CONTRIBUTION TO THE HISTORICAL BIOGEOGRAPHY OF THE ONISCIDEAN LINEAGE *MESONISCUS* (MICROCHETA, ISOPODA, CRUSTACEA)

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1. INTRODUCTION

As Emile Racovitza pointed out in his classical *Essai sur les problèmes biospéologiques*: "...on ne pourra se livrer à l'étude chorologique des Cavernicoles pris en bloc; car les faunes et les flores souterraines sont des faunes et des flores dérivées, formées par une agglomération d'êtres absolument différents, dont l'origine, l'âge, l'ancienneté d'immigration sont très divers. On sera donc réduit à faire des chorologies spéciales pour chaque groupe homogène, ce qui ne sera pas moins intéressant." (E. GH. RACOVIȚĂ, 1907, p. 459).

The genus *Mesoniscus* represents such a "homogeneous group": it is a morphologically well-defined group and clearly apart from the other groups of terrestrial isopods. Moreover, it has only a small number of species with the distribution strictly limited to the alpino-carpathic chain and, as such, particularly interesting from a biogeographical point of view.

2. SHORT CHARACTERIZATION OF THE GENUS *MESONISCUS* CARL, 1906

Completely depigmented body surface covered by numerous tubercles. No eyes. On the head, the tubercles have an irregular disposition, while on the pereion and pleon they form more or less regular transversal rows. The vertex is separated from the frons by a distinct frontal edge, slightly curved toward the posterior part. Antenna without squama. Antennar flagellum has up to eight articles. The antennae articles 2–5 present small tubercles with short hairs. Excepting the last 2–3 articles, all the antennar flagellum articles present distally a crown of hairs; articles 2–4 with a transversal row of sensitive rods. Antennula with two very wide basal articles and the terminal article reduced to a small sclerite with aestetascs.

Inner endite of the maxillule has 2 penicilli, the third one replaced by a terminal lobe with hairs. Maxilipeds have a wide truncated endite and a palpus of four articles. Maxilipedal segment completely fusioned with the cephalon. Head lacking the occipital furrow.

Elongated and narrow stomach; the superolateralia present fine hairs and a tooth directed toward the median part, on the ventral side there is a caudal row of tubercles; superomedianum elongated and narrowed in the middle. Superolateralia with

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strongly developed fringes with serrated tips; long clatri setarum anteriores, the two anterior filtratory plates are so close to each other so the anteromedianum is barely visible. The sides of the lamella dorsalis are curved toward the ventral part and the apex is convexely rounded.

Pereiopode I (at both sexes) present a field of characteristic scales on the external side of the carpus and propodus. Pereiopodes VI and VII have a row of dense hairs along the dorsal edge of the propodus. Pereiopodes have simple claws.

Male genital papillae reduced, the vasa deferentia open separately on two small cones close to each other and placed on the posterior edge of pereomere VII. Unique spermatophore formed by joining two spermatophores.

All pleopodes lack a tracheal system. Pleopode 1 presents the same conformation at both sexes. Pleopode 1 (at both sexes) with a big, triangular exopodite with rounded corners and a much smaller endopodite. Only the second male pleopode modified for the sexual function with a very long and thin endopodite with three articles vaguely distinguishable and, slightly before the middle, with a notch bearing a prominent lobe. Pleopodes 3–5 endopodite is split in two (pleopode 3) respectively in three (pleopodes 4 and 5) oval, elongated lobes.

Telson prolonged distally in a tip and laterally like two wings. Both uropodal rami shaped like rods with a slight distance between their articulations and greatly exceeding the telson.

The characters that distinguish the genus *Mesoniscus* (and thus the section Microcheta Schmalfuss, 1989) from the other sections of the Oniscidea led to an intense debate concerning its phylogenetic position. In the present, there are four main opinions concerning the position of the section Microcheta in the framework of the suborder Oniscidea: (1) WÄGELE (1989) considers the Mesoniscidae as a sister-group of the Tylidae, together forming the sister-group of the Ligiidae, on the other hand, Synocheta is the sister-group of Crinocheta and, together, they form the sister-group of Tylidae + Mesoniscidae + Ligiidae; (2) SCHMALFUSS (1989) regards Diplocheta (Ligiidae) as the sister-group of the ensemble Microcheta + Synocheta + Crinocheta, inside this group, Microcheta is the sister-group of the Synocheta + Crinocheta; (3) TABACARU & DANIELOPOL (1996a and b) following the classification of Vandel (1943) divide Oniscidea into Tylomorpha (Tylidae) and Ligiamorpha in which Diplocheta is the sister-group of the monophylum Orthogonopoda, in its turn, Orthogonopoda is divided in Monospermophora (Microcheta and Synocheta) and Dispermophora (Crinocheta); (4) ERHARD (1998) sees Diplocheta as a sister-group for his new taxon, Holoverticata, in which the Tylidae represent the sister-group of Orthogonopoda, but he considers Microcheta as the sister-group of Euoniscoidea, a monophyletic ensemble formed by Synocheta + Crinocheta.

As the phylogenetic position of the Microcheta created, and still creates, an intense debate, similarly the geographic distribution of the genus *Mesoniscus* raises interesting biogeographical problems.

3. GEOGRAPHIC DISTRIBUTION OF THE GENUS *MESONISCUS*

According to GRUNER & TABACARU (1963) the genus *Mesoniscus* contains only two species: *Mesoniscus alpicola* (HELLER, 1858) and *Mesoniscus graniger* (Frivaldsky, 1865). *Mesoniscus alpicola* is characterized by the presence of 7 short aesthetascs on the terminal article of the antennula, long and narrow scales on the carpus and propodus of the first pereiopode, uni/bipennaceous spines on the propodus of the pereiopode VII, the endopodite of the second male pleopode presents a dented lobe and, distally, one more row of short spines on the external edge, the pleopode V has a shallow notch on the external edge and the uropodal propodus with one short rod in the inner distal corner.

Mesoniscus graniger is distinguished from M. *alpicola* by the following characters: 3 aesthetascs on the terminal article of the antennula, the hand-like shape of the scales on the carpus and propodus of the first pereiopode, rod-like spines on the propodus of the pereiopode VII, a smooth lobe and, distally, more rows of short spines on the external edge, the pleopode V has a deep notch on the external edge and the uropodal propodus bearing one long rod and a short one in the inner distal corner.

An overall regard (Fig. 1) on the spreading of the two species belonging to the genus *Mesoniscus*, allows us to notice a series of characteristic aspects:

– *Mesoniscus alpicola* is found exclusively in the Alps where it has a disjunct distribution, respectively in a restricted limestone region from the Southern Centre Alps, between the Maggiore and Garda Lakes (the Bergamasc or Lombard Alps) and in a larger region represented by the Northern Calcareous Alps from the Inn Valley to Vienna and to Graz in the South. As KARL HOLDHAUS (HOLDHAUS 1954 quoted by TABACARU, 1969) had underlined, the distribution of this species emphasizes a feature typical for the Alpine cavernicolous fauna, namely that of a discontinuous areal with two marginal refugium areas.

– *Mesoniscus graniger* is spread in the whole Carpathic chain, beginning from the Northern Carpathians (Slovakia), the Romanian Carpathians, South Danube Carpthians (Serbia), the Dinarids (Serbia, Bosnia and Hertzegovina) and the Iulian Alps (Slovenia and Italy). South of the Danube, the spreading of the species *Mesoniscus graniger* does not cross the line Nişava–Timok. Also, we have to point out there is no record from Bulgaria, Macedonia, Albania and Greece.

– between the two species there is a clear separation: in the north by the Győr Depression, by the Vienna Basin and the Morava corridor while in the south by the upper basins of the Drava and Sava Rivers (the Carinthian Depression) and the basins of the Adige and Piave Rivers (the Dolomitic and the Venetian Alps)

Beginning from GRUNER's statement (1966), namely the genus *Mesoniscus* is an ancient Alpine element, we consider the species *Mesoniscus alpicola* as th

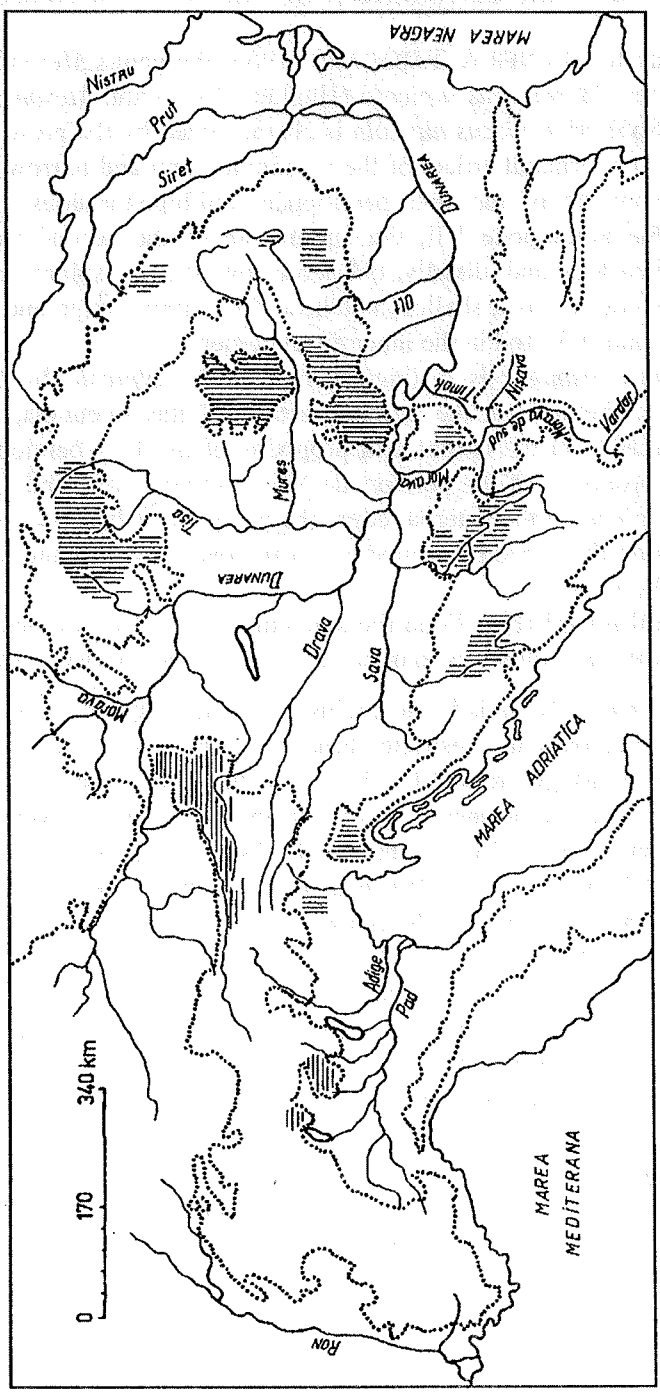

Fig. 1. – Spreading of the species belonging to the genus *Mesoniscus*: *M. graniger* (vertical hatchings) and *M. alpicola* (horizontal hatchings).

most primitive species of the genus, a statement sustained also by a series of morphological and systematical arguments (TABACARU, 1969). At *M. alpicola*, the hairs found on the propodus of the pereiopodes VI and VII are formed by thin, uni- or bi-pennaceous hairs (see Fig. 2, A). On the contrary, at *M. graniger*, the hairs from the propodus of the pereiopodes VI and VII are formed by club-like hairs, only distally equipped with fringes (see Fig. 2, B). Pennaceous hairs are widespread among the Isopoda so we can regard this as a primitive condition. Evolutionarily speaking, it is easier to derivate the condition existing at *M. graniger* (by simplification or reduction of the pennaceous hairs) from the condition found in *M. alpicola* than other way.

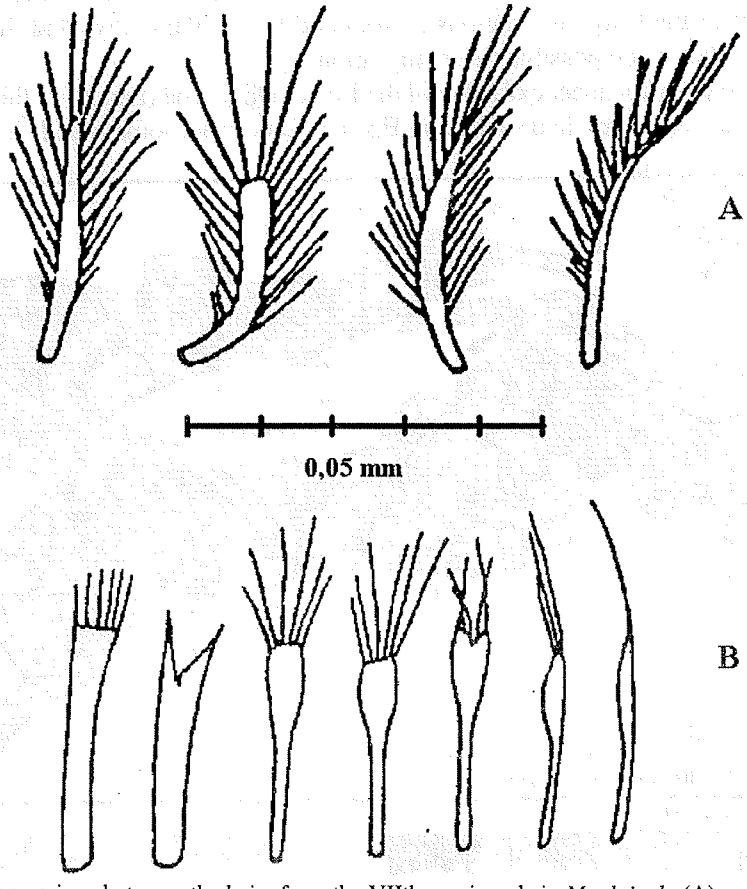

Fig. 2. – Comparison between the hairs from the VIIth pereiopode in *M. alpicola* (A) and *M. graniger* (B) (after GRUNER & TABACARU, 1963, modified).

Out of these features, emerges the following question: the species *Mesoniscus graniger* has a Northern Carpathian origin, or, maybe, a Bohemian one (and from

there it spread southward along the Carpathic chain to the Dinarids and the Iulian Alps) or, on the contrary, it has an Illyric origin (from where by the Dinarids and the South-Danube Carpathians, it went northward through the Romanian Carpathians up to the Northern Carpathians)?

4. PALEOGEOGRAPHIC EVOLUTION OF EUROPE

In order to outline the migrations leading to the apparition of the two species (along with their present-day distributions) belonging to the genus *Mesoniscus*, we have to take into account the data concerning the paleogeographic evolution of Europe (after RÖGL, 1984; STEININGER & RÖGL, 1985; RÖGL, 1998), respectively the isolation of the Carpathic regions surrounded by the Paratethys and the various land bridges that made possible these migrations.

No European continent existed until the Lower Oligocene (Fig. 3). In this moment (25–23 million years ago), in the Chattian-Egerian-Caucasian, some island chains of the

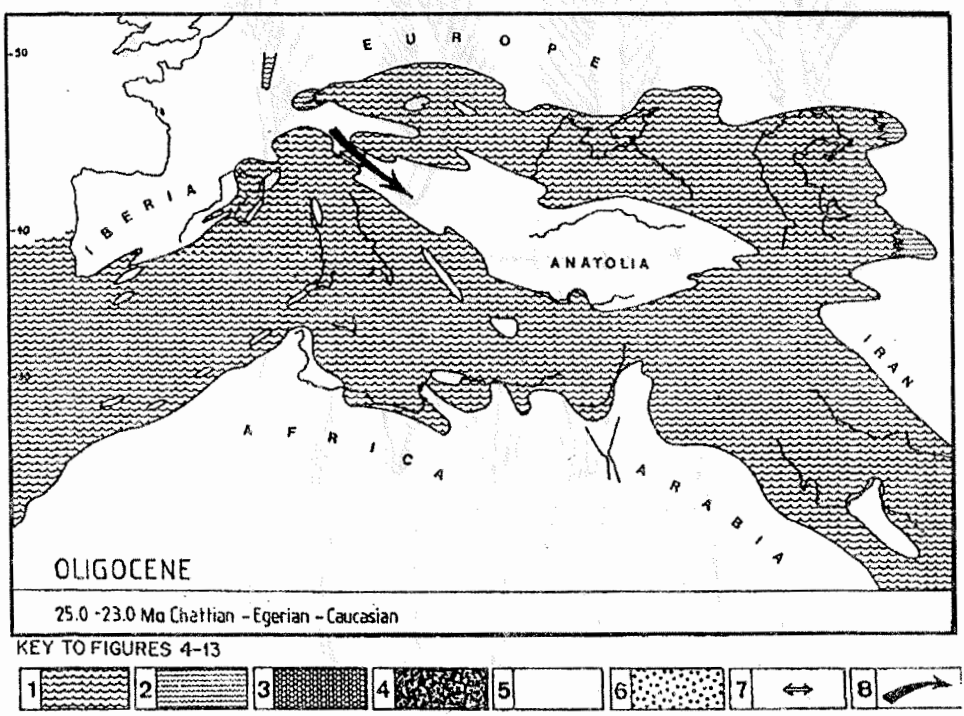

Fig. 3. – Palinspastic reconstruction of the Circum-Mediterranean Region in the Upper Oligocene. Explanation of symbols: (1) marine realms; (2) marine realms with reduced salinity; (3) endemic facies of the Paratethys; (4) eavaporitic realms; (5) continental realms; (6) important areas of fluvio-terrestrial sedimentation; (7) basins narrowed by tectonic processes; (8) principal direction of migration pathways; the same explanation holds for the rest of the figures (after RÖGL & STEININGER, 1984).

rising Alpine System began to emerge. Up until the Upper Oligocene no communication existed between the European Archipelago and Asia as a consequence of the Turgai Strait that extended on a north-south direction along the Ural Mountains. In the south-east of Europe, there was the huge Dinarian-Pelagonian-Anatolian landmass, linked to the rest of Europe by recurring landbridges across the Slovenian corridor.

In the Lower Miocene (Middle Burdigalian-Upper Burdigalian, 20–17 million years ago) the Paratethys opened a new short-lived seaway along the western Alpine foredeep to the Rhone Basin and to the Mediterranean (Fig. 4).

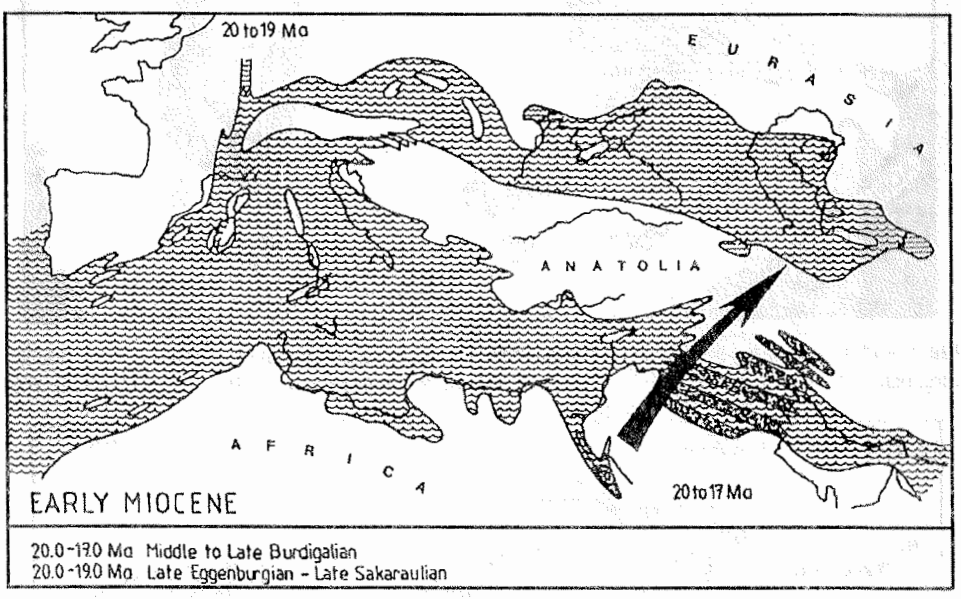

Fig. 4. – Palinspastic reconstruction of Europe in the Lower Miocene: the Eurasian-African collision (after RÖGL & STEININGER, 1984).

The African-Eurasian collision from the Upper Ottnagian (Lower Miocene) profoundly altered the basins of the Paratethys by the destruction of the seaways to the oceans (Fig. 5). Thus, the seaway along the western Alpine foredeep was closed in Bavaria, breaking the Mediterranean connection from the Alpine molasse trough. The only remaining marine connection to the Mediterranean passed through northern Yugoslavia, so preventing any contact between the Alps and the Dinarides.

Ulteriorly, the sea withdrew from the Alpine-Carpathian molasse basin and only the most central part in Hungary remained marine. This is the first connection between the Alps, the Bohemian Massif and the Carpathians.

During the Karpatian (approx. 16, 8 million years ago), a short transgression forms an embayment into the Austrian-Bohemian molasse trough but without interrupting the connection between the Alps, the Bohemian Massif and the Carpathians (Fig. 6).

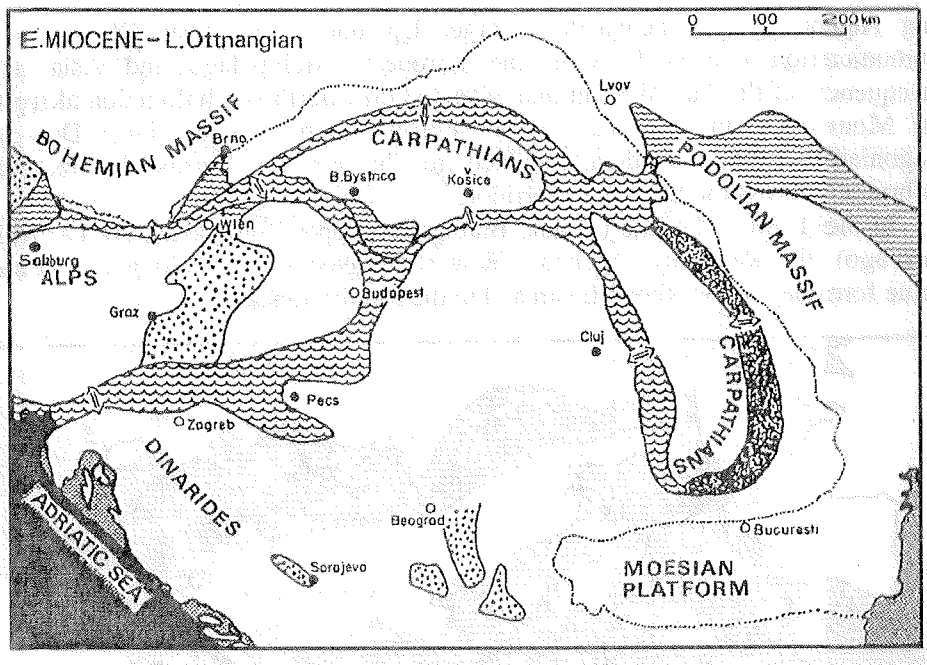

Fig. 5. – Palinspastic reconstruction of Europe in the Upper Ottnagian: marine conditions remained in the central part of the Paratethys which was connected with the Mediterranean (after RÖGL & STEININGER, 1984).

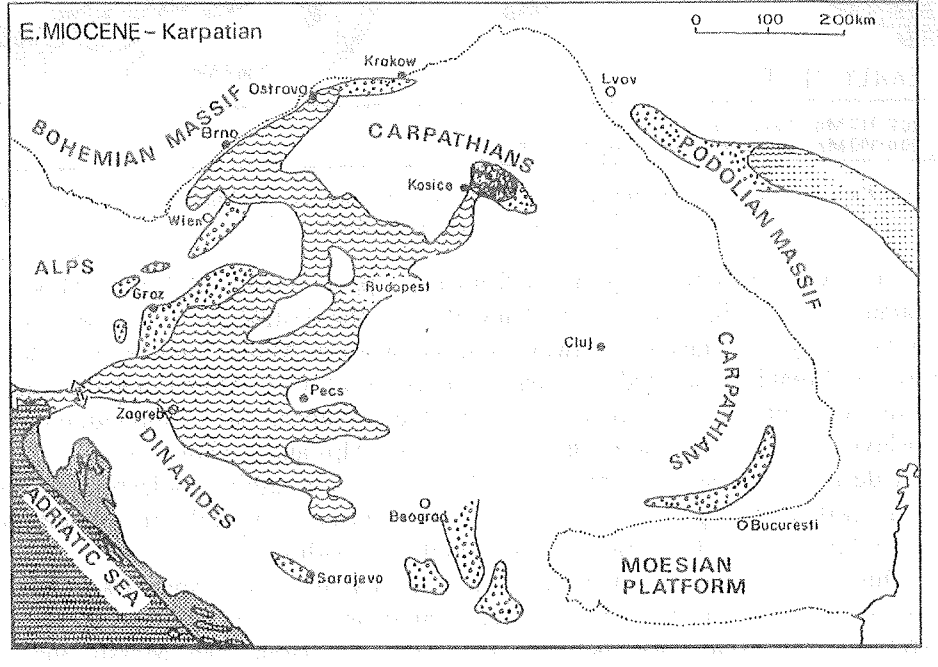

Fig. 6. – The Karpatian transgression (after RÖGL & STEININGER, 1984).

In the Middle Miocene (Langhian-Lower Badenian-Tarkhanian, 16,8–16 million years ago), the Adriatic plate, including the Dinarides was in a south-eastward position and a deep-water connection from the Mediterranean to the Central Paratethys existed to the north of it ("the Slovenian corridor"). At this point, the Carpathian arc system developed and created a series of extensional basins (*e.g.*, Vienna Basin, Transsylvanian Basin, Pannonian Basin) (Fig. 7).

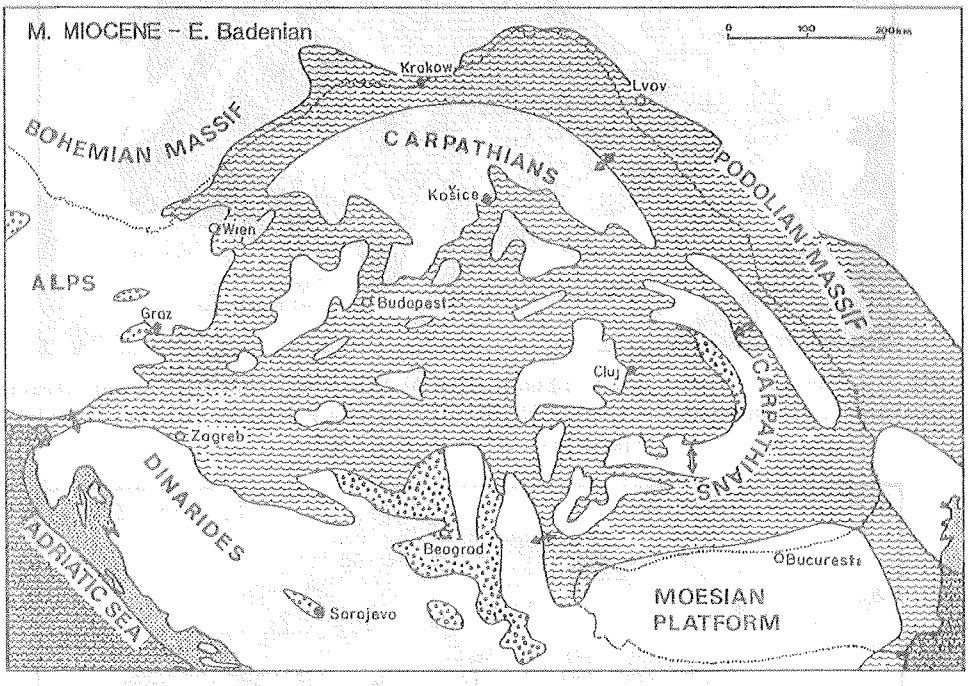

Fig. 7. – Palinspastic reconstruction of Europe in the Lower Badenian: flooding of the entire Central Paratethys, formation of the Vienna, Pannonian and Transylvanian basins (after RÖGL & STEININGER, 1984).

Also, in the Lower Badenian, a major transgression filled the Carpathian foredeep and interrupted, temporarily, the connection between the Carpathians and the Bohemian Massif. The seaway connecting the Paratethys with the Mediterranean remained open. This marine connection to the Mediterranean along the northern Yugoslavian corridor was retained also in the Middle Badenian.

In the Middle Badenian (Fig. 8), the marine connection along the northern Carpatians was restricted (and interrupted) by the rising Carpathians and by sills formed by volcanic activity and by growth of corallinacean reefs in the Carpathian foredeep and the adjoining satellite basins from Transylvania and Eastern Slovakia, where vast areas of evaporites were formed. The connection Alps–the Bohemian Massif–the Carpathians is definitively established.

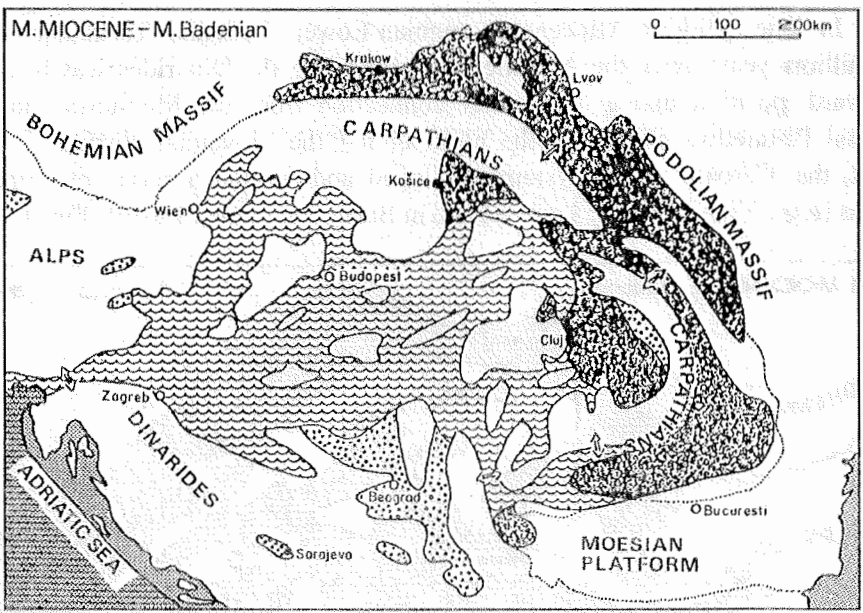

Fig. 8. – Palinspastic reconstruction of Europe in the Middle Badenian: formation of vast areas of evaporate in the Carpathian foredeep and the adjoining basins of Eastern Slovakia and Transylvania (after RÖGL & STEININGER, 1984).

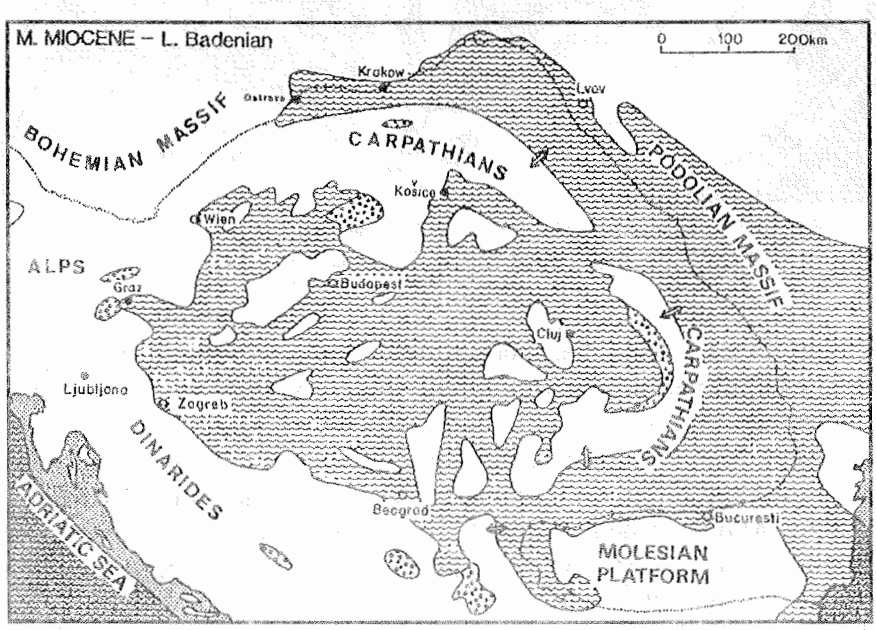

Fig. 9. – Palinspastic reconstruction of Europe in the Upper Badenian: re-flooding of the eastern and Central Paratethys, the gateway to the Mediterranean at the northern Slovenian corridor was closed (after RÖGL & STEININGER, 1984).

Ulteriorly, in the Upper Badenian (Fig. 9), (approx. 14, 5 million years ago) a strong transgression was recorded in the entire Paratethys basin but without the interruption of the connection between the Carpathians and the Alpino–Bohemian system. In turn, the gateway to the Mediterranean at the northern Yugoslavian corridor was closed: this is the first connection between the Alps and the Dinarides (Fig. 10). Of contrary, there was still no connection between the Carpathians and the Dinarides.

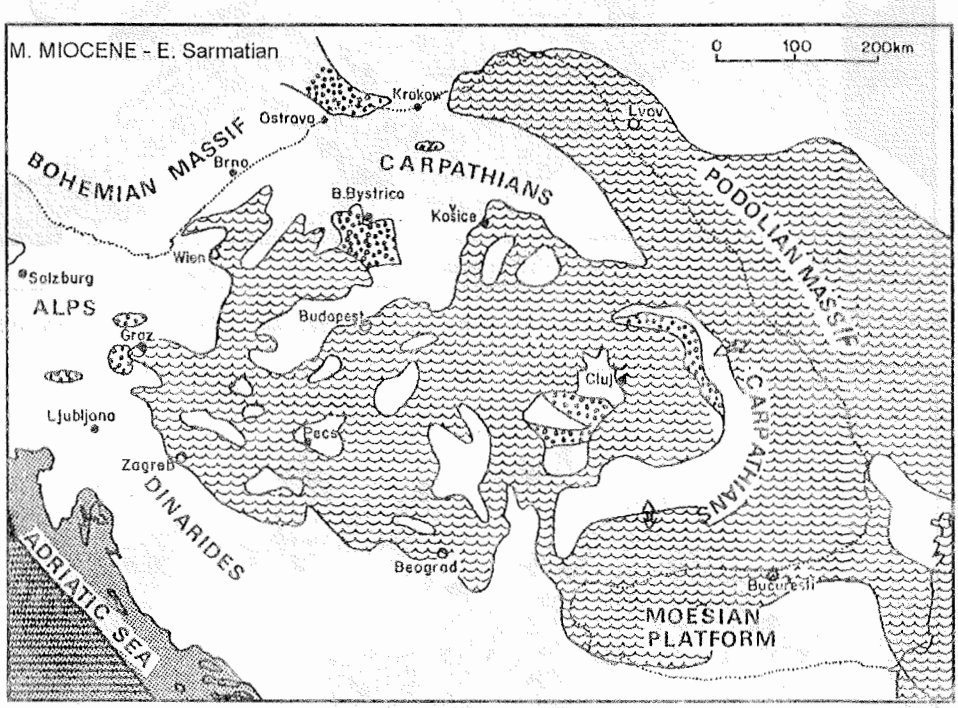

Fig. 10. – Palinspastic reconstruction of Europe in the Lower Sarmatian: the paleogeographic configuration shows no distinct differences to the Upper Badenian (after RÖGL & STEININGER, 1984).

In the Upper Miocene (Lower Tortonian-Pannonian-Upper Bessarabian 12–11 million years ago) (Fig. 11) the Carpathian foredeep was uplifted; the marine seaway separating the Carpathians from the Dinarides was maintained, an aspect supported by the interfingering of the typical *Congeria-Melanopsis* facies of the Vienna and Pannonian Basins with the euryhaline facies from the Dacian Basin.

Also in the Upper Miocene, but in Messinian-Upper Pontian (6–5.5 million years ago) (Fig. 12), the closure of the Atlantic-Mediterranean gateway resulted in the Messinian salinity crisis and, as a result, of the Mediterranean desiccation. The Paratethys started to divide into isolated basins. This fact led to the first connection between the Carpathians and the Dinaric plate (Carpathians-Dinarides). The geography of modern Europe was manifested in the Pliocene.

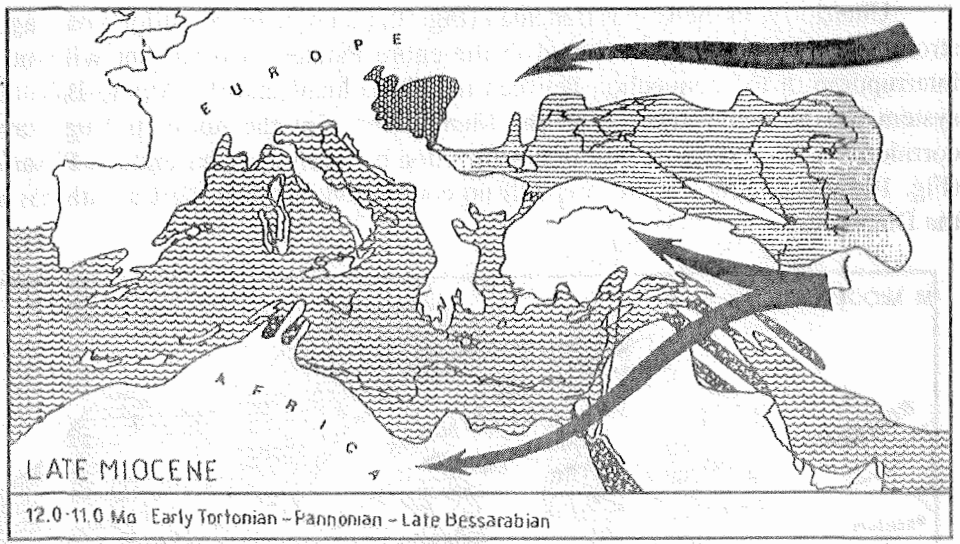

Fig. 11. – Palinspastic reconstruction of Europe in the Upper Miocene (after RÖGL & STEININGER, 1984).

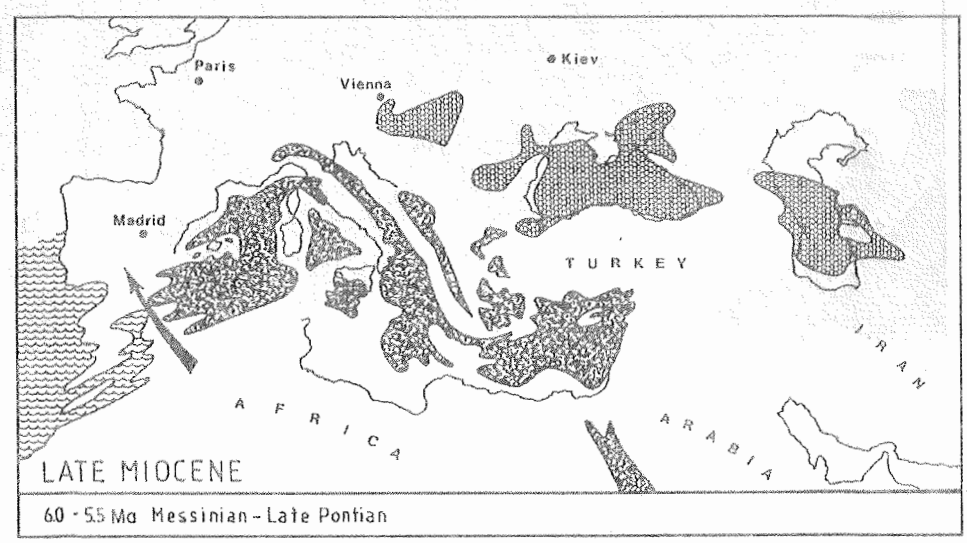

Fig. 12. – Palinspastic reconstruction of Europe in the Upper Pontian (the Messinian salinity crisis (after RÖGL & STEININGER, 1984).

5. COMMENTS ON THE HISTORIC DISTRIBUTION OF THE GENUS *MESONISCUS*

Taking into consideration the paleogeographic evolution of the European continent (after RÖGL, 1984; STEININGER & RÖGL, 1985; RÖGL, 1998) and starting with the statements of GRUNER (1966) and TABACARU (1969), we regard as more

probable a North-Carpathian or a Bohemian origin for the species *Mesoniscus graniger* (and a subsequent migration along the Carpathian chain to the Dinarides and the Iulian Alps) than an Illyric origin and a northward migration from here.

The following facts endorse our affirmation: the Alps established at first a connection with the north of the Carpathians (by the agency of the Bohemian Massif) approximately 17 million years ago. Of contrary, the connection between the Alps and the Dinarides was established much later: the Slovenian corridor was closed only in the Upper Badenian, so approximately 14.5 million years ago. The connection between the Alps and the Carpathians is interrupted temporarily during the strong Lower Badenian transgression (that filled the Carpathian foredeep), but in the Middle Badenian, in correlation with the uplift of the Carpathians, the Alpino-Carpathian connection is definitively established. We also have to point out that the connection between the Alps and the Dinarides was established in the Upper Badenian, therefore, after the definitive formation of the Alpino-Carpathian connection. Moreover, we have to point to a much later establisment of the connection between the Carpathians and the Dinarides in the Messinian-Upper Pontian (6–5.5 million years ago).

In our opinion, a northern origin (or maybe a Bohemian one) for the species *Mesoniscus graniger* is supported by an earlier connection, and so for a longer period of time, between the Alps (especially the Eastern Alps) and the Carpathians. The establishment of the connection Dinarides-Carpathians is much younger than the connection Alps-Carpathians, hence another argument in favor of a northern origin.

Mesoniscus graniger is not the sole species from our fauna with a northern (Bohemian) origin: based on zoogeographical studies on the Coleoptera, R. Jeannel (1942, 1943) had pointed to the presence in the Carpathians of lineages originating in the ancient Hercinic massif of Bohemia. These lineages colonized the Carpathians from the North to the South.

Likewise, we can take into consideration the possibility of a Bohemian origin for the common ancestor of both species of *Mesoniscus* but the data concerning the fauna of Bohemia – obviously, strongly affected by the glaciations (TABACARU 1970) – are not enough in order to argue this hypothesis.

Starting from R. Jeannel's statement (1942), namely the Egeides (and especially the Northern Egeide) represented a very important dispersion center, we can not ignore the hypothesis of an egeidian (or illyrian) origin for the species *Mesoniscus graniger*. Concomitently, Jeannel underlined the impossibility of the egeidian lineages to colonize the Southern Carpathians before the end of the Pliocene.

In the Chattian-Egerian-Caucasian (25–23 million years ago), a huge southeastern European Dinarian-Pelagonian-Anatolian landmass was populated by recurring landbridges across the Slovenian corridor. These connections, maintained in the interval between the Middle Burdigalian and the Upper Sakaraulian, were interrupted ulteriorly in the Upper Ottnagian (preventing any link between the Alps and

the Dinarides) and re-established only in the Upper Badenian. The first connection Carpathians-Dinarides took place only in Messinian-Upper Pontian (Upper Miocene).

These recurring landbridges from the Chattian-Egerian-Caucasian might have led to the colonization of the European Dinarian-Pelagonian-Anatolian landmass with the ancestral Alpine form of the species *Mesoniscus alpicola*. The subsequent breaking, in the Upper Ottnagian, of these landbridges, led to the fragmentation of the ancestral Alpine form into two populations which will evolve differently: in the Alps, into *Mesoniscus alpicola* and into *Mesoniscus graniger* in the Dinarides. In the Upper Badenian, with the re-establishment of the connection between the Alps and the Dinarides, the two forms where reproductively isolated. As the Dinarides established a connection with the Carpathians (in the Messinian-Upper Pontian), the species *Mesoniscus graniger* went northward in the Carpathians but without crossing eastward in the Balkans.

The presence of these landbridges between the Alps and the Dinarian-Pelagonian-Anatolian landmass before the formation of the Alps-Bohemian Massif-Carpathians connection, might suggest and argue for a southern (Illyric) origin of the species *Mesoniscus graniger*. The subsequent isolation of the Dinarides from the Alps and also from the Carpathians, further argues for this hypothesis. Therefore, we might regard the species *Mesoniscus graniger* as an ancient Dinaric element and not a Carpathian one.

However, this hypothesis presents two drawbacks. The first one regards the existence and the duration of the land bridges between the Alps and the Dinarides. These lanbridges figure on the paleogeographic maps given by RÖGL in 1984 and by STEININGER & RÖGL in 1985 but they are not figured in the paleogeographic maps given by RÖGL in 1998 so rising question marks about their existence and duration.

Secondly, there is a time gap between the formation of the Alps-Carpathians connection (Lower Carpatian, approx. 17.3–16.4 million years ago) and the establisment of the first certain connection between the Alps and the Dinarides (Upper Badenian, approx. 14–13 million years ago). Even considering a colonization of the Carpathians after the Lower Badenian transgression and the definitive establishment of the Alps-Carpathians connection from the Middle Badenian (approx. 15–14 million years ago), there is still a time interval until the formation of the Alps-Dinarides connection. It seems unlikely for the ancestral form of the species *Mesoniscus graniger* not to "use" this time interval in order to colonize the Carpathians and later on to migrate after the establishment of the Alps-Dinarides connection.

6. CONCLUSIONS

The earlier establishment of the connection between the Alps and the Carpathians and its longer duration, represents the main reason why we chose for the first hypothesis, that of a north-western Carpathian (or maybe Bohemian) origin for

the ancestral form of the species *Mesoniscus graniger*, subsequently followed by a southward migration along the Carpathian chain to the Dinarides and the Iulian Alps.

In our opinion, *Mesoniscus graniger* represents an ancient Carpathian element and not a Dinaric one.

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