cold steppe or, vice versa, species which reached the Turanian basin from southern areas.

Pleistocene and post-Pleistocene environmental changes may have substantially affected, in different ways, southern species, belonging to various chorotypes, especially EME and SWA ones. Among species with these chorotypes, Syro-Anatolian and Irano-Anatolian distribution types are dominant. Both these distributions could be related to ice refuges, but the post-Pleistocene increasing aridity may have forced some species into such distributions. Also, there is a present ecological continuity between East Anatolia and Iran, as well as between South East Anatolia and Syria.

On the other hand, the low percentage of species largely distributed in Mediterranean or North African areas towards west (MED and NAF chorotypes) supports a substantial isolation of the Anatolian pimeliine fauna from western areas, as also observed by Kwieton (1986a).

Therefore, the Messinian salinity crisis seems to have scarcely favored dispersal or vicariance between West Mediterranean and Anatolian faunas. However, Messinian effects could be actually underestimated, because they may have originated unrecognized sister taxa. In particular, taxa endemic to the Anatolia peninsula could have originated as a result of vicariance between populations isolated by restored sea levels after Messinian conditions. Unfortunately, lack of phylogenetic investigation makes difficult to test such models.

Ball (1975) suggested that all biogeographical studies develop through three stages: descriptive, narrative and analytical. In the descriptive stage the complexities of contemporary distributions are recognized and described, but little effort is made to explain their historical causes. In the narrative stage present distributions are described as patterns and historical factors are claimed to explain them. Such explanations are formed by inductive observations of the distribution patterns. The pages you are reading are of this type. Such explanations can be rational (I hope!), but they are rational only in a retrospective manner, and thus cannot be tested. In other words, they lack predictive power. In the analytical stage, testable propositions are formulated: these propositions (*i.e.*, predictions) are tested against other observations (including experiments) in conjunction with background knowledge, and a preference established between competing hypotheses. To be testable biogeographical studies must be based on carefully hypothesized phylogenies, so that only real evolutionary units are compared.

Unfortunately, lack of phylogenetic information on the Anatolian Pimeliinae makes impossible, today, any testable approach. However, I hope phylogenetic studies will be available in the future and present "narrative" hypotheses will be revised from new points of view.

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REFERENCES

Aldryhim Y.N., Mills C.W. III, Aldawood A.S. 1992 - Ecological distribution and seasonality of darkling beetles (Coleoptera: Tenebrionidae) in the central region of Saudi Arabia. J. Arid Environ., **23**: 415-422.

Ardoin P. 1978 - Contribution a l'etude des *Adesmia* (Coleoptera: Tenebrionidae) du Sinai, d'Israel et de Jordaine. Nouv. Rev. Entomol., **8** (3): 295-313.

Ayal Y., Merkl O. 1994 - Spatial and temporal distribution of tenebrionid species (Coleoptera) in the Negev Highlands, Israel. J. Arid Environ., **27**: 347-361.

Ball I.R. 1975. Nature and formulation of biogeographical hypotheses. Syst. Zool., **24**: 407-430.

Banarescu P. 1977 - Position zoogeographique de l'ichthyofaune d'eau douce d'Asie occidentale. Cymbium, 3e Série, **2**: 35-55.

Baran I. 1976 - Türkiye yilanlarinin taksonomik revizyonu ve cografi dagilislari, Proie No: TBAG-53. Alexander von Humboldt-Stiftung Deutschland. Türkiye Bilimsel ve Teknik Arastirma Kurumu. Matematik, Fiziki ve Biyolojik Bilimler Arastirma Grubu: 177 pp.

Basoglu M., Baran I. 1977 - Türkiye Sürüngenleri. Kisim I. Kaplumbaga ve Kertenkeleler. (The Reptiles of Turkey, Part I. The turtles and lizards). Ege Üniversitesi Fen Fakültesi Kitaplar Serisi No. 76: 1-272.

Basoglu M., Baran I. 1980 - Türkiye Sürüngenleri. Kisim II. Yilanlar. (The Reptiles of Turkey, Part II. The snakes). Ege Üniversitesi Fen Fakültesi Kitaplar Serisi No. 81: 1-218.

Basoglu M., Özeti N. 1973 - Türkiye Amphibileri. (The Amphibians of Turkey). Ege Üniversitesi Fen Fakültesi Kitaplar Serisi No. 50: 1-155.

Biondi M. 1998 - Comparison of some methods for a cladistically founded biogeographical analysis. In: Cristofolini G., Minelli A. (eds), Atti 1° Colloquio Nazionale di Sistematica Cladistica. Verona, 6-7 febbario 1998. Memorie Mus. Civ. Stor. Nat. Verona, 2 serie, Sezione Scienze della Vita, **13**: 9-31.

Brice W.C. (ed.) 1978 - The environmental history of the Near and Middle East since the Last Ice Age. Academic Press, London: 384 pp.

Brown J.H., Gibson A.C. 1983 - Biogeography. The C.V. Mosby Company, St Louis, Toronto, London: 643 pp.

Burakowski B. 1993 - Laboratory methods for rearing soil beetles (Coleoptera). Memorabilia Zool., **46**: 1-66.

Butler M.A. 1949 - Observations on the biology of *Palorus ratzeburgi* Wissman, with comparative notes on Tenebrionidae in general (Coleoptera). Trans. R. Entomol. Soc. Lond., **100**: 249-273.

Butzer K.W. 1978 - The late prehistoric environmental history of the Near East. In: W.C. Brice (ed.), The environmental history of the Near and Middle East since the Last Ice Age. Academic Press, London: 5-12.

Bytinski-Salz H. 1953 - The zoogeography of the ants in the Near East. Istanbul Üniversitesi Fen Fakültesi Mecmuasi, B, **28**: 67-74.

Bytinski-Salz H. 1956 - 1. Coleoptera and Hymenoptera from a journey through Asia Minor. 1. Istanbul Üniversitesi Fen Fakültesi Mecmuasi, B, **31**: 211-229.

Canzoneri S. 1970 - I Tenebrionidae delle Isole Egadi (XXII Contributo allo studio dei Tenebrionidi). Mem. Mus. Civ. Stor. Nat. Verona, **18**: 55-89.

Colombini I., Chelazzi L., Fallaci M., Palesse L. 1994 - Zonation and surface activity of some Tenebrionid beetles living on a Mediterranean sandy beach. J. Arid Environ., **28**: 215-230.

Cook L.M. 1997 - Geographic and ecological patterns in Turkish land snails. J. Biogeogr., **24**: 409-418.

Cox B. 1998 - From generalized tracks to ocean basins- how useful is Panbiogeography? J. Biogeogr., **25**: 831-828.

Croizat L. 1958 - Panbiogeography, vol. 1, vol. 2a, b. Published by the author, Caracas: 1018 pp., 1731 pp.

Croizat L. 1982 - Vicariance/vicariism, panbiogeography, "vicariance biogeography," etc.: a clarification. Syst. Zool., **31** (3): 291-304.

Croizat L., Nelson G., Rosen D.E. 1974 - Centers of origin and related concepts. Syst. Zool., **23**: 265-287.

Daszak P., Cawthraw S. 1991 - A review of the reptiles and amphibians of Turkey, including a literature survey and species checklist. Brit. Herpetol. Soc. Bull., **36**: 14-26.

Davis P.H. 1971 - Distribution patterns in Anatolia with particular reference to endemism. In: Davis P.H., Harper P.C., Hedge I.C. (eds). Plant life of South-West Asia, Edinburgh: 15-27.

De Freina J.J. 1979 - 1. Beitrag zur systematischen Erfaussung der Bombyces- und Sphinges-Fauna Kleinasiens. Atalanta, **10** (3): 175-224.

Dermitzakis, M.D. 1990 - Paleogeography, geodynamic process and event stratigraphy during the late Cenozoic of the Aegean area. Atti Conv. Lincei, **85**: 263-288.

Dettner K. 1987 - Chemosystematics and evolution of beetle chemical defenses. Annu. Rev. Entomol., **32**: 17-48.

Doyen J.T. 1993 - Cladistic relationships among pimeliine Tenebrionidae (Coleoptera). J. New York Entomol. Soc., **101** (4): 443-514.

Doyen J.T., Lawrence J.F. 1979 - Relationships and higher classification of some Tenebrionidae and Zopheridae (Coleoptera). Syst. Entomol., **4**: 337-377.

DOYEN J.T., MATTHEWS E.G., LAWRENCE J.F. 1989 - Classification and annotated checklist of the Australian genera of Tenebrionidae (Coleoptera). Invertebr. Taxon., **3**: 229-60.

DOYEN J.T., ROGERS E. 1984 - Environmental determinants of size variation in *Eusattus muricatus* (Coleoptera: Tenebrionidae). J. Kansas Entomol. Soc., **57** (3): 483-489.

DOYEN J.T., TSCHINKEL W.R. 1982 - Phenetic and cladistic relationships among tenebrionid beetles (Coleoptera). Syst. Entomol., **7**: 127-183.

EISNER T., MEINWALD J. 1966 - Defensive secretions of arthropods. Science, **153**: 1341-1350.

ENDRÖDY-YOUNGA S. 1988 - Revision of the *Anomalipus* Latreille, 1846 (Coleoptera: Tenebrionidae: Platynotini): Transvaal Mus. Monogr., **6**: 129 pp.

ENDRÖDY-YOUNGA S. 1996 - Revision of the tribe Caenocrypticini (Coleoptera: Tenebrionidae: Tentyriinae). Transvaal Mus. Monogr., **11**: 72 pp.

EPPS T.M, BRITTEN H.B., RUST R.W. 1998 - Historical biogeography of *Eusattus muricatus* (Coleoptera: Tenebrionidae) within the Great Basin, western North America. J. Biogeogr., **25**: 957-968.

ERINÇ S. 1978 - Changes in the physical environment in Turkey since the end of the Last Glacial. In: W.C. Brice (ed.), The environmental history of the Near and Middle East since the Last Ice Age. Academic Press, London: 87-110.

ESPAÑOL COLL F. 1943 - Misión Cientifica E. Morales Agacino, Ch. Rungs y B. Zolotarevsky a Ifni y Sáhra Español. Tenebrionidae (Col.) I.a Parte. EOS, **19**: 119-148.

FABBRIS L. 1997 - Statistica multivariata. Analisi esplorativa dei dati. McGraw-Hill, Milano: 437 pp.

FALLACI M., COLOMBINI I., PALESSE L., CHELAZZI L. 1997 - Spatial and temporal strategies in relation to environmental constraints of four tenebrionids inhabiting a Mediterranean coastal dune system. J. Arid Environ., **37**: 45-64.

FARAGALLA A.A. 1999 - Seasonal occurrence and habitat distribution of Tenebrionid beetles (Coleoptera: Tenebrionidae) in Khulais Valley, western Saudi Arabia. Elytron, **12** (1998): 105-112.

FATTORINI S., LEO P., SALVATI S. 1998 - The Aegean Islands as a transition area between Balkans and Anatolia: ecogeographic and historic aspects of the Darkling beetle fauna (Coleoptera, Tenebrionidae). XXXII Congresso Società Italiana di Biogeografia. Abstracts: 35-36.

FATTORINI S., MANGANARO A., PIATTELLA E., SALVATI L. 1999a - Role of the beetles in raptor diets from a Mediterranean urban area (Coleoptera). Fragm. Entomol., **31** (1): 57-69.

FATTORINI S., LEO P., SALVATI L. 1999b - Biogeographical observations on the Darkling beetles of the Aegean Islands (Coleoptera, Tenebrionidae). Fragm. Entomol., **31** (2): 339-375.

FATTORINI S., LEO P., SALVATI S. 2000 - Levels of endemism in the Aegean Tenebrionids (Coleoptera, Tenebrionidae). Biogeographia, **21**: 429-440.

FRAIRE M. 1994 - Metodi di analisi multidimensionale dei dati. Aspetti statistici e applicazioni informatiche. CISU, Roma: 217 pp.

FISHELSON L. 1987 - Biogeography and ecology of the acridofauna of Israel and neighbouring countries (Acridoidea, Orthoptera). In: F. Krupp, W. Schneider, R. Kinzelbach (eds.), Proceedings of the Symposium on the Fauna and Zoogeography of the Middle East, Mainz 1985: 124-147.

GARDINI G. 1995 - Coleoptera Polyphaga XIII (Lagriidae, Alleculidae, Tenebrionidae), pp. 1-13. In: A. Minelli, S. Ruffo, S. La Posta (eds.), Checklist delle specie fauna italiana, 58. Calderini, Bologna.

GEBIEN H. 1937 - Katalog der Tenebrioniden. Teil I. Pubbl. Mus. Entomol. P. Rossi, Duino, 2.

GEBIEN H. 1938-43 - Katalog der Tenebrioniden. Teil II. Mitt. Münch. Entomol. Ges., **28-34**.

GOLVAN Y.J. 1969 - Éléments de parasitologie médicale. Éditions médicales Flammarion, Paris: 579 pp.

GRIDELLI E. 1933 - Spedizione scientifica all'Oasi di Cufra (Marzo-Luglio 1931). Coleotteri. Ann. Mus. Civ. Stor. Nat. Genova, **56**: 155-258.

GRIDELLI E. 1937 - Coleotteri raccolti dal Prof. G. Scortecci nel Fezzan (Missione R. Società Geografica 1934). Atti Soc. Ital. Sci. Nat., **76**: 17-74.

GRIDELLI E. 1939 - Coleotteri del Fezzan e dei Tassili d'Aggèr (Missione Scortecci 1936). Atti Soc. Ital. Sci. Nat., **78**: 385-456.

GRIDELLI E. 1953 - Note illustranti varie specie di Tenebrionidi della Persia e dell'Arabia (Coleopt. Tenebrionidae). Doriana, **1** (43): 1-14.

GRIDELLI E. 1954 - Catalogo ragionato delle specie della famiglia Tenebrionidae a me note dell'Afghanistan. Atti Mus. Civ. Stor. Nat. Trieste, **19** (4): 169-292.

GRIMM R. 1981 - Die Fauna der Agais-Insel Santorin. Teil 2. Tenebrionidae (Coleoptera). Stuttg. Beitr. Naturkd., Ser. A (Biologie), **348**: 1-14.

GRIMM R. 1991 - Tenebrioniden von der Insel Zypern (Insecta: Coleoptera). Biocosme Mésogéen, Nice, **8** (1): 15-49.

HACINI S., DOUMANDJI S. 1998 - Place des Insectes dans le régime alimentaire de l'Hirondelle de cheminée Hirundo rustica Linné, 1758 (Aves, Hirundinidae) dans un milieu agricola à Bordj-El-Kiffan région du littoral algérois. L'Entomologiste, **54** (3): 105-111.

HACKER H. 1990 - Die Noctuidae Vorderasiens (Lepidoptera). Neue Entomologische Nachrichten aus dem Entomologischen Museum Dr Ulf Eitschberger, **27**: 707 pp.

HERNÁNDEZ A., ALEGRE J., SALGADO J.M., GUTIERREZ A. 1991 - El papel de los Coleópteros en el régimen alimentario de algunos Vertebrados en el Noroeste de España. Elytron Suppl., 5 (1): 231-237.

HESSELBARTH G., VAN OORSCHOT H, WAGENER S. 1995 - Die Tagfalter der Türkei unter Berücksichtigung der angrenzenden Länder. Dem Volk der Türkei, 3 vols.: 1354 pp. (vols. 1-2), 847 pp. (vol. 3).

HOLM E., SCHOLTZ C.H. 1980 - Structure and pattern of the Namib Desert dune ecosystem at Gobabeb. Madoqua, 12 (1): 5-39.

HOVENKAMP P. 1997 - Vicariance events, not areas, should be used in biogeographical analysis. Cladistics, **13**: 67-79.

JOLIVET P. 1998 - Manipulation du comportament chez les Fourmis et les Coléoptères sous l'influence de leurs parasites. L'Entomologiste, 54 (5): 211-222.

JUAN C., PETIPIERRE E. 1991 - Chromosome numbers and sex-determining systems in Tenebrionidae (Coleoptera). In: M. Zunino, X. Bellés, M. Blas (eds.), Advances in Coleopterology. AEC, Barcelona: 167-179.

JUAN C., OROMÍ P., HEWITT G.M. 1995 - Mitochondrial DNA phylogeny and sequential colonization of Canary Islands by darkling beetles of the genus *Pimelia* (Tenebrionidae). Proc. R. Soc. Lond. Ser. B, **261** (1361): 173-180.

JUAN C., OROMÍ P., HEWITT G.M. 1996 - Phylogeny of the genus *Hegeter* (Tenebrionidae, Coleoptera) and its colonization of the Canary Islands deduced from Cytochrome Oxidase I mitochondrial DNA sequences. Heredity, **76** (Pt 4): 392-403.

KASZAB Z. 1938 - Beiträge zur Kenntnis der Tenebrioniden-Fauna Kleinasiens. Folia Entomol. Hung., 5 (1, 4): 1-7.

KASZAB Z. 1939 - Vasvári Mihlós kisázsiai gyüjtoútjainak állattani eredményei. II. Gyászbogarak (Tenebrionidae). - Zoologische Ergebnisse der ersten (VI. - X. 1936) und zweiten (V. - VIII. 1937) Forschungsreise N. Vasvári's in Kleinasien. Math. Naturw. Anz. Ung. Akad. Wiss., **58**: 578-590.

KASZAB Z. 1957 - Zehn neue Tenebrioniden aus Asien. Ann. Hist. Nat. Mus. Natur. Hung., N.S., **8**: 289-299.

KASZAB Z. 1960a - Wissenshaftliche Ergebnisse der zoologischen Expedition des National Museums in Prag nach der Türkei. Acta Ent. Mus. Nat. Pragae, **33**: 69-82.

KASZAB Z. 1960b - Die Tenebrioniden Afghanistans auf Grund der Ergebnisse der Sammelrreise des Herrn J. Klapperich in den Jahren 1952/53. Entomol. Arb. Mus. G. Frey Tutzing Bei Münch, **11**: 1-179.

KASZAB Z. 1961a - Zwei neue Tenebrioniden (Coleoptera) as Arabien und Kleinasien. Entom. Abh. Ber. Mus. Tierk. Dresden, **26** (20): 169-175.

KASZAB Z. 1961b - Neue Tenebrioniden aus der Zoologischen Staatssmmlung in München. Mitt. Münch. Ent. Ges., **51**: 213-230.

KASZAB Z. 1968 - Ergebnisse zoologischer Sammelreisen in der Türkei. Coleoptera: Tenebrionidae. Ann. Nathist. Mus. Wien, **72**: 451-463.

KASZAB Z. 1974 - Neue Angaben zur Kenntins der Tenebrioniden von Afghanistan. Ann. Hist. Natur. Mus. Natur. Hung., **66**: 187-203.

KASZAB Z. 1982 - Insects of Saudi Arabia. Coleoptera: Fam. Tenebrionidae. Fauna Saudi Arabia. 4: 124-243.

KOCH C. 1935 - Wissenschaftliche Ergebnisse der entomologischen Expedition seiner Durchlaucht des Fürsten A. Della Torre e Tasso nach Aegypten und auf die Halbinsel Sinai. VII. Tenebrionidae (Coleoptera). Bull. Soc. R. Entomol. Egypte, Kairo, **19**: 2-111.

KOCH C. 1937 - Wissenschaftliche Ergebnisse über die während der Expedition Seiner Durchlaucht des Fürsten Alessandro C. della Torre e Tasso in Lybien aufgefundeden Tenebrioniden. Pubbl. Mus. Entomol. P. Rossi, Duino, **2**: 285-500.

KOCH C. 1939 - Die Käfer der libyschen Ausbeute des Herrn Georg Frey. Mitt. Münch. Ent. Ges., **29**: 216-293.

KOCH C. 1940 - Phylogenetische, biogeographische und systematische Studien über ungeflügelte Tenebrioniden. (Col. Tenebr.) Mitt. Münch. Ent. Ges., **30** (2): 683-750.

KOCH C. 1948 - Die Tenebrioniden Kretas. Mitt. Münch. Entomol. Ges., **34** (1944): 255-363.

KOCHER L. 1958 - Catalogue commenté des Coléoptères du Maroc, 6, Tenebrionides. Trav. Inst. scient. chérif. (Sér. Zool.), **12**: 7-185.

KOSSWIG C. 1955 - Zoogeography of the Near East. Syst. Zool., **4**: 49-73.

KOSWIG C. 1972 - Neue Beiträge zur Fauna Anatoliens, 2. Teil: Gibt es in Anatolien eine Irano-Turaniche Region? Istanbul Üniversitesi fen Fakültesi Mecmuasi, B, **37** (1-2): 97-107.

KRASNOV B., SHENBROT G. 1998 - Structure of communities of ground-dwelling animals at the junction of two phytogeographic zones. J. Biogeogr., **25**: 1115-1131.

KRASNOV B., WARD D., SHENBROT G. 1996 - Body size and leg length variation in several species of darkling beetles (Coleoptera: Tenebrionidae) along a rainfall and altitudinal gradient in the Negev Desert (Israel). J. Arid Environ., **34**: 477-489.

KÜHNELT W. 1965 - Tenebrionidae. In: A. Kanellis (ed.), Catalogus Faunae Graeciae. To Vuno, 60 pp.

KWIETON E. 1976 - Une espèce nouvelle du genre *Pimelia* F. (Coleoptera, Tenebrionidae). Annot. Zool. Bot., **113**: 1-3.

KWIETON E. 1977a - Révision phylogénétique du groupe de *Pimelia granulata*. Annot. Zool. Bot., **121**: 1-29.

KWIETON E. 1977b - Révision phylogénétique du groupe de *Pimelia obsoleta* (Col., Tenebrionidae). Bull. Soc. Entomol. Mulhouse, Avril-Juin: 17-24.

KWIETON E. 1977c - Esquisse phylogénétique de genere *Pimelia* F. Acta Entomol. Mus. Nat. Pragae, **39**: 559-589.

KWIETON E. 1978a - Espèces nouvelles des genres *Adesmia* Fish., *Pimelia* Sol. et *Vieta* (Col. Tenebrionidae). Bull. Soc. Entomol. Mulhouse, Janvier-Mars: 8-12.

KWIETON E. 1978b - Sur la division de l'ancien genre *Pachyscelis* Sol. (Col., Tenebrionidae). Bull. Soc. Entom. Mulhouse, Juillet-Septembre: 28-34.

KWIETON E. 1978c - Essai synoptique sur le genre *Thriptera* Solier (Col., Tenebrionidae). Annot. Zool. Bot., **123**: 1-15.

KWIETON E. 1980a - Révision du genre *Pachyscelis* Solier et notes sur des rélations inter-génériques chez les Pimeliini. Annot. Zool. Bot., **137**: 1-16.

KWIETON E. 1980b - Genre et espèces noveaux des Pimeliini (Col., Tenebrionidae) de l'Arabie. Fauna Saudi Arabia, **3**: 402-407.

KWIETON, E. 1981a - Exposé sommaire des faits concernant la phylogenèse et la paléogéographie de la sous-famille des Pimeliinae de l'Ancien Monde. Bull. Soc. Entomol. Mulhouse, Janvier-Mars: 1- 7.

KWIETON E. 1981b - Coléopères Tenebrionidae constatés par l'expédition de Tis au Pakistan. Annot. Zool. Bot., **143**: 1-20.

KWIETON E. 1981c - Esquisse entomogéographique de l'Algérie et de l'historie du désert Saharie, à la base des Coléoptères Tenebrionidae. Publicações do Instuto de Zoologia "Dr. Augusto Nobre". Fac. Cienc. Porto, **161**: 5-53.

KWIETON E. 1982a - Notes sur les Tenebrionidae Pimeliinae du Pakistan. Bull. Soc. Entomol. Mulhouse, Avril-Juin: 21-26.

KWIETON E. 1982b - Contributions ultérieures à la connaissance du genre *Pimelia* F. (Col. Tenebrionidae). Annot. Zool. Bot., 145: 1-38.

KWIETON E. 1983 - Zoogéographie historique de l'Arabie à la base des Coléoptères Tenebrionidae. Türk. Bit. Kor. Derg., 7: 3-16.

KWIETON E. 1986a - Esquisse de la zoogéographie dynamique de la Turquie, à la base des Coléoptères Tenébrionidae. Acta Entomol. Bohemoslov., **83**: 279-293.

KWIETON E. 1986b - Notes faunistiques sur les *Adesmia* du Pakistan (Col. Tenebrionidae). Bull. Soc. entomol. Mulhouse, Octobre-Décembre: 62-64

KWIETON E. 1987 - Mise au point sur la phylogénie et la paléogéographie du g. *Pimelia* F. (Col. Tenebrionidae). Bull. Soc. Entomol. Mulhouse, Janvier-Mars: 9-15.

LA GRECA M. 1964 - Le categorie corologiche degli elementi faunistici italiani. Mem. Soc. Entomol. Ital., **43**: 147-165.

LA GRECA M. 1996 - Storia biogeografica degli ortotteri d'Italia: origine e distribuzione (Insecta, Orthoptera). Boll. Mus. Civ. Stor. Nat. Verona, **20** (1993): 1-46.

LAWRENCE J.F., SPILMAN T.J. 1991 - Tenebrionidae (Tenebrionoidea). In: F.W. Stehr (ed.), Immature Insects. Vol. 2: 520-524.

LEO P., FATTORINI S., 2000 - The zoogeographical composition and distribution of the Anatolian Pimeliini (Coleoptera, Tenebrionidae). Biogeographia, **21**: 399-427.

LOVARI S. 1975 - The feeding habits of four raptors in Central Italy. Raptor Res., 8 (3-4) (1974): 45-57.

MALICKY H. 1985. The distribution of Caddisflies (Insecta, Trichoptera) in the South Aegean Arch of islands (Südägäischer Inselbogen). Biol. Gallo-Hell., **10**: 95-101.

NAUMANN C.M. 1987 - Distribution patterns of *Zygaena* Moths in the Near and Middle East (Insecta, Lepidoptera, Zygaenidae). In: F. Krupp, W. Schneider, R. Kinzelbach (eds.), Proceedings of the Symposium on the Fauna and Zoogeography of the Middle East, Mainz 1985: 200-212.

NICOLSON S.W. 1990 - Water relations of the Namib tenebrionid beetles. In: M.K. Seely (ed.), Namib ecology: 25 years of Namib research. Transvaal Mus. Monogr., 7: 173-178.

NOONAN G.R. 1979 - The science of biogeography with relation to Carabids. In: T.L. Erwin, G.E. Ball, D.R. Whitehead, A.L. Halpern (eds.), Carabid beetles: their evolution, natural history, and classification. Dr W. Junk Publishers, The Hague: 295-317.

NOONAN G.R. 1988 - Biogeography of North American and Mexican insects, and a critique of vicariance biogeography. Syst. Zool., 37 (4): 366-384.

NORMAND H. 1936 - Contribution au Catalogue des Coéoptères de la Tunisie. 10. Tenebrionidae. Bull. Soc. Hist. Nat. Afr. Nord, 27: 178-191.

OOSTERBROEK P., ARNTZEN J.W. 1992 - Area cladograms of Circum-Mediterranean taxa in relation to Mediterranean palaeogeography. J. Biogeogr., **19**: 3-20.

ORMIÈRES R. 1967 - A propos de quelques grégarines de *Blaps* de Grèce. Vie Milieu, 18, sèrie C (1): 247-250.

OROMÍ MASOLIVER P. 1982 - Los Tenebriónidos de las Islas Canarias. Istituto de Estudios Canarios (C.E.C.E.L.) Aula de Cultura del Excmo. Cabildo Insular de Tenerife: 267-292.

PENRITH M.L. 1983 - Revision of the Zophosini (Coleoptera: Tenebrionidae). Part 8. The palaearctic species group of the subgenus *Oculosis* Penrith, the subgenus *Cheirosis* Deyrolle, and a monotypical subgenus from Socotra. Cimbebasia, ser. A, **6**: 369-384.

PENRITH M.L. 1984 - Revision of the Zophosini (Coleoptera: Tenebrionidae). Part 9. The remaining species of the subgenus *Septentriophosis* Penrith. Cimbebasia, ser. A, **6** (9): 385-416.

PETIPIERRE E., JUAN C., ALVAREZ-FUSTER A. 1991 - Evolution of chromosomes and genome size in Chrysomelidae and Tenebrionidae. In: M. Zunino, X. Bellés, M. Blas (eds.), Advances in Coleopterology. AEC, Barcelona: 129-144.

PIERRE F. 1964a - Contribution a la connaisance de la faune du Moyen-Orient (Missions G. Remaudière 1955 et 1959). II. Coléoptères Ténébrionides. Vie Milieu, **15** (4): 1043-1055.

PIERRE F. 1964b - *Storthocnemis* nouveaus de la zone sahélienne et du Sahara. Remarques concernant les Leucolaephini, trib. nov. (Col. Tenebrionidae). Bull. Inst. Fr. Afr. Noir, Ser. A Sci. Nat., **26** (3): 865-874.

PIERRE F. 1974 - Contribution a la faune de l'Iran. Insectes Coléoptères du désert du Lut. Ann. Soc. Entomol. Fr., n.s., **10** (1): 229-235.

PIERRE F. 1982 - Variation spécifique des *Pimelia* du groupe d'*interstitialis* dans le nord de l'Afrique et au Sahara avec description de noveaux taxa (Col. Tenebrionidae). Bull. Soc. Entomol. Fr., **87**: 2-13

POLIS G.A. 1981 - The evolution and dynamics of intraspecific predation. Annu. Rev. Ecol. Syst., **12**: 225-251.

POR F.D. 1987 - The Levantine Landbridge: historical and present patterns. In: Krupp F., Schneider W., Kinzelbach R. (eds.), Proceedings of the Symposium on the Fauna and Zoogeography of the Middle East, Mainz 1985: 23-28.

RATTI E. 1986 - Ricerche faunistiche del Museo Civico di Storia Naturale di Venezia nell'Isola di Pantelleria. I - Notizie introduttive; Coleoptera Tenebrionidae. Boll. Mus. Civ. Stor. Nat. Venezia, **35** (1984): 7-41.

REITTER E. 1900 - Bestimmungs-Tabellen der Tenebrioniden-Abtheilungen: Tentyriini und Adelostomini, aus Europa und der angrenzenden Gebieten. Heft 42. Paskau.

REITTER E. 1916 - Bestimmungs-Tabellen der europäeischen Coleopteren. Heft 79. Tenebrionidae. X Teil. Zopherini, Elenophorini, Leptodini, Stenosini und Lachnogyini aus der paläarktischen Fauna. Paskau. Wiener Entomol. Zeitung, **35** (5-7): 129-171.

RICKARD W.H. 1971 - Observations on the distribution of *Eleodes hispilabris* (Say) (Coleoptera: Tenebrionidae) in relation to elevation and temperature in the Rattlesnake Hills. Am. Midl. Nat., **85** (2): 521-526.

SÁNCHEZ-PIÑERO F., GÓMEZ J.M. 1995 - Use of ant-nest debris by darkling beetles and other arthropod species in an arid system in south Europe. J. Arid Environ., **31**: 91-104.

SANTOS A. DE LOS. 1994 - Generic diversity patterns in the Tenebrionid beetle communities (Col: Tenebrionidae). Ecol. Mediterr., **20** (3-4): 125-136.

SCHAWALLER W. 1982 - Tenebrionidae aus dem Vorderen Orient I (Insecta, Coleoptera). Stuttg. Beitr. Naturkd. (ser. A), 359: 1-14.

SCHAWALLER W. 1987 - Revision westpaläartktischer Tenebrionidae (Coleoptera). Teil 1. Die Arten der Gattung *Akis* Herbst. Stuttg. Beitr. Naturkd. (Ser. A), **403**: 1-21.

SCUPOLA A. 1984 - Una nuova *Idastrandiella* Strand di Grecia (Coleoptera Tenebrionidae) (II Contributo alla conoscenza dei Tenebrionidae). Boll. Mus. Civ. Stor. Nat. Verona, **11**: 69-75.

SKOPIN N.G. 1973 - Revision der Tenebrioniden-Gattungsgruppe *Trigonoscelis-Sternoplax* (Coleoptera). Entomol. Arb. Mus. G. Frey Tutzing bei Münch, **24**: 104-185.

SLIPINSKI S.A., LAWRENCE J.F. 1997 - Genera of Colydiinae (Coleoptera: Zopheridae) of the Australo-Pacific region. Ann. Zool. (Wars.), 47 43/47: 341-440.

SLOBODCHIKOFF C.N. 1978 - Habitat use by mimetic coastal tenebrionid beetles. Am. Midl. Nat., **99** (1): 45-57.

STAPP P. 1997 - Microhabitat use and community structure of darkling beetles (Coleoptera: Tenebrionidae) in shortgrass prairie: effects of season, shrub cover and soil type. Am. Midl. Nat., **137** (2): 298-311.

VIGNA TAGLIANTI A., AUDISIO P.A., BELFIORE C., BIONDI M., BOLOGNA M.A., CARPANETO G.M., DE BIASE A., DE FELICI S., PIATTELLA E., RACHELI T., ZAPPAROLI M., ZOIA S. 1993 - Riflessioni di gruppo sui corotipi fondamentali della fauna W-paleartica ed in particolare italiana. Biogeographia, **16** (1992): 159-179.

VIGNA TAGLIANTI A., AUDISIO P.A., BIONDI M., BOLOGNA M.A., CARPANETO G.M., DE BIASE A., FATTORINI S., PIATTELLA E., SINDACO R., VENCHI A., ZAPPAROLI M. 1999 - A proposal for a chorotype classification of the Near East fauna, in the framework of the Western Palearctic region. Biogeographia, **20** (1999): 31-59.

VILENKIN B. YA., CHIKATUNOV V.I. 1998 - Co-occurrence of species with various geographical ranges, and correlation between area size and number of species in geographical scale. J. Biogeogr., **25**: 2745-284.

VIÑOLAS A. 1994 - El género *Pimelia* Fabricius, 1775 en la Península Ibérica y Baleares, con nota sistemática sobre una especie de Canarias (Coleoptera, Tenebrionidae, Pimeliinae). Ses Entom. ICHN-SCL, **8** (1993): 125-140.

WAGENER S. 1995 - Allgemeiner Teil. In: Hesselbarth G., van Oorschot H, Wagener S. (eds), Die Tagfalter der Türkei unter Berücksichtigung der angrenzenden Länder. Dem Volk der Türkei, vol. 1: 1-139.

WATT J.C. 1974 - A revised subfamily classification of Tenebrionidae (Coleoptera). N. Z. J. Zool., **1**: 381-452.

WOLFART R. 1987 - Late Cretaceous through Quaternary palaeogeographic evolution of the Middle East. In: F. Krupp, W. Schneider, R. Kinzelbach (eds.), Proceedings of the Symposium on the Fauna and Zoogeography of the Middle East, Mainz 1985: 9-22.

ZUNINO M., ZULLINI A. 1995. Biogeografia. La dimensione spaziale dell'evoluzione. Casa editrice Ambrosiana, Milano: 310 pp.

APPENDIX 1 - CHECKLIST OF ANATOLIAN PIMELIINAE

Chorotypes follow Vigna Taglianti et al. (1999): EME = East Mediterranean; NAF = North African; NAS = North East African-Sindian; SWA = South West Asiatic; TUE = Turano-European; TUM = Turano-Mediterranean; TUR = Turanian, E = endemic species (species restricted to the Anatolian peninsula or to the Anatolian peninsula and near islands). Only Pimeliini endemic species are referred to general chorotypes (reported in parentheses) based on the distributions of their relatives.

	Chorotype	**Distribution range**
CNEMEPLATINI		
Cnemeplatia atropos A. Costa, 1847	TUM	
STENOSINI		
Dichillus araxidis Reitter, 1889	TUR	Ponto-Caspian
Dichillus carinatus (Küster, 1848)	EME	Ponto- Mediterranean
Dichillus cylindricus Baudi, 1874	SWA	Syro-Anatolian
Dichillus iranicus Kaszab, 1963	SWA	Irano-Anatolian
Dichillus pertusus Kiesenwetter, 1861	EME	
Dichillus subsetulosus Reitter, 1916	E	
Eutagenia smyrnensis (Solier, 1838)	EME	Aegean
Eutagenia minutissima Pic, 1903	EME	Aegean
? **Microtelus asiaticus** Solier, 1838 (1)	EME	Aegean
Stenosis comata Reiche and Saulcy, 1857	SWA	Syro-Anatolian
Stenosis dianae C. R. and J. Sahlberg, 1907-8	SWA	Syro-Anatolian
Stenosis dilutipes Reitter, 1887	SWA	Syro-Anatolian
Stenosis esau C. R. and J. Sahlberg, 1907-8	E	
Stenosis orientalis Brullé, 1832 (2)	EME	Aegean
Stenosis punctiventris Eschscholtz, 1831	TUR	Ponto-Caspian
Stenosis quadraticollis Desbrochers des Loges, 1881	TUR	Ponto-Caspian
Stenosis cretica Koch, 1940 (3)	E	
Stenosis sardoa (Küster, 1848) (4)	MED	
ZOPHOSINI (5)		
? **Zophosis acuminata** Fisher, 1832 (6)	SWA?	
? **Zophosis asiatica** Miller, 1861 (7)	SWA	Syro-Anatolian?
Zophosis dilatata Deyrolle, 1867	EME	Aegean
Zophosis oblonga Solier, 1834	SWA	Irano-Anatolian
Zophosis punctata Brullé, 1832	TUM	
? **Zophosis rugosa** Faldermann, 1837 (8)	TUR	Ponto-Caspian
ERODIINI		
Amnodeis asiaticus Miller, 1858	E	
Amnodeis grandis Miller, 1858	SWA	Irano-Anatolian
Amnodeis intermedius Reitter, 1914	SWA	Syro-Anatolian
Amnodeis milleri Reitter, 1914	E	
? **Apentanodes globosus** (Reiche and Saulcy, 1857) (9)	EME	Aegean
Erodius orientalis Brullé, 1832 (10)	EME	Aegean
Erodius semenovi Bogacev, 1950	SWA	Irano-Anatolian

EURYCHORINI

Adelostoma sulcatum Duponchel, 1827	NAF	
Adelostoma ovalipenne Chevrolat, 1878	E	

CERATANISINI

Ceratanisus funebris Reitter, 1898	E	
Idastrandiella allardi (Reitter, 1884) (11)	EME	Aegean
Idastrandiella mucoreus (Waltl, 1838)	EME	Aegean

AKIDINI (12)

Akis elongata Brullé, 1832	EME	Aegean
Akis latreillei Solier, 1836	SWA	Irano-Anatolian
Cyphogenia lucifuga (Adams, 1817)	TUE	

PIMELIINI (13)

Graecopachys quadricollis (Brullé, 1832) (14)	EME	Aegean
Pachyscelis musiva (Ménétriés, 1832) (15)	SWA	Irano-Anatolian
Pachyscelis villosa (Drapiez, 1820)	EME	Aegean
Pimelia akbesiana Fairmaire, 1884	E (EME)	
Pimelia bajula Klug, 1830 (16)	SWA	Irano-Anatolian
Pimelia dubia Faldermann, 1837	E? (TUR)	Ponto-Caspian?
Pimelia timarchoides Ménétriés, 1832	E (EME)	
Pimelia repleta Reitter, 1915	E (EME)	
Pimelia robusta Kraatz, 1865	E (TUR?)	
Pimelia subglobosa Pallas, 1781 (17)	EME	Ponto-Mediterranean
Pimelia werneri (Ganglbauer, 1905)	E (TUM)	
Sternoplax nicomedia (Reitter, 1908)	E (TUR)	
Trachyderma lima (Petagna, 1819)	MED	
Trachyderma philistina Reiche and Saulcy, 1857	NAS	
Trachyderma setosa (Fischer, 1832)	TUR	Ponto-Caspian

ADESMIINI (18)

Adesmia audouini Solier, 1835	SWA	Syro-Anatolian
Adesmia anthracina (Klug, 1830)	SWA	Syro-Anatolian
Adesmia carinata Solier, 1835 (19)	SWA	Irano-Anatolian
Adesmia fisheri Faldermann, 1837	TUR	Ponto-Caspian
Adesmia gibbula Reitter, 1916	SWA	Syro-Anatolian
Adesmia metallica (Klug, 1830) (20)	NAF	
Adesmia procera Miller, 1861	SWA	Irano-Anatolian
Adesmia servillei Solier, 1835	SWA	Irano-Anatolian

TENTYRIINI

Calyptopsis capnisiformis Reitter, 1903	E	
Calyptopsis capnisoides Reitter, 1896	EME	Aegean
Calyptopsis caucasica Kraatz, 1865	TUR	Ponto-Caspian
Calyptopsis deplanata Faust, 1875	TUR	Ponto-Caspian
Calyptopsis escherichi Reitter, 1900	E	
Calyptopsis pandaroides Reitter, 1896	EME	Ponto- Mediterranean

Calyptopsis solieri Reiche, 1857	SWA	Syro-Anatolian
Dailognatha caraboides Solier, 1835	EME	Ponto- Mediterranean
Dailognatha crenata Reiche and Saulcy, 1857	SWA	Syro-Anatolian
Dailognatha minuscula Desbrochers des Loges, 1881	E	
Dailognatha planata Miller, 1861	SWA	Syro-Anatolian
Dailognatha pumila Baudi, 1874	E	
Dailognatha quadricollis (Brullé, 1832) (21)	EME	Ponto- Mediterranean
Dailognatha rugipleuris Reitter, 1896	E	
Dichomma dardanum (Steven, 1829)	EME	Aegean
Stegastopsis microderoides Reitter, 1898	E	
Tentyria cylindrica Solier, 1835	SWA	Syro-Anatolian
Tentyria rotundata Brullé, 1832 (22)	EME	Aegean
? **Tentyria taurica** Tausch, 1812 (23)	TUR ?	
Tentyria tessulata Tausch, 1812 (24)	SWA	Syro-Anatolian
Tentyria wiedemanni Ménétries, 1838	E	

ANNOTATIONS

Note 1. The genus *Microtelus* was never quoted from Anatolia. However, based on its general distribution, Kwieton (1986a) suggested that this genus probably occurs also in this region. Reitter (1916) cited *M. asiaticus* from Crete and Greece and, dubiously, from Lebanon. The occurrence of this species in Anatolia is possible, but not proved.

Note 2. According to Koch (1940), this species includes two subspecies. The nominal form occurs in Greece and Asia Minor, while the Ionian Islands are inhabited by ssp. *jonica* Koch, 1940.

Note 3. According to Koch (1948), this species includes two subspecies: the nominal form is recorded from Crete; ssp. *shusteri* Koch, 1940 from Asia Minor. This species was cited by Kaszab (1968) as *S. silvestrii* Koch, 1935 ssp. *shusteri* Koch, 1940.

Note 4. This species, wrongly cited by Koch (1940) as *S. brenthoides* (Rossi, 1790), includes three subspecies (Canzoneri, 1970; Ratti, 1986). The Anatolian populations should be referred to ssp. *laeviventris* Desbrochers des Loges, 1881, while the typical form and ssp. *ardoini* Canzoneri, 1970 have W-Mediterranean distributions.

Note 5. Systematics of the genus *Zophosis* follows Penrith (1983).

Note 6. This species was cited by Gebien (1937) from Transcaucasus and Syria. According to Kwieton (1986a), it probably occurs also in the Anatolian peninsula. However, according to Penrith (1983), it is so far recorded with certainty only from Iran.

Note 7. This species was quoted by Gebien (1937) from Syria, Iran and Asia Minor. However, according to Penrith (1984), only one definite locality, in Syria, is available.

Note 8. Gebien (1937) cited this species from Turkestan, Iran, Transcaucasus and Armenia. My colleague P. Leo (1999 pers. comm.) knows this species from a locality in the Armenian Republic very close to the Turkish borderline.

Note 9. According to Kwieton (1986a), this species, known from Lebanon, Cyprus, Rhodes, Crete, Gavdos near Crete, and Karpathos (cf. Grimm, 1991), probably occurs also in the Anatolian peninsula.

Note 10. This species includes four subspecies differently distributed in the Aegean area (cf. Koch, 1948): ssp. *brevicostatus* Solier, 1834, ssp. *boyeri* Solier, 1834, ssp. *oblongus* Solier, 1834; and ssp. *orientalis* Solier, 1834. The Anatolian populations are referred by Kaszab (1968) to ssp. *oblongus.*

Note 11. Systematics and distribution of the genus *Idastrandiella* follow Scupola (1984).

Note 12. Systematics and distribution of the genus *Akis* follow Schawaller (1987).

Note 13. Systematic and distribution of the tribe Pimeliini follow Leo and Fattorini (2000).

Note 14. A number of subspecific and infrasubspecific taxa are known for this species (cf. Koch, 1948). According to Koch (1948), the Anatolian populations should be referred to a distinct subspecies: ssp. *smyrnensis* Kraatz, 1865.

Note 15. A number of subspecific taxa were described for this species, but their true taxonomic value is uncertain. According to Kwieton (1980a), the South West Iranian populations should be referred to ssp. *achaemenia* Bogacev, 1949, while all the other populations have to refer to the typical form.

Note 16. This species includes two subspecies (cf. Leo and Fattorini, 2000): the nominal form is distributed in Lebanon, Palestine and Jordan, while ssp. *solieri* Mulsant, 1852 is distributed in Anatolia, Cyprus, Syria, Kurdistan, and W Iran. According to Kwieton (1977c), *P. zarudnyi* Bogacev, 1953, described from Iran, should be regarded as a subspecies of *P. bajula.*

Note 17. This species includes a number of subspecies in need of revision. However, the Anatolian populations seem to be referable to three subspecies: a Central Anatolian subspecies, and two Western Anatolia subspecies (cf. Leo and Fattorini, 2000).

Note 18. Systematics and distribution of *A. anthracina*, *A. carinata*, *A. gibbula* and A. *metallica* follow Ardoin (1978) and Kwieton (1986b).

Note 19. The Anatolian populations of this species should be referred to the typical form (cf. Kwieton, 1986b). Ssp. *stokleni* Koch 1940 is distributed in Israel, Jordan, Kweit and Syria (Ardoin, 1978).

Note 20. This species includes a number of subspecies (cf. Ardoin, 1978). The Anatolian populations should be referred to the typical form.

Note 21. This species includes a number of subspecies differently distributed in the Aegean area (cf. Koch, 1948). The Anatolian populations should be referred to ssp. *carceli* Solier, 1834.

Note 22. This species includes a number of subspecies differently distributed in the Aegaen area (cf. Koch, 1948). The Anatolian populations should be referred to the following subspecies: ssp. *mittrei* Solier, 1835, ssp. *winkleri* Koch, 1936, ssp. *daghestris* Koch, 1948, and ssp. *convexipennis* Koch, 1948. According to Koch (1948) all these subspecies are strictly related to ssp. *angulata* Brullé, 1832 and ssp. *paganettii* Schuster, 1915.

Note 23. This species was quoted from Turkey, Southern Russia and Crimea by Reitter (1900), but its true taxonomic value and actual distribution, are uncertain (cf. Koch, 1948; Kühnelt, 1965).

Note 24. This species includes two subspecies: the nominal form (occurring in Caucasus and Iran) and spp. *rugipleuris* Bogdanov-Katjkov, 1916 (which should be restricted to Northern Iran), but nothing is known about the taxonomic status of the Anatolian populations (cf. Kwieton, 1986a).