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On the Structure of the Distribution Area of Flea Species (*Aphaniptera*) of the Superfamily *Ceratophylloidea*

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Abstract. On the basis of recent investigations the author concludes that fleas *(Aphaniptera)* of the superfamily *Ceratophylloidea* parasitizing on rodents and insectivores are a suitable object for determining territorial geographical units, because they form clearly defined geographical subspecies like other terricolous insects. The author further deals with the phenomenon of substitution of one flea host by another and demonstrates the possible application of the geographical distribution of fleas of the said superfamily for a detailed zoogeographical subdivision of Central Europe and the Balkan Peninsula.

Modern taxonomic aphanipterological papers clearly indicate that most flea species *(Aphaniptera)* belonging to the superfamily *Ceratophylloidea* from rodents and insectivores form distinct geographical subspecies (WAGNER, ROTHSCHILD, JORDAN, IOFF, SMIT, HOLLAND, PEUS, MIKULIN, ROSICKÝ etc.) It remains to be seen whether the fleas of the superfamily *Ceratophylloidea* can be considered a separate and suitable object for determining territorial geographical units and for solving other zoogeographical problems (see also BEIRNE 1952, HESSE 1924, HOLDHAUS 1928, RENSCH 1932, SCHILDER 1936, ROSICKÝ 1957, etc.).

The method of confronting the distribution areas of flea species with the distribution areas of their hosts indicates that there exist several types of such distribution areas:

1. The distribution area of the flea species fully coincides with the distribution area of the host species, for example *Monopsyllus sciurorum* (Schrank) on squirrel (*Sciurus vulgaris* L.), *Ctenophthalmus bisoctodentatus* on mole (*Talpa europaea* L.) etc.
2. The distribution area of the flea species is wider than the distribution area of the main host species and overlaps the distribution areas of other hosts. For example the distribution area of *Ctenophthalmus orientalis* overlaps the distribution area of *Citellus citellus* L., that of *Citellophilus simplex* (Wagn.) overlaps the distribution area of *Citellus suslica* (Güld.) etc.
3. The distribution area of the flea species covers the distribution areas of several

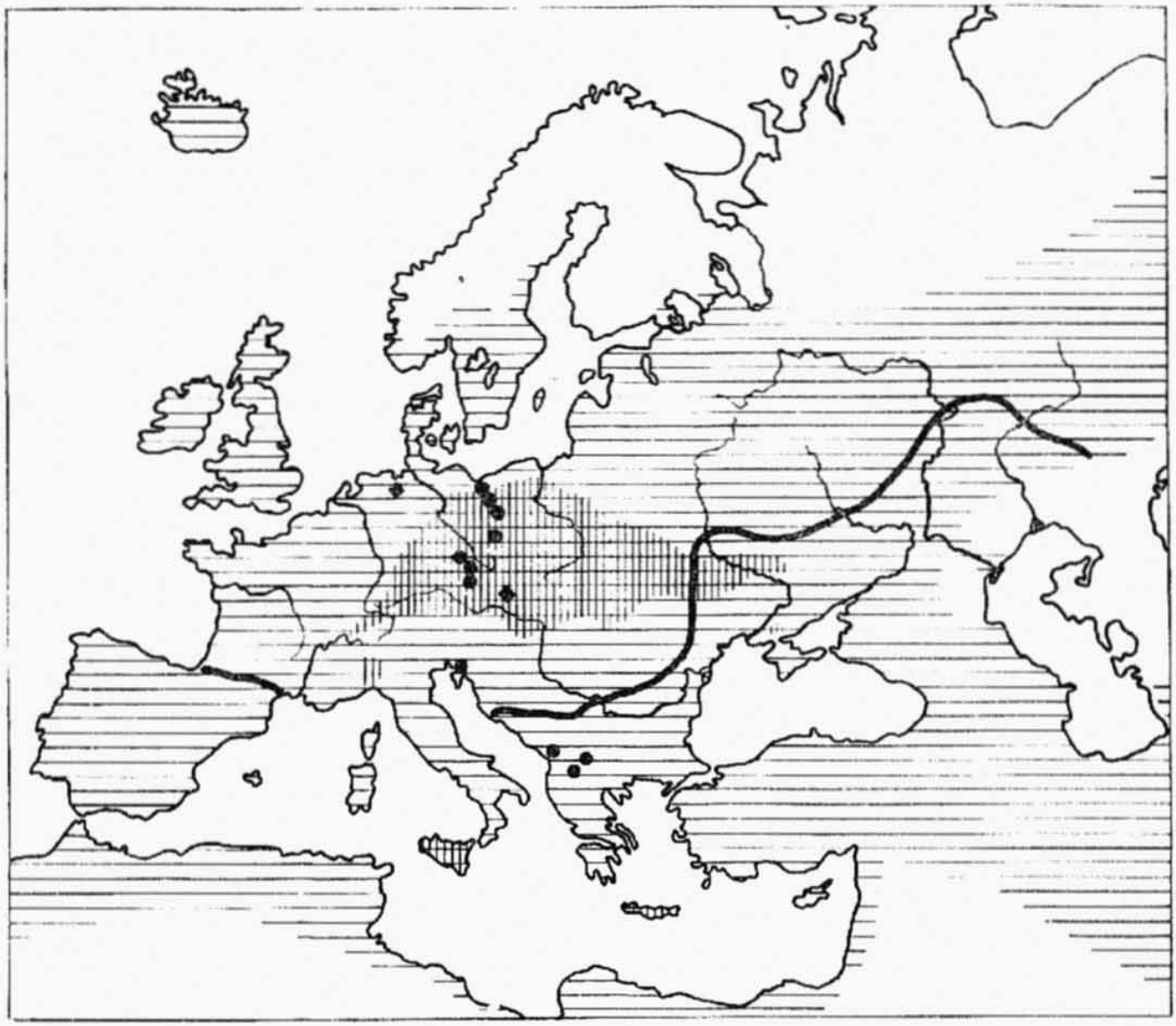

Fig. 1. The distribution area of *Apodemus sylvaticus* L. as compared with the distribution areas of some main flea species parasitizing on this rodent.
The distribituon area of *A. sylvaticus* (horizontal lines). The distribution area of the flea species *Ctenophthalmus solutus* J. et R. (vertical lines). The eastern boundary of the distribution area of the West European flea species *Typhloceras poppei* Wag. (●), a characteristic Atlantic type of distribution. The northern boundary of the continuous distribution area of the flea species *Triainapsylla taschenbergi* (Wagn.) (thick line). A patch-like distribution outside the continuous distribution area in Central Europe (◆) in the localities Vranov n./D., Vegesack.

host species which live mostly together. A typical example are the fleas *Palaeopsylla soricis* (Dale) and *Doratopsylla dasycnema* (Roths.) on shrews of the genera *Sorex* and *Neomys* in Europe.

4. The distribution area of the flea species does not coincide with the distribution area of the main host and continuously covers only a part of this area. This type of the distribution area is to be found in a number of flea species parasitizing on *Apodemus sylvaticus* (L.), *Talpa europaea* (L.), *Clethrionomys glareolus* (Schr.). (See Fig. 1, 2, 3.)
5. The distribution area of the flea species is not identical with the distribution

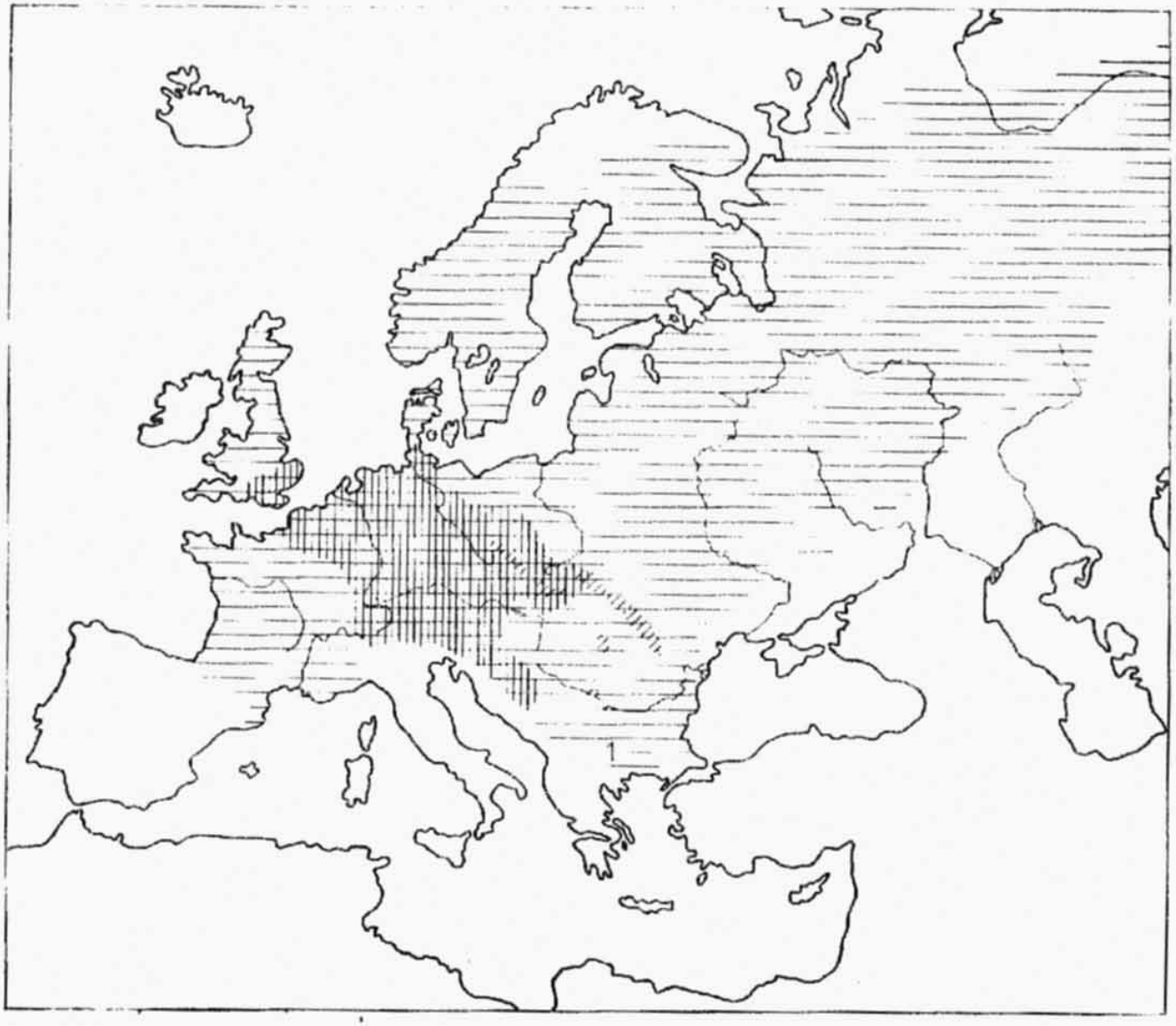

Fig. 2. The distribution area of *Clethrionomys glareolus* (Schr.) as compared with the distribution areas of some main flea species parasitizing on this host in Europe.
The distribution area of *C. glareolus* (horizontal lines). The distribution area of the nominate form of *Ctenophthalmus congener congener* Roths. (vertical lines).
1 — geographical subspecies *C. congener bureshi* Ros. from the mountain range Pirin and Rila (Bulgaria) isolated from the distribution area of the nominate subspecies. The distribution area of *C. obtusus* J. et R. (diagonal lines).

area of the main host and is broken up in the form of islets (patches). For example the distribution area of *Atyphloceras nuperus* (Jord.), *Rhadinopsylla mesa* (J. et R.) etc.

6. The distribution area of the flea species is divided into two parts: one in the north and the other in the mountainous regions of Central Europe and the Balkan Peninsula (Boreo-Alpine type — Holdhaus 1912, 1954). For example *Megabothris rectangulatus* (Wahlgr.), *Amphipsylla sibirica* (Wagn.), *Ceratophyllus lunatus* (J. et R.), *Ceratophyllus balati* Ros. etc. (See Fig. 4, 5.)

Such a structure of the distribution area is met with not only within the boundaries of a definite geographical landscape (for example in the zone of

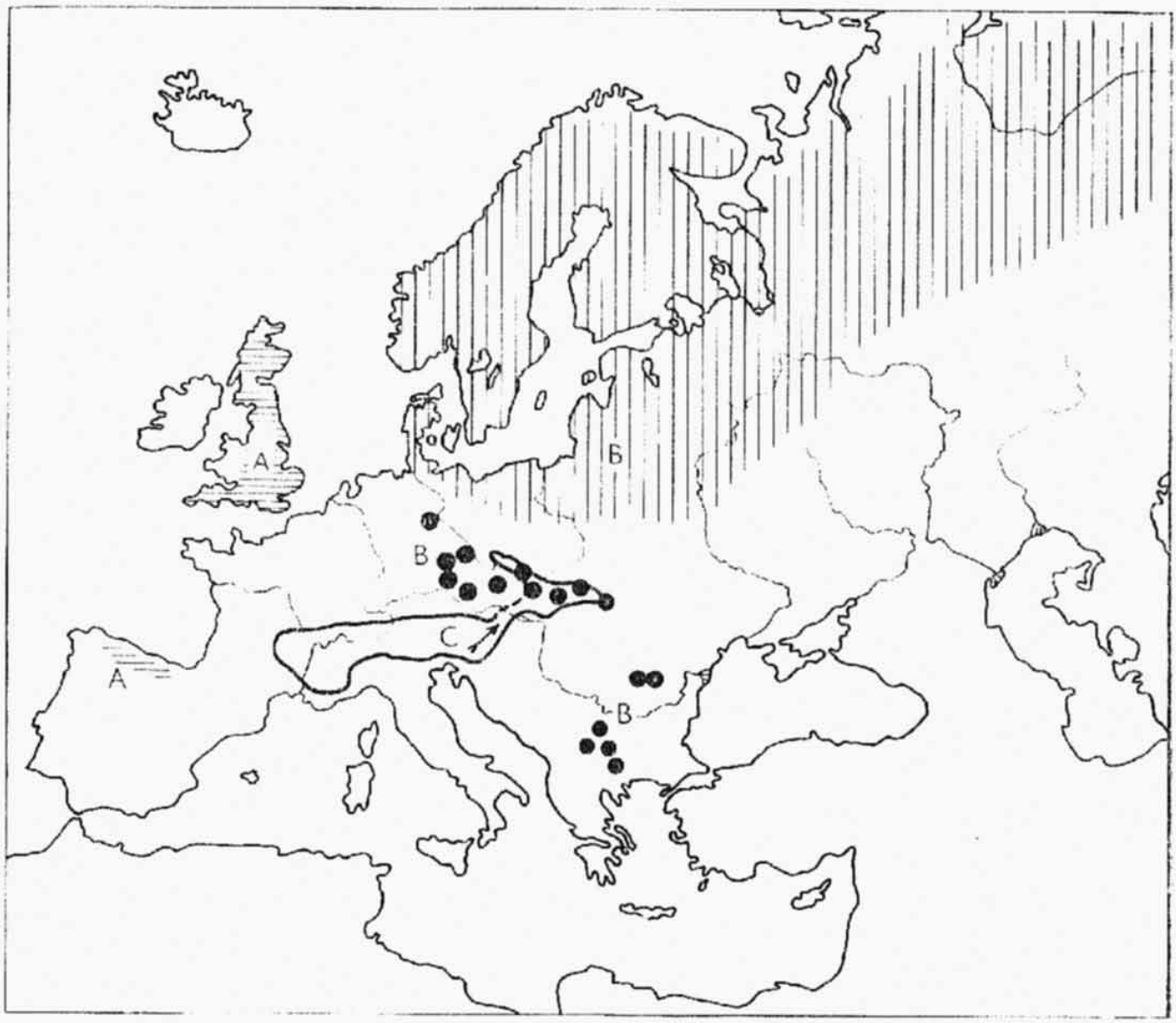

Fig. 3. The distribution area of 3 species of the genus *Peromyscopsylla:* A –(horizontal lines)– *P. spectabilis* (Roths.) B–(vertical lines)–*P. silvatica* (Mein.), a part of the distribution area with continuous distribution. B–(black dots)–*P. silvatica* –occurrence in Central European and Balkan mountains, where this species is absent in lower altitudes. Localities: Harz (Peus in litt.), Krušné hory, Doupovské hory, Tepelské hory, Český les, Šumava, Českomoravská vysočina (Žďárské hory), Jeseníky, Beskydy, Vysoké Tatry, Nízké Tatry, Minčol, Východné Karpaty, Transylvánské Alpy (Babele, Sinaia), Vitoša, Rila, Pirin, Stara Planina, Suva Planina (Rosický). In Central Europe only main mountain massifs are marked (Boreo-montane type of distribution). C–*P. fallax* (Roths.)–localities are marked with a thick line. Arrow–supposed direction of the species distribution in post-glacial period in the territory where both species occur in the same locality at present

the European deciduous forest, in the steppe zone etc.), but it can include several zones also. All these types of the distribution areas of flea species belonging to the mentioned superfamily, with the exception of type 1, indicate that in most cases the host does not solely and universally determine the distribution area of a flea species, but also prove that the fleas of small rodents and insectivores, as far as their demands for the conditions of external environment are concerned, are subject to the same rules and natural laws as terricolous insects (JEANNEL 1942).

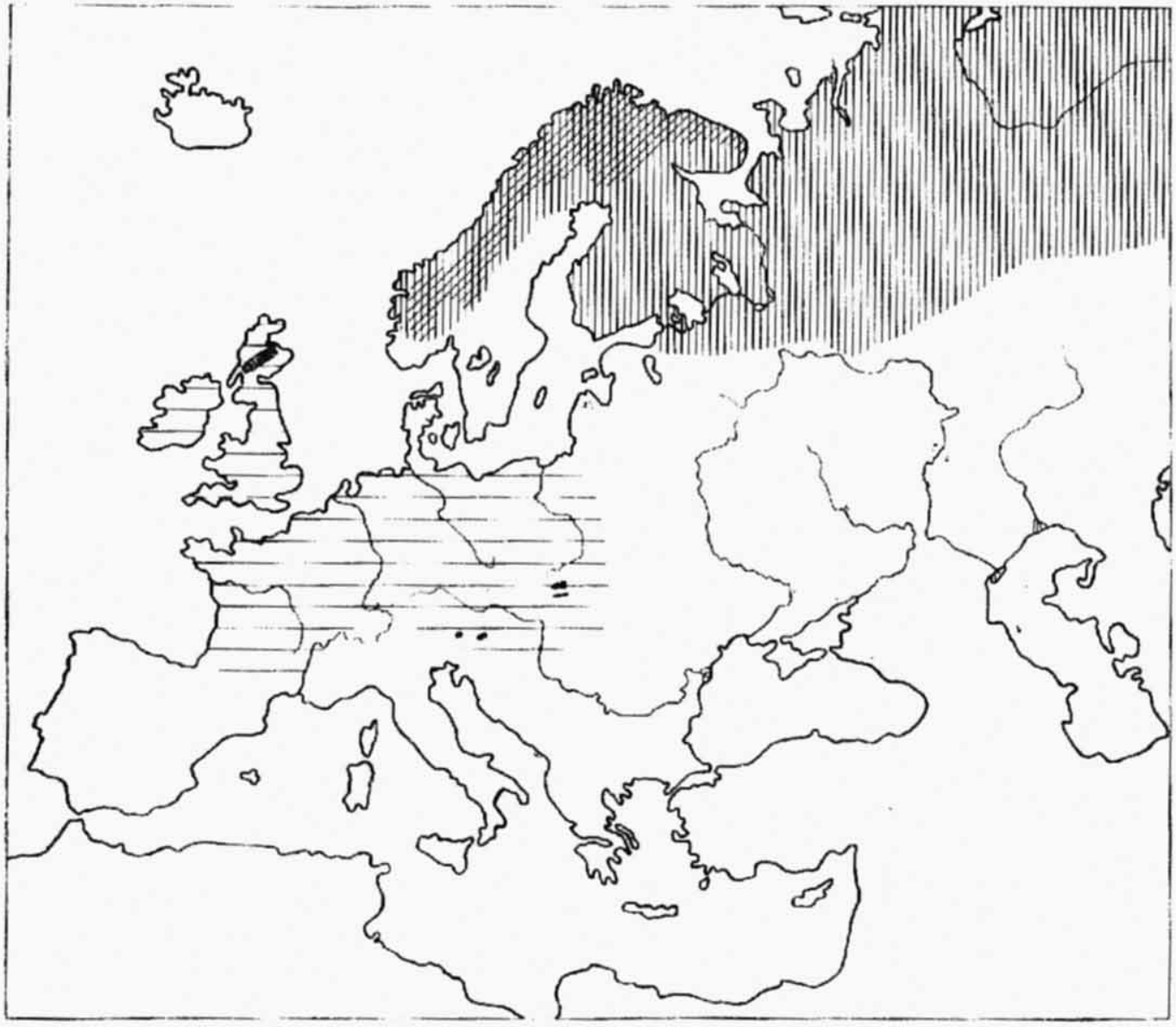

Fig. 4. Boreo-Alpine type of distribution of the species *Megabothris rectangulatus* (Wahlgr.). Black spots in Central Europe and Scotland – isolated relic occurrence of the species. Vertical lines – distribution of the species in northern Europe. Diagonal lines – present occurrence of *Lemmus lemmus* L. in the distribution area of *M. rectangulatus*. The distribution area of the flea species is different and larger than the distribution area of its main host – distribution by means of host substitution. Horizontal lines – Pleistocene distribution of *L. lemmus* in Europe according to fossils.

These very conditions have given rise to geographical subspecies, even in those cases when the host species remains the same and is not differentiated in geographical races. Many flea species develop within the boundaries of their distribution area a number of geographical subspecies, the distribution areas of which do not coincide with the distribution areas of the host subspecies. The geographical subspecies of the flea species *Ctenophthalmus agyrtes*, *C. congener*, *Amphipsylla sibirica* may serve as classical examples.

The factors of external environment exert influence upon these ectoparasites, primarily during the period of their larval stage (as is the case of most terricolous insects). The fleas, being real parasites, could not exist without a host anywhere, and in the course of a long evolution of flea species and subspecies a substitution

Fig. 5. Boreo-Alpine type of distribution of the species *Amphipsylla sibirica* (Wagn.) A — northern population of the subspecies *A. sibirica sibirica* (Wagn.). B — populations of the subspecies *A. sibirica sepifera* J. et R. in the Alps. C — populations of the subspecies *A. sibirica hetera* Jord. in the High Tatras. D — populations of the subspecies *A. sibirica intermedia* Ros. in the Krkonoše Mountains. An example of ancient differentiation of populations which has resulted in the formation of clearly defined subspecies.

of one host species by another inside a definite ecological group of mammals necessarily resulted and played an important role. This substitution was promoted by the group specificity of fleas to a certain ecological unit of hosts (it is specially pronounced in the aphanipteria zone of small terrestrial mammals).

The substitution of one flea host by another takes place when a flea species can live on different host species which are taxonomically closely related and similar in their nidicolous bionomics, primarily within the framework of a definite faunal complex. Such host substitution existed and still exists now in vast territories of various aphanipteria zones.

Clearly defined subspecies have been formed in case of fleas infesting both fur

Fig. 6. Scheme of districts in steppe subregion of the palearctic region: I. The Pannonian district, II. the Macedonian district, III. the Black Sea district. Horizontal lines – distribution of the steppe flea complex. Thick line – boundary of the steppe district (Lavrenko 1952). A – West Balkan complex of flea fauna. B – Mediterranean subregion (East Mediterranean provinces).

and nests (Ioff 1941) and in case of species with a wide ecological valency, occurring from lowest geographical localities to highest mountainous regions, or in case of species associated with a certain biotopes or group of biotopes.

On the basis of the distribution of fleas of the superfamily *Ceratophylloidea*, typical for insectivores and rodents in the territory of Central Europe and the Balkan Peninsula, the following 4 faunal complexes may be distinguished:

1. The faunal complex of deciduous forest which predominates here.
2. The steppe complex which covers this territory in 3 regions: a) the Pannonian, most western region, b) the Macedonian region and c) the Black Sea region. These regions are considerably influenced by human activities. (Fig. 6.)
3. The Mediterranean faunal complex in the Balkan Peninsula.
4. The complex of European mountainous fauna, in which the following groups

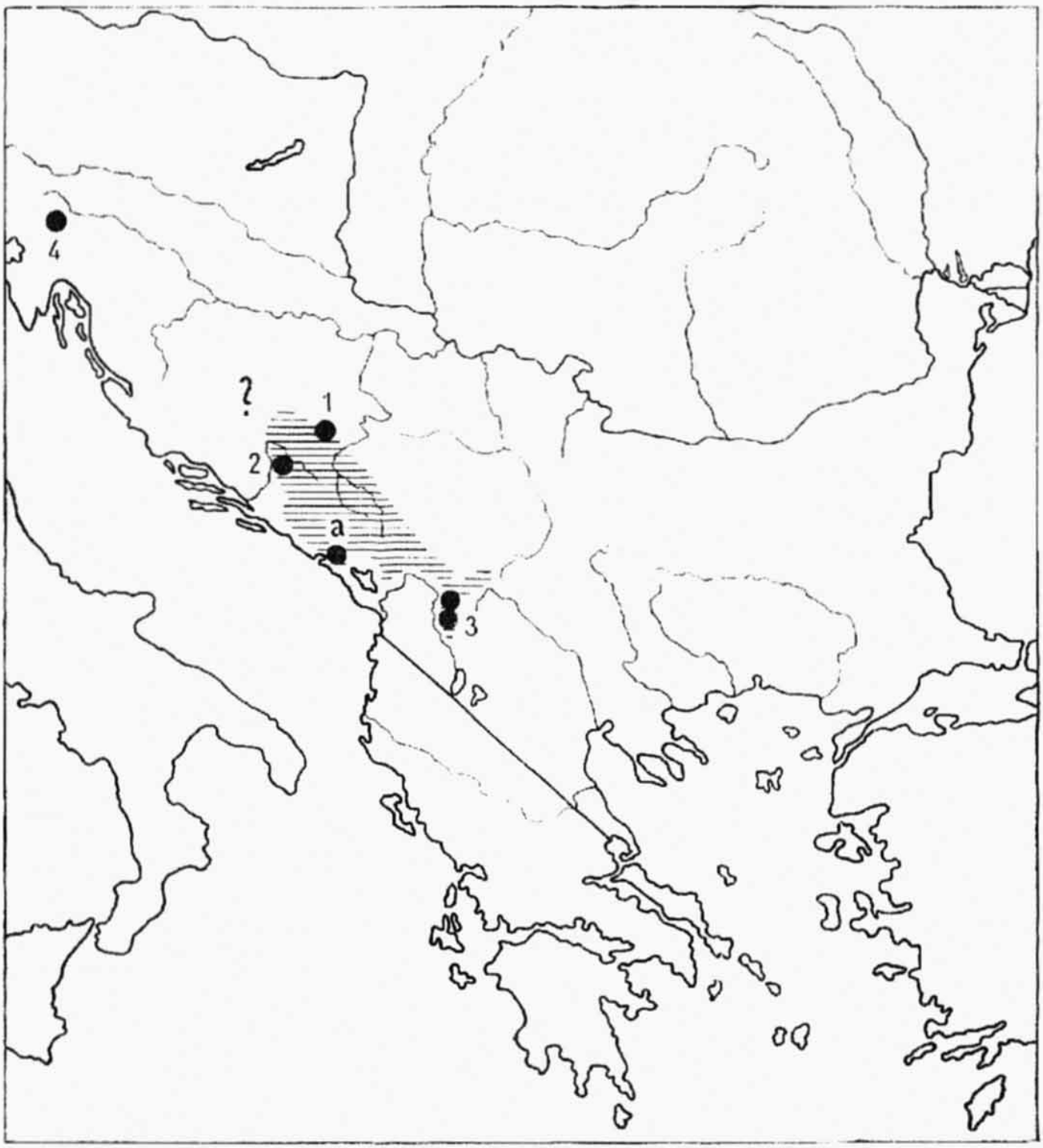

Fig. 7. Geographical subspecies of *Ctenophthalmus nifetodes* Wagn.: 1—*C. nifetodes nifetodes* Wagn. (Trebević). 2—*C. nifetodes eugeniae* Wagn. (Crno Polje, Prenj Planina). 3—*C. nifetodes martinorum* Smit (Velika Korabska Vrata, Korab). 4—*C. nifetodes brelihi* Ros. et Car. (Hotedršćica). a—locality of 1 ♀ *C. nifetodes nifetodes* Wagn. (Cetinje). Horizontal lines—known distribution of *Dolomys bogdanovi* Martino—potential locality of the species of the genus *Dolomys*, distant from its hitherto known distribution area, according to the finding of its specific flea in Hotedršćica. Diagonal line—position of the supposed division of the North and South Aegea by a strait.

of flea species can be marked out according to origin: a) species of the Alpine Eurasian complex (of the Alpine and Asia Minor origin), b) species originating from the Variscean mountains, c) species of the faunal complex of northern

tundra and forest-tundra, d) species of the taiga faunal complex, e) species of the faunal complex of the European deciduous forest.

The analysis of the mountainous faunal complex indicates its different origin and the resulting rich forms. Considering also other entomofauna (MAŘAN 1945, 1956) the following provinces can be noted in the mountainous region: 1. the province of the Variscean mountains, 2. the province of the Alpine mountains, 3. the province of the Carpathian mountains, 4. the province of the Stara Planina and the East-Serbian mountains, 5. the province of the Thracian-Macedonian mountains, 6. the province of the Albanian-Greek mountains and 7. the province of the Dinaric mountains. The present aphanipterological material referring to the last mentioned province (Fig. 7) proves that this province should be considered as an independent, higher zoogeographical unit (see BERG 1933 and his survey of zoogeographical distribution of fishes).

Hence it appears that the fleas parasitizing on rodents and insectivores are a suitable object for determining territorial geographical units in the territory of Europe and that they can be studied separately, because their species and geographical subspecies are considerably older than species and subspecies of mammals or birds.

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