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Fossil Tortoises of the Genus *Geoemyda* GRAY, 1834 (s. lat.) of Europe

[Plates XXIX—XXXIII, 1 mape and 7 text-figures]

Żółwie kopalne z rodzaju *Geoemyda* GRAY, 1834 (s. lat.) Europy

Европейские ископаемые черепахи рода *Geoemyda* GRAY, 1834 (s. lat.)

CONTENTS

I. INTRODUCTION

Remains of tortoises of the genus *Geoemyda* are fairly often found in the Tertiary and the youngest Pleistocene strata of Europe. HOOLEY (1905) was the first to ascertain the occurrence of this form in the Eocene of England. It was not till the third decade of the twentieth century that the presence of comparatively numerous geoemyds was found in Central Europe (GLAESSNER, 1926), SZALAI (1932, 1934) and HUMMEL (1935) also gave attention to the occurrence of the members of this genus. In the latest period of some dozen years the presence of remains of geoemyds have been reported from new localities in the countries of Central (THENIUS, 1951) and Eastern Europe (TELEPNEVA, 1964). A new species has recently been described from the Polish Pliocene (MŁYNARSKI, 1964).

During the examination of fossil materials of tortoises in the collections of Germany, Poland, Czechoslovakia, Hungary, Romania and the USSR we found some more remains of tortoises under discussion and had an opportunity to get better acquainted with the descriptive material (types) of a few forms.

Both in the title and in the text we use the name *Geoemyda* sensu lato, treating it as a collective genus for related forms. This is connected with the revision of this systematic unit carried out by McDOWELL (1964), who divided it into three distinct genera. These genera are regarded here as subgenera. Our opinion on this matter will be presented in the part given up to systematics.

In the taxonomic part of this paper we offer a method, which makes it possible to identify fossil remains of geoemyds relatively assuredly, even if the materials are fragmentary. In the systematic part we give a survey of all the forms described so far, including the revision of their systematic position and the description.

The tortoises of the genus *Geoemyda* form a morphologically distinct and characteristic group with two Recent evolutionary centres, situated in the Oriental Region and on the border of the Sonarian Region with the Neotropical. In the Tertiary their range was considerably more extensive and shifted in relation to the present one, which is evidenced by the occurrence of their remains both in Europe and in north-western Asia (MATSUMOTO, 1922; SHIKAMA, 1956).

We wish to express our heartfelt thanks to Prof. H. MATTHES (Geiseltal Museum at Halle, G. D. R.), Prof. N. MACAROVICI (Institute of Geology, Al. I. Cusa University, Iași, Romania) and Prof. M. KRETZOI (Hungarian Institute of Geology, Budapest) for the use of material from their institutions and for photographs of specimens.

We are also indebted to Miss S. ROLLIUS of Halle University for valuable information and to Dr W. SZYMCZAKOWSKI from Kraków for examining contemporary materials in Vienna Museum. We also used contemporary materials of the collections in Berlin (Zoologisches Museum) and Leningrad (Institute

of Zoology, Academy of Sciences of the U. S. S. R.). We desire to express our gratitude to the Managements of these scientific institutions for permission to do it.

II. SYSTEMATIC POSITION

According to WERMUTH and MERTENS'S (1961) classification of contemporary tortoises, the genus *Geoemyda* GRAY includes 15 species. On the basis of very detailed morphological studies on the members of the family *Emydidae* (= *Emydinae* auct.) MCDOWELL (1964) has recently distinguished three genera of geoemyds: *Geoemyda* GRAY, 1854; *Heosemys* STEJNEGER, 1902 and *Rhinoclemys* GRAY, 1863. He based himself, above all, on craniological material, but also took into account the taxonomic characters of the morphology of the shell. The division offered by MCDOWELL makes a distinction between the American *(Rhinoclemys)* and the Asiatic species *(Geoemyda* and *Heosemys)*. The European fossil forms from the late Tertiary probably belong to the second group of species, but the position of many of them is not clear. The fairly close determination of systematic position on the basis of the shell or its isolated elements is often impossible, whereas the identification of general „geoemydal" characters common to all these forms does not present major difficulties. For this reason we propose to use the notion of one collective genus tentatively. The most important character common to the forms belonging to this genus is the presence of neurals tapering cephalad, which occur in comparatively large numbers in all the specimens examined of one species along with a number of other characters found in them (see Taxonomy). As has already been mentioned, the genera distinguished by MCDOWELL (1964) are treated here as distinct subgenera of the genus *Geoemyda* analogically, for instance, to the subgenera of the fossil testudinids of AUFFENBERG (1963). For a few forms described in this paper we erect two new subgenera based on characters absent from contemporary species. The systematic division given here is of practical importance and connected with the specific nature and the limitedness of palaeontological taxonomy. It seems to us that the systematic position of fossil forms cannot be treated in the same way as the position of contemporary forms, where the possibility of analysis of characters and their selection are considerably greater. Consequently, the opinion of WILLIAMS (1954, p. 8) that the generic position of European fossil emydids is uncertain and their division into genera and species rather reflects some evolutionary tendencies seems to us reasonable.

III. TAXONOMY

The European fossil members of the genus under study have been identified exclusively on the basis of shells. These remains exhibit distinct characters of the *Batagurinae* of the „*Geoemyda* Complex" (MCDOWELL, 1964) and those of *Geoemyda* s. lat. The taxonomy of these forms is based on distinctive characters of the shell, assuming that they are homologous to other, unknown, parts of the skeleton.

The shell of fossil geoemyds is as a rule characterized by the massive structure of plates, which are always evidently separated by sutures and sculptured. Reflecting the structure of the horny shields, the sculpture may be characteristic of species and taxonomically significant. In this case the appearance of lines of the horny layer surrounding the areolae of centrals and laterals is particularly characteristic.

The carapace is distinctly convex except for the forms with a dubious position, in which it is flat. In most of the species there is a neural keel. Pleural (lateral) keels are absent or hardly marked. The peripheral margin of the cranial and, especially, pygal parts may be undulate or serrate. The proneurals (all the names of plates and shields after STAESCHE, 1961) have often a marked nuchal notch. A large number of neurals (except N — I and the last ones) broaden caudad. There is always only one metaneural joined with the narrow, often convex pygal. The edges of lateral pleurals are parallel to each other. The bridge buttresses of the carapace are for the most part well visible, set a short or somewhat longer distance appart. In larger fragments they may be traced on the inner surface of pleurals and peripherals.

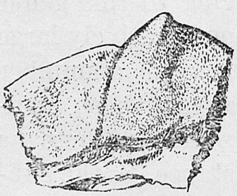


Fig. 1. Epiplastron of *Geoemyda mossoczyi* MŁYNARSKI (nat. size). Del. J. ŚWIECIMSKI

The plastron is massive and united to the carapace by a wide bridge. It has not been found as yet whether the posterior lobe is marked by mobility, which has been demonstrated in contemporary species and might constitute an important sexual (MERTENS, 1941) or specific character (our own observations concerning the specimens of G. *(Rhinoclemys) punctularia* (DAUDIN) from the collection of the Institute of Zoology, Academy of Sciences of the USSR in Leningrad). Special attention should be given to the so-called epiplastral lips, which are well developed in most of the forms under study and have the shape of cylinders symmetrical in relation to each other and slightly pointed at the ends. Such cylinders are also characteristic of many contemporary geoemyds and can readily be noticed on the inner side of the epiplastra (in contemporary forms they are very well developed, e. g., *G. (G.) spengleri* (GMELIN); *G. (Heosemys) depressa* ANDERSON (holotype), *G. (Rhinoclemys) annulata* (GRAY); *G. (R.) areolata* (DUMÉRIL, BIBRON et DUMÉRIL) and *G. (R.) pulcherrima* (GRAY).

The entoplastron is broad, tetragonal in outline, and it elongates or broadens with growth. It is traversed by the humeropectoral sulcus more or less medially on the external surface. In all the specimens the xiphiplastra had a distinct anal notch.

Fig. 2. Entoplastrons of *Geoemyda mossoczyi* MŁYNARSKI (A) and *G. eureia* (WEGNER) (B). Nat. size. Del. J. ŚWIECIMSKI

The grooves of horny shields are very well seen. The precentrals are always broad and the lateromarginal grooves run on the surface of the peripherals. The axillaries and inguinals are well developed. The grooves of postcentrals cross the surface of the metaneurals at a considerable height in the pygal portion of the carapace (the character of the *Batagurinae*).

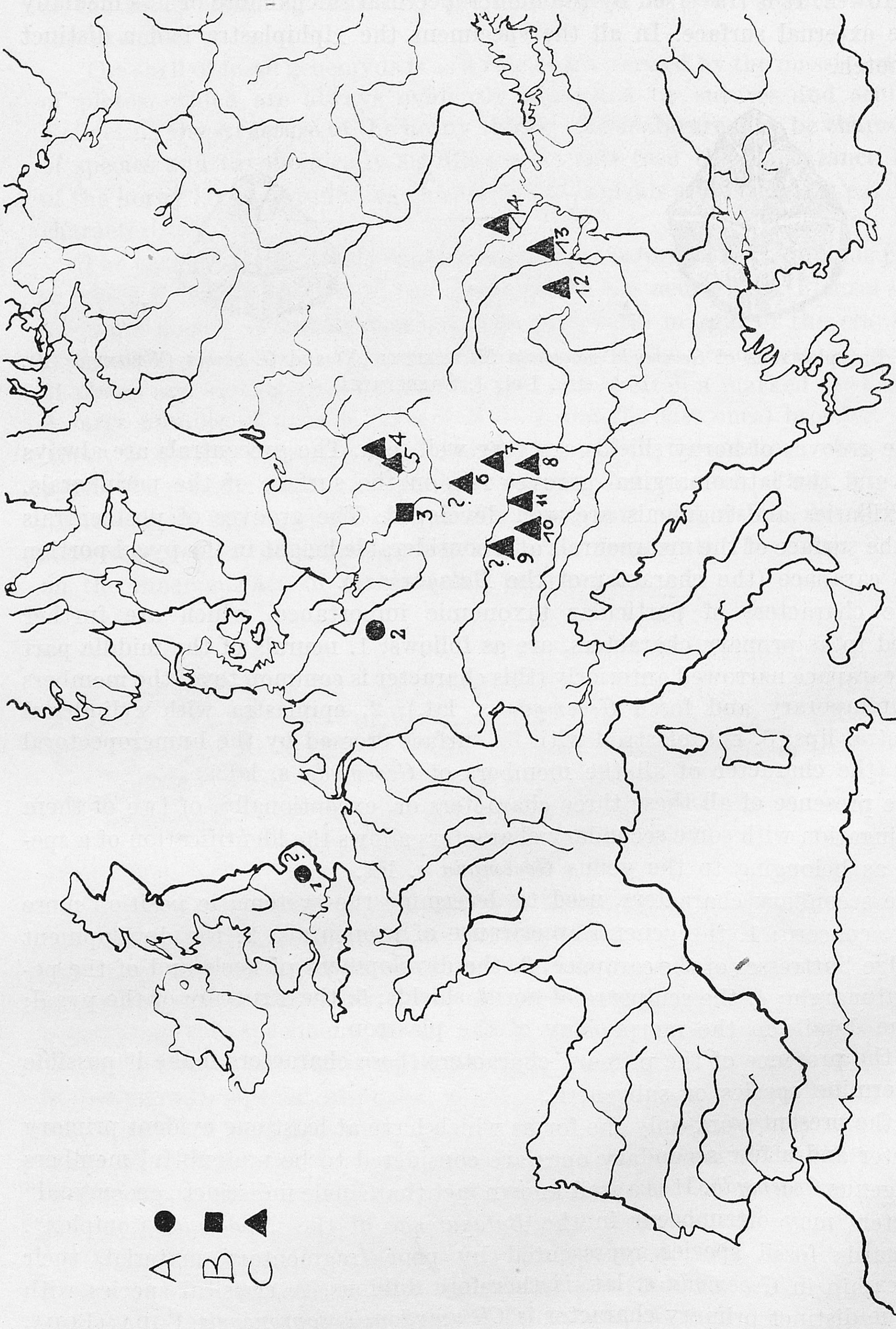
The characters of particular taxonomic importance, which are further referred to as primary characters, are as follows: 1. neurals of the middle part of the carapace narrowed anteriorly (this character is common to all the members of contemporary and fossil *Geoemyda* s. lat.); 2. epiplastra with cylindrical epiplastral lips; 3. entoplastron with its surface crossed by the humeropectoral sulcus (the character of all the members of *Geoemyda* s. lat.).

The presence of all these three characters or, exceptionally, of two of them in conjugation with some secondary characters allows the identification of a specimen as belonging to the genus *Geoemyda* s. lat.

The secondary characters, used to determine the systematic position more closely, concern: 1. the general appearance of proneurals; 2. the development of bridge buttresses of the carapace; 3. the development of keels and of the peripheral margin; 4. the sculpture of horny shields; 5. the structure of the pygal; 6. some details in the morphology of the plastron.

In the presence of the primary characters these characters make it possible to determine species or subgenera.

In the present work only the forms which have at least one evident primary character and a few secondary ones are considered to be undoubtful members of the genus *Geoemyda*. It is a well-known fact that single indistinct „geoemydal" characters may often occur in the *Batagurinae* of the „*Geoemyda*-Complex". As regards fossil species represented by poor fragmentary material, their membership in *Geoemyda* s. lat. is therefore dubious. A classical species with only one distinct primary character is *Clemmydopsis sopronensis* BODA (BODA, 1926). Forms with similar geoemydal characters are mentioned by GLAESSNER



Map 1

(1926), and MŁYNARSKI (1959), and KUHN (1964) reckons them in the genus *Geoemyda* as doubtful.

The tortoises under study have a characteristic tendency to developmental anomalies. These anomalies most frequently concern the shape of the neurals and the hypertrophy of the centrals, accompanied occasionally by an increase in their number. The abberations and differentiation of the general habitus of the shell, the presence or absence of keels, and a change in the outlines and shape of the carapace and plastron can also be observed. These last differences are particularly pronounced in young specimens dating back to old geological periods.

IV. SYSTEMATIC SURVEY

1. Species of established systematic position

Subgenus *Geiselemy* subgen. nov.

Type species: *Geoemyda ptychogastroides* HUMMEL, 1935.

Diagnosis: Broad epiplastra forming a distinctive gular notch; epiplastral lips poorly developed; xiphiplastra with a narrow but deep anal notch.

Geoemyda ptychogastroides HUMMEL, 1935

1927. *Ptychogaster* sp., BARNES, p. 14, Figs 4a-b, Pl. 1, Fig. 8.
1935. *Geoemyda ptychogastroides* n. sp., HUMMEL, p. 457—465.
1964. *Geoemyda ptychogastroides*, KUHN, p. 87 (synonymy).
1964. *Geoemyda ptychogastroides*, MŁYNARSKI, p. 340.

Holotype: Heavily damaged fragment of carapace and fragments of plastron. Geiseltal Museum, No. 6970, Halle-Saale, Germany.

←

Map 1. Find localites of the Fossil *Geoemyda*-Tortoises in Europe. A — Eocene, B — Upper Miocene, C — Pliocene and Villafranch. 1. Lower Headon Beds of Hordwell, Hunts (?*Geoemyda headonensis* (HOOLEY)). 2. Valey of the Geisel River in Saxony, Germany (*Geoemyda ptychogastroides* HUMMEL and *G. saxonica* HUMMEL). 3. Nowa Wieś Królewska in Opole, Poland (*Geoemyda eureia* (WEGNER)). 4. Rębielice Królewskie, Poland (*Geoemyda mossoczyi* MŁYNARSKI). 5. Węże near Działoszyn, Poland (*Geoemyda* sp.). 6. Ivanovce near Trenčin, Slovakia, ČSSR (?*Geoemyda* sp.). 7. Hajnáčka near Filákovo, Slovakia, ČSSR (*Geoemyda* cf. *mossoczyi* MŁYNARSKI by MŁYNARSKI, 1966). 8. Galgamacsa, Komitat Pest, Hungary (*Geoemyda* sp., MŁYNARSKI, 1966). 9. Brunn-Wösendorf near Viena, Austria (*Clemmydopsis (Geoemyda?)* sp.). 10. Sopron in Hungary (*Clemmydopsis sopronensis* BODA). 11. Csákvar in Komitat Féjér, Hungary (*Geoemyda* sp., MŁYNARSKI 1966). 12. Irimești, Region Oltănia, „Fîntîna lui Mitilan", Romania (*Geoemyda* cf. *mossoczyi* MŁYNARSKI). 13. Malușteni near Berești in Moldavia, Romania (*Geoemyda malustensis* (MACAROVICI et VANCA)). 14. Novopetrovka, Anastasievka and other localities in the valey of the Khuchurgan River, Odessa province, Ukrainian SSR (*Geoemyda pidoplickai* (KHOSATZKY))

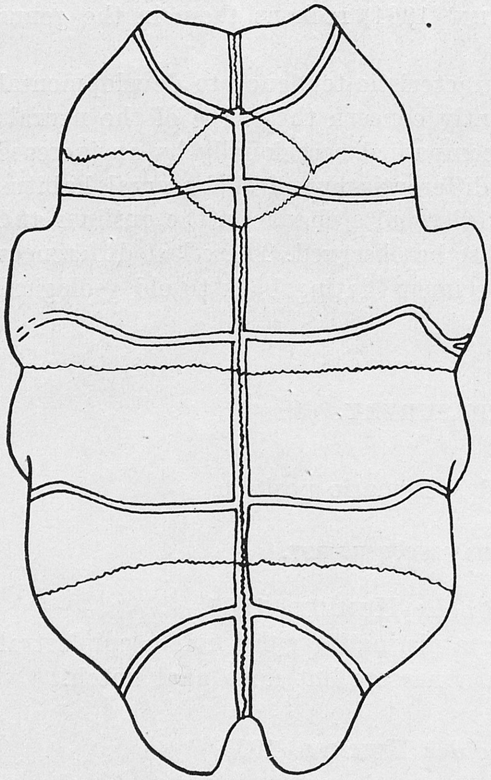


Fig. 3. Plastron of *Geoemyda ptychogastroides* HUMMEL. (1/2 nat. size). After HUMMEL (1935) and new material del. J. ŚWIECIMSKI

Type locality: The „Cecilia" Mine of brown coal in Geiseltal, Saxony, Germany. Type stratum: middle Eocene, lignites.

Diagnosis: Carapace convex, oval, roundish in juveniles. Peripheral edge even, nuchal notch visible, anal notch also present. Most specimens with medial keel, which terminates gently on the last neural or metaneural. Plastron united to the carapace by a broad bridge with a distinct lateral notch between hyo- and hypoplastra (HUMMEL, 1935). Plastron with distinct semilunar notch in anal region. Epiplastra broad, flat, without cylindrycal thickenings of epiplastral lips. Gulars broad, overlapping entoplastron. Sculpture of shields indistinct and poor; primary characters pronounced. Shell length up to 22 cm.

Geoemyda saxonica HUMMEL, 1935

1935. *Geoemyda saxonica* n. sp., HUMMEL, p. 456, Figs 13—14.
1959. *Geoemyda saxonica.*, MŁYNARSKI, p. 97.
1964. *Geoemyda saxonica.*, KUHN, p. 88 (no synonymy).
1964. *Geoemyda saxonica.*, MŁYNARSKI, p. 340.

Holotype: Almost complete carapace with large fragments of plastron. Geiseltal Museum, No. 6972, Halle-Saale, Germany.

Type locality: the „Cecilia" Mine of brown coal in Geiseltal, Saxony. Type stratum: middle Eocene, lignites.

Diagnosis: Carapace broad with even peripheral margin and gentle proneural and caudal notches. Bridge broad, not notched laterally but having distinct straight edge (after HUMMEL, 1935, p. 466). Medial keel absent (?), pleurals (after HUMMEL, loc. cit.) „testudoidal“, their long margins are not all parallel. Gulars small, not overlapping entoplastron. Sculpture of shields delicate. Primary geoemydal characters very distinct. Length up to 20 cm.

REMARKS ON SPECIES FROM GEISELTAL

The above-mentioned species are the oldest indubitable members of the genus under discussion known from Europe. Their remains are numerous in the materials from Geiseltal, not excepting those found recently. All the specimens are strongly compressed dorsoventrally, broken and deformed. It is very difficult to demonstrate specific differences and characters on this material, particularly so because its specimens exhibit great individual variation. For instance, among the materials identified by HUMMEL (1935) there are many specimens of *G. ptychogastroides* with some characters of *G. saxonica* and vice versa. Despite the statement of this author, smooth specimens and those with distinct keels may be met in both these forms.

The notches of the bridge and its lateral edges are often indistinct in these specimens. In a few of them the notches are simply caused by the mechanical dorsoventral compression. A number of specimens, besides, have a great resemblance in morphology to the species *Ocadia germanica* HUMMEL described in the same paper. Consequently, it might be supposed that in Geiseltal we have to do either with one geoemyd species or with two extremely closely related forms, characterized by great morphological variation and having numerous transitional forms. We believe that they are phylogenetically young forms in the course of intense evolution. Two evolutionary tendencies may be distinguished in the material: in some of the forms the carapace is smooth, without a trace of keels and with a very poor sculpture of horny shields, in the others the keels are well developed. In either of these groups there are specimens identified both as *G. ptychogastroides* and as *G. saxonica*. The problem concerning the occurrence of one or two forms in Geiseltal will be decided after the new material, now under preparation, has been worked out.

Subgenus: ***Heosemys*** STEJNEGER 1902, **emend.** McDOWELL, 1964

Type species: *Geoemyda spinosa* (GRAY).
Diagnosis: McDOWELL, 1964, p. 272.

Geoemyda eureia (WEGNER, 1913)

1913. *Clemmys eureia* n. sp., WEGNER, p. 213, Figs 13—18, Pl. 22, Figs 3—5.
1913. *Clemmys pacheia* n. sp., WEGNER, p. 217, Figs 1—22, Pl. 10, Figs 6—9.
1964. *Clemmys eureia.*, KUHN, p. 68, 87 (detailed synonymy).
1962. *Geoemyda eureia.*, MŁYNARSKI, p. 180, 184, 185.
1964. *Geoemyda eureia.*, MŁYNARSKI, p. 334, 338, 340.

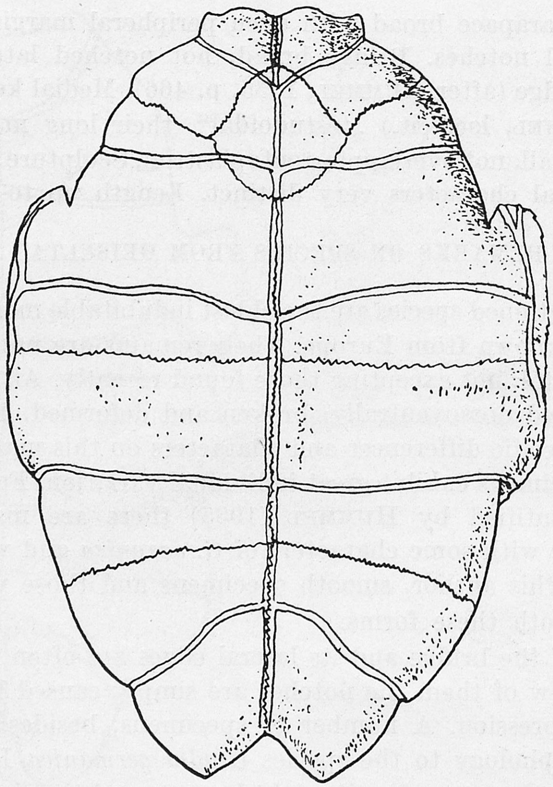


Fig. 4. Plastron of *Geoemyda eureia* (Wegner). (3/4 nat. size). After Wegner (1913) and a new material del. J. Świecimski

Holotype: not designated, Wegner's (1913) descriptive material has probably been lost. Type locality: Nowa Wieś Królewska near Opole, Upper Silesia, Poland (in lit.: Königliches Neudorf bei Oppeln, Oberschlesien). Type stratum: Upper Miocene, fresh-water silt.

Diagnosis: Carapace convex, smooth and oval, in young individuals with weak medial keel. Peripheral margin even or only slightly serrated in pygal region. Bridge buttresses of carapace distinct. Plastron broad, epiplastra with distinct cylindrical thickenings. Sculpture of shields poorly marked. Primary and secondary geoemydal characters conspicuous. Shell length 12 cm.

DISCUSSION

Wegner (1913) described two species from the above-mentioned locality. Glaessner (1926) assigned them to the genus *Geoemyda* and put forward the supposition that „*Clemmys pacheia*" is synonymous with the first species. This opinion was accepted by a few authors (see Kuhn, 1964). As may be judged by the illustrations and description given by Wegner (op. cit.), we really have to do with one species here. The features characteristic of „*Clemmys pacheia*" have been found in only one specimen. The differences ascertained by WEGNER (1913) in the structure of the pygal region of these forms have been demonstrated nowhere but in this single specimen, in which the pygal, and not the metaneural, is crossed by the groove of the postcentrals, as in the members of the *Emydinae* (sensu McDOWELL, 1964). Otherwise, however, this specimen has distinct primary and secondary geoemydal characters and differs in nothing essential from the specimens of *G. eureia* (WEGNER). In connection with the above the differences in the structure of the pygal region may be regarded as a typical individual aberration. The plastron of „*Cl. pacheia*" WEGNER presented in Plate 10 (Fig. 6) shows no distinct primary characters and the morphology of the inner surface of the epiplastra differs evidently from that of *G. eureia* WEGNER. This plastron may have belonged to quite a different member of the *Emydidae*, which even was not a member of the „*Geoemyda*-Complex" or to a remarkably „pathological" specimen. Unfortunately, the material described by WEGNER has been lost and there are no other similar remains in the fragmentary material that we have at our disposal. As all the Miocene silts have been exploited near Opole, there is no hope of any more materials from this locality.

G. eureia (WEGNER) is a very typical member of the group under discussion. The remains which have recently been found have a structure typical of *Geoemyda* s. lato with distinct primary and secondary characters. The finding of fragments of bridge buttresses makes the subgeneric determination possible (these remains are in the possession of the Institute of Systematic Zoology, Polish Academy of Sciences in Kraków).

The remains of tortoises of the same genus derived from the Upper Pliocene localities at Rębielice Królewskie and Węże I (MŁYNARSKI, 1955, 1959, 1960, 1962) have been reckoned in this species. The very large number of remains found in the first of these localities allowed the revision as well as the description of a new species, *G. mossoczyi* MŁYNARSKI (see below). Phylogenetically this form is undoubtedly closely related to the species being discussed. However, the specific membership of the remains (epiplastron and entoplastron) of *Geoemyda* from Węże I is uncertain (MŁYNARSKI, 1955, Figs 13—14), though the ecological conditions and age would rather indicate that they belong to *G. mossoczyi* MŁYNARSKI. The lack of any other materials makes the close determination of this systematic position impossible (the last mentioned remains are kept in the collection of the Muzeum Ziemi in Warsaw).

Geoemyda mossoczyi MŁYNARSKI, 1964

1959. *Geoemyda* cf. *eureia.*, MŁYNARSKI in MOSSOCZY, p. 133.
1959. *Geoemyda eureia.*, MŁYNARSKI, pp. 91—100, Figs 1—7.
1960. *Geoemyda eureia.*, MŁYNARSKI, p. 160.
1962. *Geoemyda eureia.*, MŁYNARSKI, p. 180, 184, 185.
1964. *Geoemyda mossoczyi* n. sp., MŁYNARSKI, pp. 335—341, 344, Figs 19—30 and 43 (restoration).

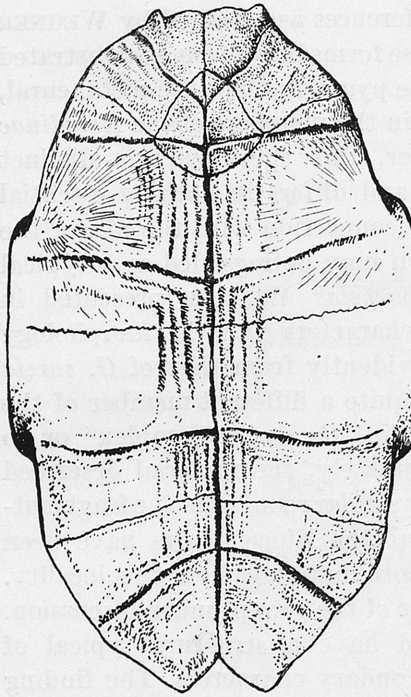


Fig. 5. Plastron of *Geoemyda mossoczyi* MŁYNARSKI (1/3 nat. size). Del. J. ŚWIECIMSKI

Holotype: Pygalpart of carapace, Institute of Systematic Zoology, Polish Academy of Sciences, Kraków (No. Rf. T. 2/63). Type locality: Rębielice Królewskie near Kłobuck in the north-western part of the Kraków—Wieluń Jurassic Ridge, Poland. Type stratum: Upper Pliocene, weathering clay of the terra rosa type filling karst crevices of jurassic limestones.

Diagnosis: Carapace strongly convex, with medial keel beginning more or less on the surface of the neural N-III and ending in a characteristic robust tubercle on the metaneural. Pygal massive, strongly convex, trough-shaped; peripherals strongly and distinctly serrate in cranial and, especially, pygal region. Bridge buttresses well-developed and overlapping pleurals. Plastron like that in *G. eureia* WEGNER, with well-developed cylindrical thickenings of epiplastra. Sculpture of horny shields very distinct, thick, concentrical and slightly undulate. Length up to 15 cm.

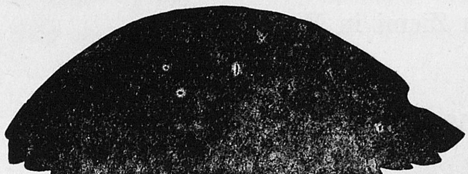


Fig. 6. *Geoemyda mossoczyi* MŁYNARSKI. The shape of the cartapace. Restoration by J. ŚWIECIMSKI

REMARKS

In the „preglacial" period the range of *G. mossoczyi* MŁYNARSKI in Europe may have been fairly wide. The remains from the Villafranchian locality at Irimeşti (Romania, Oltănia region) as well as those from Hajnáčka (Czechoslovakia), more or less from the same geological period (MŁYNARSKI, 1964, p. 340), probably belonged to the same species.

Subgenus: *Spinemys* subgen. nov.

Type species: *Geoemyda pidoplickai* (KHOSATZKY, 1946).

Diagnosis: Xiphiplastra, evidently different from the other plates of the shell, with characteristic pointed processes, which are bent down.

Geoemyda pidoplickai (KHOSATZKY, 1946)

1946. *Clemmys pidoplickai* sp. n., KHOSATZKY, p. 618—619, Fig. 2 (error lit?).
1964. *Geoemyda pidoplickai.*, TELEPNEVA, p. 70.

Holotype: Fragments of plastron of an adult specimen (epiplastra, hyo- and hypoplastra, xiphiplastra). Institute of Zoology, Academy of Sciences of the Ukrainian SSR, Kiev. Type locality: Novopetrovka in the valley of the Kuchurgan River, Odessa Province, Ukrainian SSR. Type stratum: Upper Pliocene, Kuchurgan deposits.

Diagnosis: Carapace distinctly though not strongly convex, smooth, with slightly marked medial keel and even or weakly undulate peripheral margin. Sculpture of shields distinct and concentrical. Plastron with strongly developed cylindrical thickenings of epiplastral lips. Xiphiplastra with very distinct

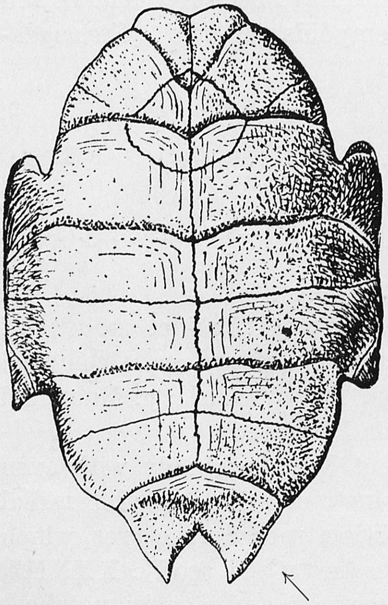


Fig. 7. Plastron of *Geoemyda pidoplickai* (KHOSATZKY) (1/2 nat. size). Del. L. I. KHOSATZKY

pointed ends, often slightly bent down (Fig. 7, indicated by an arrow), which is a character of the subgenus. Primary and secondary geoemydal characters distinct. Length of adult specimens about 20 cm.

DISCUSSION

This species was described together with another one, *Clemmys riabinini* KHOSATZKY. In the mentioned 1946 paper the description of the plastron and the explanations of the figures were probably confused. This error was subsequently found by TELEPNEVA (1964) who put the species in question in the genus *Geoemyda*. However, a comparison of the new abundant materials derived from the above-mentioned locality in the herpetological collection of the Institute of Zoology of the Academy of Sciences of the USSR in Leningrad shows that they are two separate forms. The completely different habitus of the plastra and fragmentary carapaces and the lack of sufficiently distinct primary geoemydal characters in *M. riabinini* (KHOSATZKY) indicate that they do not represent the sexual dimorphism of the same species, either.

Among the remains found in a later period and kept in Leningrad a well-preserved whole shell of a large specimen claims attention. The structure of its plastron is typical of *G. pidoplickai* (KHOSATZKY) and shows no evolutionary anomalies, whereas the carapace is characterized by the enormous hypertrophy of the centrals accompanied by the atrophy of laterals, as in the members of *Clemmydopsis* BODA. The centrals are extremely broad and about eight in number (the damaged part of the specimen), which makes them different from the above-mentioned genus. At the present time it is difficult to determine on the basis of one specimen only whether it is a distinct form related to *Clemmydopsis* BODA or rather a form with an anomalous structure characterized by the hypertrophy of the centrals. This tendency seems to have been frequent in and characteristic of the „preglacial“ European emydids of the „*Geoemyda*-Complex“.

Geoemyda malustensis (MACAROVICI et VANCA, 1960)

1960. *Clemmys malustensis* n. sp., MACAROVICI et VANCA, pp. 381—384, Pl. 3, Fig. 3—24.
1962. *Clemmys malustensis*, MŁYNARSKI, p. 185.

Lectotype: Left pleural Pl. I of small specimen with distinct grooves of centrals Centr. 1—2 and very well preserved sculpture of surface. Geological Laboratory, Al. J. Cusa University, Jaşi, Romania. Type locality: Maluşteni in Moldavia, Romania. Type stratum: ,,Upper Pliocene."

Diagnosis: Carapace vaulted, without evident keels, probably with even peripheral margin and characteristic, very distinct, concentrical and radial sculpture of shields. Centrals and laterals with distinct radial structures, which spread starrily from the areola towards the margins (lectotype, see Pl. XXXIII, Fig. 4). Precentrale very broad, pygale small, convex and deeply notched, metaneurals with distinct though delicate trace of tuberculous ending of medial keel, endings of xiphiplastra pointed. Primary and secondary characters distinct. Length probably up to 15 cm.

DISCUSSION

This species was described from fragmentary but abundant and very distinctive materials. At first sight they show distinct primary (entoplastron) and secondary (series of preneural plates, sculpture) geoemydal characters. After examining the sufficiently clear photographic material, we decided to include this species in the genus under discussion, which had already been suggested before on the basis of the data from the publication of MACAROVICI and VANCA (1960) (MŁYNARSKI, 1964, p. 340). At the same time, for the matter of routine we take the liberty to designate the lectotype, because the remains represent several specimens of various size. In redescription we, however, take into account the whole material used by these authors.

Geoemyda malustensis (MACAROVICI et VANCA) is undoubtedly a form closely related to *G. pidoplickai* (KHOSATZKY). Both these forms come from similar strata of the same geological age and both have their xiphiplastra developed in a characteristic manner. *G. malustensis* (MACAROVICI et VANCA) differs from the other species in its considerably stronger and dissimilar sculpture of carapace shields.

2. Species of doubtful systematic position

Geoemyda headonensis (HOOLEY, 1905)

1905. *Nicoria headonensis* n. sp., HOOLEY, pp. 66—68, Figs 1—3.
1935. *G. (Nicoria) haedonensis.*, HUMMEL, p. 460.
1952. *Nicoria headonensis.*, THENIUS, p. 325.
1959. *Geoemyda headonensis.*, MŁYNARSKI, p. 95.
1964. *Geoemyda headonensis.*, KUHN, p. 87.
1964. *Geoemyda headonensis.*, MŁYNARSKI, p. 340.

Holotype (material): Probably in private collections. Type locality: Lower Headon Beds of Hordwell, Hunts, England. Type stratum: middle Eocene (Lower Headon Beds).

Diagnosis: Species described from fragmentary material of slight taxonomic value probably belonging to one specimen. Peripheral margin even in pygal region; geoemydal characters very indistinct and questionable.

DISCUSSION

This species was described on the basis of very fragmentary materials, including large fragments of the pygal and medial parts of the carapace (neurals, pleurals, peripherals, a small piece of metaneurals), the right hyoplastron with a lower fragment of the entoplastron and a small fragment of the left hyoplastron. Taking for granted that this form is closely related to contemporary *Geoemyda trijuga* (GRAY), HOOLEY (1905) offered a restoration of the shell. The descriptive material being insufficient, the restoration was based on erroneous data assumed by the author. On account of the lack of fragments with distinct primary and secondary characters the systematic position is uncertain. On the basis of the existing material *G. headonensis* (HOOLEY) cannot be compared at all with any other fossil emydids of an established taxonomic value.

Clemmydopsis sopronensis BODA, 1927

1927. *Clemmydopsis sopronensis* ng., n. sp., BODA, pp. 375—383, Fig. 1—2.
1932. *Geoemyda (Nicoria) sopronensis*., SZALAI, p. 221.
1964. *Clemmydopsis sopronensis*., KUHN, p. 67 (further synonymy).
1964. *Clemmydopsis sopronensis*., SUKHANOV, p. 405, Fig. 406.
1964. *Geoemyda (Clemmydopsis) sopronensis*., MŁYNARSKI, p. 340.
1966. *Clemmydopsis sopronensis*., MŁYNARSKI, p. 249—251.

Holotype: Well-preserved though damaged carapace with inner mould and small fragments of plastron. F. Liszt Museum in Sopron, Hungary (no number). Type locality: Fresh-water Pannonian silt in the region of Sopron, north-western Hungary. Type stratum: Lower Pliocene (Upper Pannonian).

Diagnosis: Carapace somewhat convex, smooth, with weak but distinct medial keel in pygal region. Peripheral margin even. Bridge broad, with distinctly marked edge; presence of buttresses not ascertained. Owing to the hypertrophy of the first three centrals, characteristic of this genus, the surface of the pleurals Pl. I is crossed by a perpendicular groove separating lateral shields 1 and 2. Carapace shields with very delicate concentrical sculpture round areolae. Batural characters distinct, geoemydal ones (in the case of holotype) indistinct. Length: 12.8 cm.

DISCUSSION

This species was described by BODA (1927) from one relatively well preserved specimen (holotype). SZALAI (1932) placed it in the genus *Geoemyda* (GRAY) on the basis of the shape of three neurals and at the same time expressed the supposition that the remains belonged to a specimen with an anomalous structure, i.e., with the hypertrophy of the central shields. This opinion was accepted by a few authors till the recent times (see KUHN, 1964). WILLIAMS (1954) was the first to show that the generic characters given by BODA (op. cit.) are not individual and „pathological“ and that they occur in other fossil tortoises of Europe. In this genus he also included *C. turnauensis* (H. v. MEYER) from the Upper Miocene of Austria. The opinion of WILLIAMS (op. cit.) was supported by most authors except MŁYNARSKI (1956, 1959, 1964), who still supposed that the remains belonged to a geoemyd with a „symmetrical and regular“ aberration in the structure of shields. Having examined the holotype, we incline to WILLIAMS'S view, motiving this as follows: 1. The geoemydal characters of the holotype are indistinct (the geoemydal shape of the three neurals may occur sporadically in many batagurines). 2. The general habitus of the shell departs from the appearance typical of *Geoemyda* (Gray) and rather resembles the type of structure of *Mauremys* Gray.

On the other hand, the membership of the remains described by Thenius (1952) in this species is not clear. The only evidence for it is the perpendicular crossing of the horny shields of the pleural Pl. I by a groove found in a small specimen (op. cit., p. 320, Fig. 1a). The surface of these remains is, however, more strongly and distinctly sculptured and the restored plastron (p. 325, Fig. 6), which is not known from the holotype, has a typical geoemydal structure despite the somewhat weaker development of the epiplastral lips. Even if, despite the evident primary and secondary geoemydal characters, the remains represent a member of the genus *Clemmydopsis* Boda, it is evidently different from the type species of this genus and certainly resembles the Pliocene geoemyds. Similar evolutionary tendencies in *G. pidoplickai* (Khosatzky) have already been discussed.

The members of the genus *Clemmydopsis* (Boda) have characters of a very typical batagurine of the „*Geoemyda* Complex". It will not be possible to demonstrate their relationship to the members of *Geoemyda* s. lat. in detail, until some new and much more abundant materials have been obtained.

V. BIOLOGY

1. Ecological Adaptation

The Recent members of the systematic group under discussion are fairly well adapted for life on land, the degree of adaptation being however very various here. Krefft (1926) reckons them among „Vorwiegend oder periodisch landlebende Wasserschildkröten". For example, *G. (Rhinoclemys) punctularia* (Daudin) inhabiting the tropical forests of South America is a typical land species associated with woodlands. It dwells in wet regions and may stay sporadically in water. It is a remarkable vegetarian and feeds on land vegetation. *G. spengleri* (Gmelin) leads a conspicuously terrestrial life in tropical forests of Asia, often in the mountains regions of Indo-China, where it reaches an altitude of about 1000 m. (Petzold, 1963, Felix 1965).

G. (Heosemys) spinosa (Gray), to which the „preglacial" European forms (*G. mossoczyi* Młynarski) have a resemblance in morphology, is characterized by the change of environment in the course of growth. Young specimens of this species live on land, whereas the older ones gradually become water animals, which is also connected with a change in their diet.

A peculiar day rhythm was observed in *Geoemyda trijuga thermalis* (Lesson), the race living in the damp highlands of Ceylon. This animal is associated with water environment during the day, and in the night it makes long and relatively regular land excursions. The main purpose of these excursions is probably to find food. The criterion of carapace convexity, formerly very often used to determine the presumable degree of adaptation (e.g., KHOSATSKY, 1941) fails when applied for the group under study. Though we cannot agree with all the theses of SCHUBERT-SOLDERN (1962) (cf. STAESCHE, 1964), yet it is just with respect to *Geoemyda* that the criterion of shell convexity often fails.

It may be assumed in general that the tortoises discussed are forest or brushwood animals associated with damp but not necessarily water environment. Their semiaquatic biological adaptation sets them between the water *Batagurinae* and the conspicuously terrestrial *Emydinae* of the genus *Terrapene* MERREM.

The question of ecological adaptation of fossil geoemyds is especially important for the characterization of the environment and it is also of some, though limited, significance for stratigraphy. It has already been discussed rather in detail many a time (HUMMEL, 1935; MŁYNARSKI, 1959, 1964). Our species are, to be sure, similar to the contemporary species, but the morphological resemblance by itself may be apparent and even not necessarily convergent. For this reason we take into account each individual case and also base ourselves on the analysis of the faunal composition and the geological nature of the strata. All these data complete each other and allow the following conclusions:

1. All the European species of the genus *Geoemyda* s. lat. were thermophilous terrestrial, forest or brushwood animals, at most periodically associated with water environment.

2. The members of the Eocene species were inhabitants of damp forests corresponding to the tropical forests of the oriental and Neotropical Regions (the characteristics of this environment are given by HUMMEL, 1935, p. 479). There are no counterparts of these forms in the contemporary fauna.

3. The members of the Miocene species also lived in forests and riverside regions, but such as neighboured upon dry areas, more exposed to the sunlight. They have distinct resemblances to the contemporary Oriental forms.

4. The Pliocene and Pleistocene species appeared in company with a xerothermic fauna, but were always numerous together with fresh-water and amphibious vertebrates in the proximity of water (e.g., Rębielice Królewskie). With all their specific characters these species are already evidently similar to the oriental subgenus *Heosemys* STEJNEGER. In connection with this fact a periodical change of environment was possible in these forms, obviously adapted for life on land.

2. Climatic Adaptation

The contemporary geoemyds dwell exclusively in tropical and subtropical regions. None the less, a number of species, especially those living in the mountains (e.g., *G. spengleri* (GMELIN)), are distinguished by great resistance to the fluctuations of temperature. This explains the phenomenon of adaptation of European geoemyds to the deteriorating climatic conditions and their survival as long as the first glaciation. However, the thermal tolerance of this group of tortoises is not so great as that of the *Emydidae*, more closely associated with water, which lasted out or returned to the territories of Europe in the Holocene. Consequently, the remains of geoemyds may be a climatic indicator in the wide sense of the word.

VI. PHYLOGENESIS

The juxtaposition of the groups of morphological characters and those of probable biological European species shows their, perhaps apparent only, polyphyletic origin. The oldest Eocene geoemyds from Geiseltal are obviously a lateral evolutionary branch of vague origin and have no characters in common with the younger forms. Accordng to Hummel (1935), they resemble the members of the genus *Ptychogaster* Portis in some characters. In contradistinction to them the Miocene and „preglacial“ species are quite evidently related to each other. They bear a great resemblance to the contemporary Oriental forms from the Asiatic evolutionary centre. It may be supposed that their ancestors were some primitive batagurines with still indistinct primary geoemydal characters. In this case the climatic and biological changes taking place towards the end of the Tertiary were the main factor causing the formation of new species.

According to the scheme offered by Loveridge and Williams (1957, p. 185, Fig. 2), *Geoemyda* would derive directly from *Clemmys (Mauremys)*. Considering the results of McDowell (1964) and our own studies on the fossil *Batagurinae*, we suppose that *Geoemyda* is a considerably older form. Consequently, we assume that this group evolved directly from the hypothetical „protoemydines“ (Loveridge and Williams, 1957) parallel to but separate from the group of species of the „*Orlitia* Complex“ (McDowell, 1964). It may well be that the *Ptychogastridae (Ptychogaster)* also branched from the same trunk. Their specialization and probably more advanced adaptation for life on land proceeded in a different way and the specific type of ossification, never occurring to this degree in other tortoises, was somehow connected with the rapid and complete extinction of this peculiar and enigmatic group.

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STRESZCZENIE

Praca niniejsza zawiera krytyczny przegląd gatunków żółwi kopalnych z rodzaju *Geoemyda* GRAY poznanych i opisanych z terenów Europy. Autorzy sami przebadali dokładnie materiały znajdujące się w zbiorach Czechosłowacji, Niemiec, Polski, Węgier i ZSRR. Uwzględniono również materiały znajdujące się w Rumunii i Austrii. Równolegle do studiów nad szczątkami kopalnymi przebadano również pancerze większości współczesnych przedstawicieli omawianej grupy.

Zarówno w tytule jak i w tekście użyto terminu *Geoemyda* s. lat. Jest to związane z przedstawioną ostatnio przez McDOWELLA (1964) rewizją i podziałem omawianego rodzaju. Autorzy stanęli tu jednak na stanowisku, że w przypadku gatunków kopalnych, znanych niestety na razie tylko na podstawie szczątków pancerza, ze względów czysto praktycznych celowe będzie zachowanie dla tych wszystkich form dużego, wspólnego rodzaju „zbiorczego", podobnie jak dotychczas uznawano w neoherpetologii (WERMUTH & MERTENS 1961). Pozostałe rodzaje geoemyd, zdefiniowane przez McDOWELLA (op. cit.), sprowadzono do podrodzajów. Równocześnie dla kopalnych form europejskich opisano dwa nowe podrodzaje, *Geiselemys* i *Spinemys*.

W części poświęconej taksonomii dokonano próby zebrania w grupach cech morfologicznych, pozwalających nawet w przypadku materiału fragmentarycznego na oznaczenie przedstawicieli omawianego rodzaju oraz na oznaczenie ich gatunków w przypadku lepiej zachowanych szczątków. Wymienione tu „cechy geoemydalne" służą równocześnie do pełniejszej definicji rodzaju i podrodzajów.

W części systematycznej omówiono krótko gatunki o ustalonym stanowisku systematycznym. Osobno też bliskie geoemydom formy o niepewnym stanowisku systematycznym. Najstarsze, pewne geoemydy z Geiseltal w Saksonii

zaliczono do podrodzaju *Geiselemys*. Gatunki te, opisane przez HUMMELA (1935) wykazują duże wzajemne podobieństwo przy równoczesnej dużej zmienności morfologicznej. W związku z tym nie jest wykluczone, że mamy w tym przypadku do czynienia z jedną tylko formą. Żółwie z Geiseltal przy wyraźnych cechach geoemydalnych różnią się wyraźnie od wszystkich pozostałych, młodszych gatunków europejskich.

Do współczesnego podrodzaju *Heosemys* STEJNEGER (sensu MCDOWELL 1964) zaliczono mioceński gatunek *Geoemyda eureia* (WEGNER) i plioceński *G. mossoczyi* MŁYNARSKI. Ta ostatnia forma reprezentowana jest prawdopodobnie w szeregu górnoplioceńskich i młodoplejstoceńskich („preglacjalnych") stanowisk południowo-wschodniej części Europy środkowej.

Do nowego podrodzaju *Spinemys* zaliczono dwa gatunki plioceńskie z Mołdawii i Ukrainy *G. pidoplickai* (KHOSATZKY), *G. malustensis* (MACAROVICI et VANCA)). Charakteryzuje je obecność ostrych zakończeń ksifiplastrów, nie spotykanych u form współczesnych ani u innych kopalnych przedstawicieli omawianej grupy. U pierwszego z wymienionych gatunków stwierdzono wyraźną tendencję do przerostu tarczek centralnych przy związanym z tym uwstecznieniem lateralnych. Podobne cechy występują u przedstawicieli kopalnego rodzaju *Clemmydopsis* BODA.

Do form o niepewnym stanowisku systematycznym zaliczono gatunki *G. headonensis* (HOOLEY) i *Clemmydopsis sopronensis* BODA. Pierwszy z nich został opisany na podstawie zbyt fragmentarycznego i nie mającego znaczenia taksonomicznego materiału (fragmenty drobne pancerza). Drugi z omawianych gatunków, którego stanowisko systematyczne było już wielokrotnie dyskutowane przez różnych autorów i ostatnio zostało ugruntowane przez WILLIAMSA (1954), jest formą bliską omawianym żółwiom, należącą do tego samego „*Geoemyda*-complex". Dokładniejsze określenie jego stanowiska jest trudne, gdyż ze stanowiska klasycznego w Sopron znany jest tylko jeden okaz. Nie wydaje się równocześnie, aby do tego samego gatunku należały szczątki z Brunn Vösendorf w Austrii, na podstawie których THENIUS (1951) wykonał rekonstrukcję plastrona.

W części ogólnej omówiono problem adaptacji ekologicznej, który ma znaczenie dla charakterystyki środowiska oraz może też mieć ograniczone znaczenie stratygraficzne. Kopalne geoemydy Europy były prawdopodobnie zwierzętami dosyć silnie związanymi z życiem lądowym, żyjącymi w środowisku leśnym lub zaroślowym w pobliżu wody. Nie wyklucza się też możliwości, że przedstawiciele niektórych gatunków mogli okresowo zmieniać środowisko z lądowego na wodne, podobnie jak to obserwujemy u współczesnych geoemyd azjatyckich. Cecha ta różniłaby je ekologicznie od amerykańskich przedstawicieli rodzaju *Terrapene* MERREM, którzy są bardziej już związani ze środowiskiem lądowym. Omawiane żółwie to wprawdzie zwierzęta związane z klimatem gorącym, głównie tropikalnym i subtropikalnym, ale doskonale dostosowane do życia w chłodniejszych górskich rejonach. Podobną odpornością na ochłodzenia i wahania temperatury musiały odznaczać się też omawiane gatunki kopalne, gdyż tylko w ten sposób możemy wytłumaczyć sobie fakt ich przetrwania do początków plejstocenu (Villafranchiano ČSSR i Rumunii).

Omawiając filogenezę rodzaju autorzy dochodzą do wniosku, że wbrew przypuszczeniom HUMMELA (1935) nie jest on w jakiś sposób bliżej spokrewniony z rodzajem *Ptychogaster* PORTIS. Nie jest jednak wykluczone, że oba te rodzaje odgałęziły się osobno ze wspólnego pnia prymitywnych emydidów. W świetle badań McDOWELLA (1964) oraz własnych autorów nie można też przyjąć za LOVERIDGE'EM i WILLIAMSEM (1957) aby omawiane żółwie miały pochodzić od przedstawicieli rodzaju *Clemmys* RITGEN (*Mauremys* GRAY). Fakty z dziedziny paleontologii i zoogeografii wskazują, że są to starsze formy batagurinów *(Batagurinae)*, których główne centrum rozwojowe znajduje się w południowo-wschodniej, tropikalnej Azji.

РЕЗЮМЕ

Настоящая работа содержит критический обзор известных в науке и описанных ископаемых черепах рода *Geoemyda* GRAY из европейских территорий. Сами авторы исследовали подробно материалы, находящиеся в разных собраниях в Чехословакии, Германии, Польше, Венгрии и СССР, а также учли материалы из Румынии и Австрии. Одновременно с изучением ископаемых остатков были исследованы панцыри большинства современных представителей данной группы.

И в заглавии, и в тексте применяется термин *Geoemyda* s. lat., что связано с ревизией и делением данного рода, выдвинутым в последнее время (1964) МАК ДОВЕЛЛОМ. Авторы придерживались однако мнения, что в случае ископаемых видов, известных к сожалению пока-что только по обломкам панцыря, по чисто практическим рассуждениям полезно будет сохранить для всех этих форм крупный общий, „сборный" род, подобно тому, как до сих пор наблюдается в неогерпетологии (ВЕРМУТ и МЕРТЕНС 1961). Остальные роды геоэмыд, установленные МАК ДОВЕЛЛОМ (ук. соч.), были сведены до подродов. Одновременно были описаны два новые подроды европейских форм: *Geiselemys* и *Spinemys*.

В части, посвященной таксономии, была сделана попытка собрать в группы морфологические признаки, которые даже в случае фрагментарного материала позволили бы обозначить представителей данного рода, а в случае лучшего сохранениа остатков — определить их вид. Приведенные здесь „геоэмыдальные признаки" способствуют также более полной дефиниции рода и подрода.

В систематической части дается краткое обсуждение видов с определенным систематическим отношением. Отдельно были разработаны также близкие к геоэмыдам формы с сомнительным систематическим отношением. Самые древние, надежные геоэмыды из Гейзельталя в Саксонии были причислены к подроду

Geiselemys. Эти виды, описанные Гуммелем (1935), обнаруживают большое взаимное сходство при одновременной большой морфологической переменчивости. В связи с этим не исключено, что в данном случае имеется дело только с одной формой. Черепахи Гейзельталя при отчетливых геоэмыдальных признаках решительно отличаются от всех остальных, более молодых европейских видов.

К современному подроду *Heosemys* Stejneger (sensu McDowell 1964) был причислен миоценский вид *Geoemyda eureia* (Wegner) и плиоценский *G. mossoczyi* Młynarski. Последняя форма представлена повидимому в ряду верхнеплиоценских и младоплеистоценских („преглациальных“) находок юго-восточной части Центральной Европы.

К новому подроду *Spinemys* были причислены два плиоценские вида из Молдавии и Украины (*G. pidoplickai* (Khosatzky), *G. malustensis* (Macarovici et Vanca)). Характерным для них является наличие острых окончаний ксифипластов, не встречающихся ни у современных форм, ни у других ископаемых представителей данной группы. У первого из этих видов была обнаружена отчетливая тенденция к гипертрофии центральных щитков при вызванной этим атрофии латеральных щитков. Подобные признаки известны у представителей ископаемого рода *Clemmydopsis* Boda.

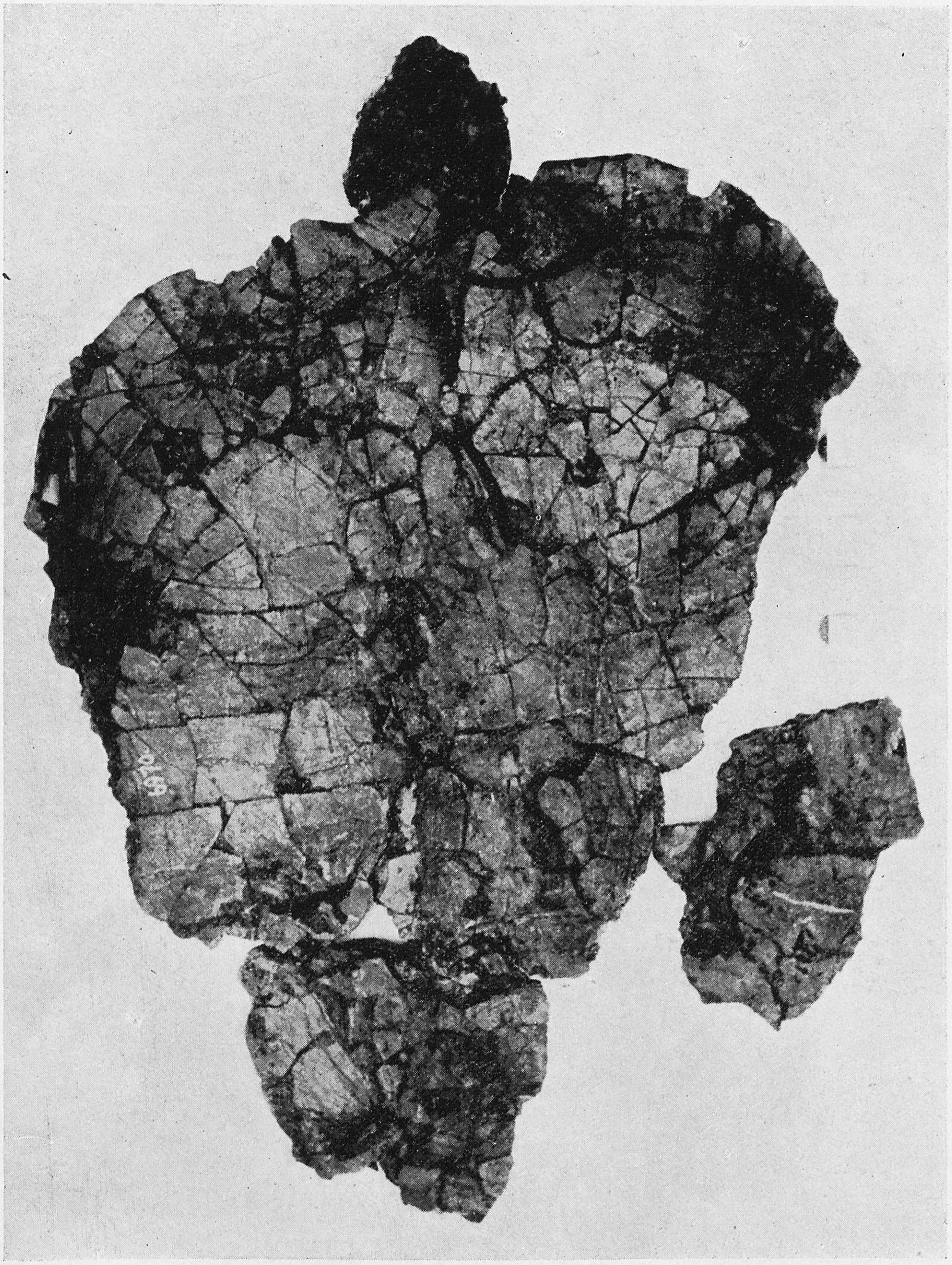
К формам с надежным систематическим отношением были причислены виды *G. headonensis* (Hooley) и *Clemmydopsis sopronensis* Boda. Первый из них был описан на основании слишком фрагментарного и лишенного значения таксономического материала (мелкие фрагменты панцыря). Второй из обсуждаемых видов, систематическое отношение которого уже многократно оспаривалось разными авторами, а в последнее время было обосновано Вилльямсом (1954), является формой близкой к обсуждаемым черепахам, принадлежащей к тому же самому „*Geoemyda*-complex“. Определить более точно его систематическое отношение трудно, так-как из классического места находки в Шопрон известен только один экземпляр. Вряд ли принадлежат к этому виду остатки из Брунн Вёзендорф в Австрии, на основании которых Тениус (1951) дал реконструкцию пластрона.

В общей части обсуждается вопрос о экологической адаптации, важной для характеристики среды, а также — в ограниченном размере — для стратиграфии. Ископаемые геоэмыды Европы являлись повидимому животными довольно тесно связанными с жизнью на суше, обитающими в лесной среде, или же в близких к воде кустах. Не исключена также возможность, что представители отдельных видов могли временно переходить из лесной среды в водную, подобно тому, как наблюдается у современных геоэмыд Азии. Признаком этим они в некоторой степени отличаются в экологическом отношении от американских представителей рода *Terrapene* Merrem, теснее связанных с континентальной средой. Обсуждаемые черепахи, хотя и обитают в горячем тропическом и субтропическом климате, отлично приспособлены к жизни в более холодных горных районах. Подобной стойкостью на охлаждение и колебания температуры отличались повидимому и исследованные здесь ископаемые виды, так-как только таким образом можно объяснить то, что они сохранились до начала плеистоцена (Villafranchiano Чехословакии и Румынии).

Рассматривая филогенез рода, авторы приходят к заключению, что вопреки предположениям Гуммеля (1935) он не сроднен ближе с родом *Ptychogaster* Portis. Возможно однако, что оба эти рода отдельно ответвились от общего ствола примитивных эмыдидов. В свете наблюдений МакДовелла (1964) и собственных наблюдений авторов нельзя также согласиться с мнением Ловериджа и Вилльямса (1957) о том, что обсуждаемые черепахи происходят от представителей рода *Clemmys* Ritgen (*Mauremys* Gray). Факты из области палеонтологии и зоогеографии указывают на то, что это более древние формы батагуринов *(Batagurinae)*, главный центр развития которых находится до сих пор в юго-восточной тропической Азии.

Plate XXIX

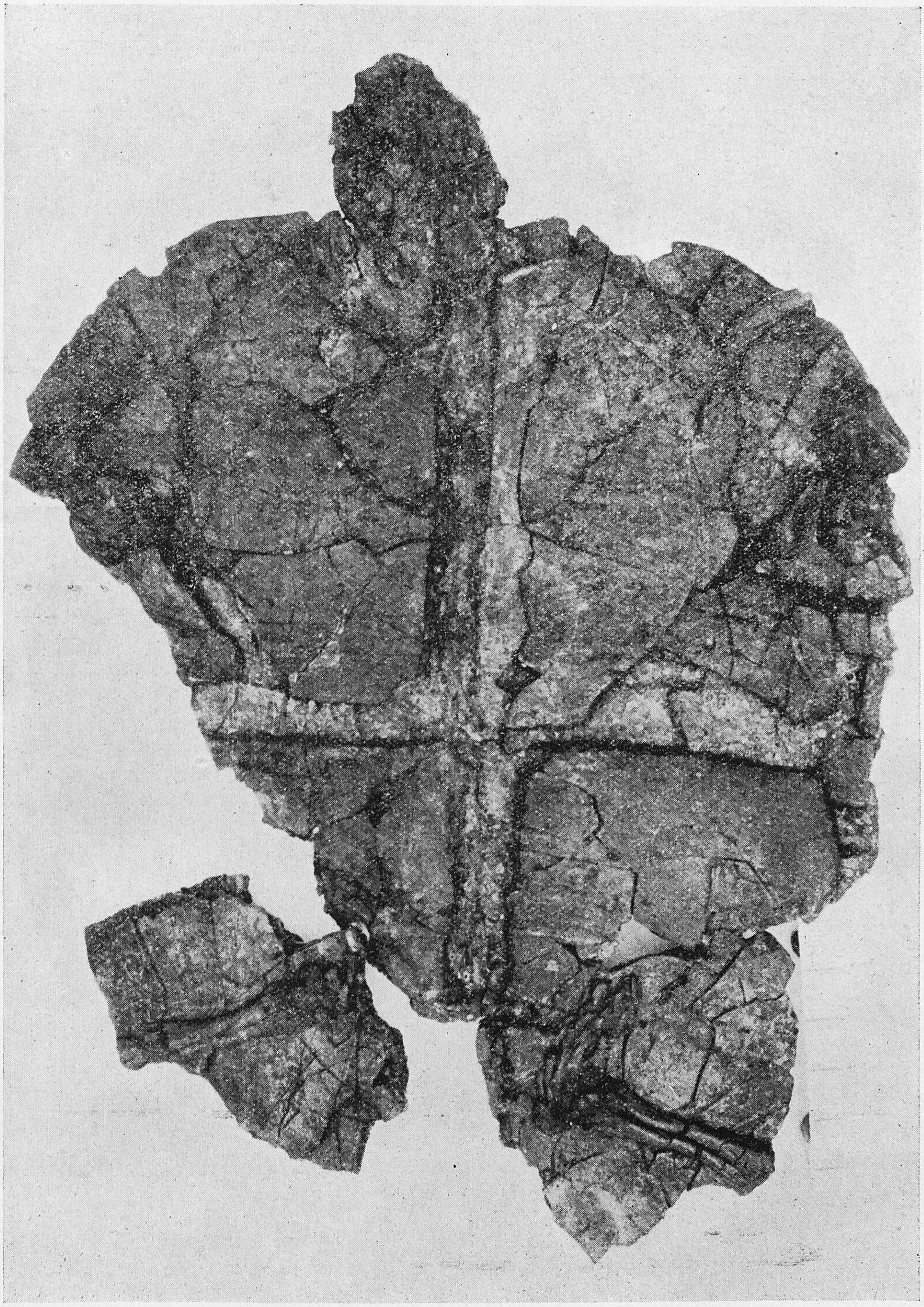
Geoemyda ptychogastroides HUMMEL. External part of the holotype.



L. I. Khosatzky & M. Młynarski
Phots: Univ. Halle Phot. Service

Plate XXX

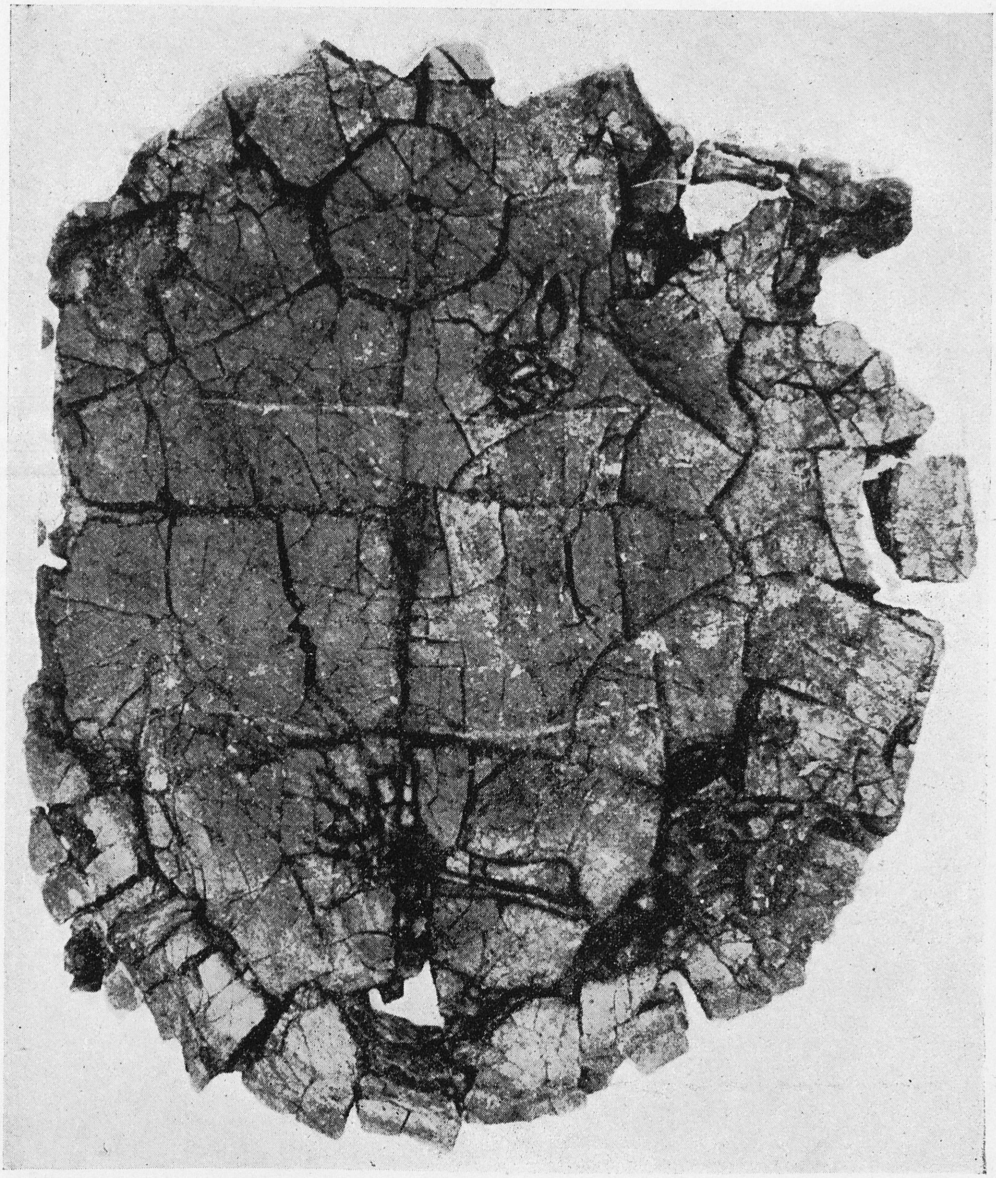
Geoemyda ptychogastroides HUMMEL. Internal part of the holotype.



L. I Khosatzky & M. Młynarski
Phots: Univ. Halle Phot. Service

Plate XXXI

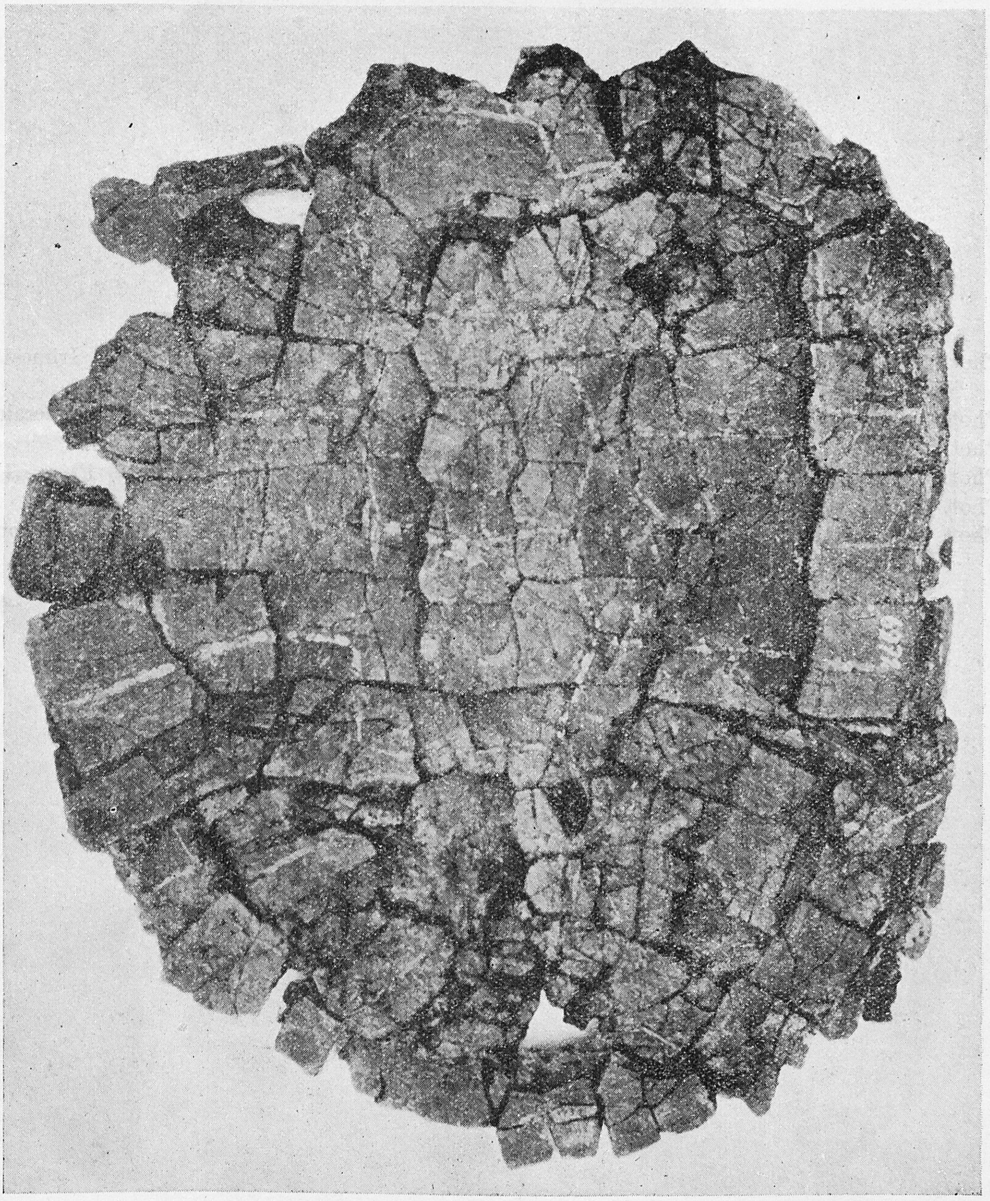
Geoemyda saxonica HUMMEL. External part of the holotype.



L. I. Khosatzky & M. Młynarski
Phots: Univ. Halle Phot. Service

Plate XXXII

Geoemyda saxonica HUMMEL. Internal part of the holotype.



L. I. Khosatzky & M. Młynarski
Phots: Univ. Halle Phot. Service

Plate XXXIII

Phot. 1—2. Pygal part of the carapace of *Geoemyda* cf. *mossoczyi* MŁYNARSKI from Irimeşti, Romania.

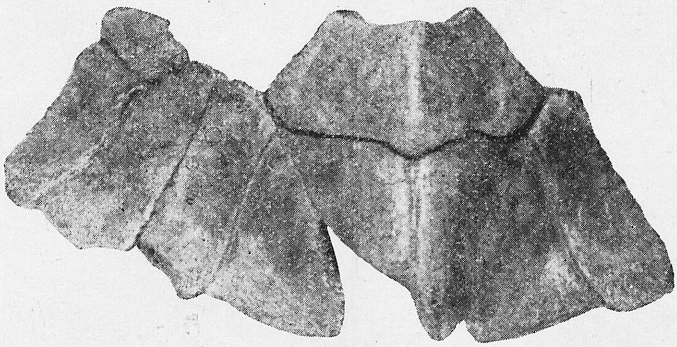
Phot. 3. *Geoemyda mossoczyi* MŁYNARSKI from Rębielice Królewskie, Poland. Pronuerale.

Phot. 4. *Geoemyda malustensis* (MACAROVICI et VANCA) Proneurale.

Phot. 5. Lectotype of *Geoemyda malustensis* (MACAROVICI et VANCA). (Pleural Pl. — 1).

Phot. 6. *Geoemyda malustensis* (MACAROVICI et VANCA). Pleural Pl. — 1.

Phot. 7. *Geoemyda malustensis* (MACAROVICI et VANCA). Pointed process of the xiphiplastron.



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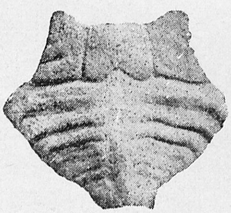

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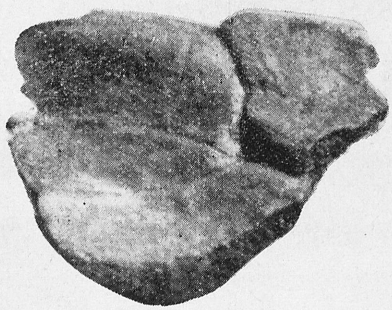

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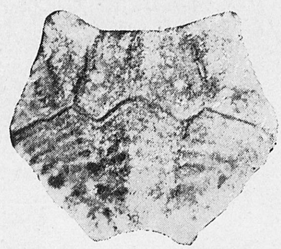

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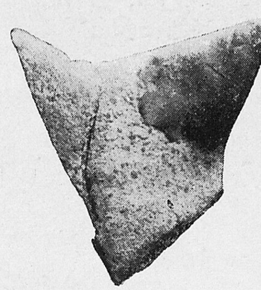

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L. I. Khosatzky & M. Młynarski
Phot. 1—3 L. Sych; 4—7 University of Jasi Phot. Service

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