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Notes on the Amphibian and Reptilian Fauna of the Polish Pliocene and Early Pleistocene

(Pl. XIV)

Uwagi o plioceńskiej i wczesnoplejstoceńskiej faunie płazów i gadów Polski

Замечания о плиоценских и раннеплейстоценских амфибиях и рептилиях Польши

Abstract. This paper is the summing-up of the investigations on the Pliocene and early Pleistocene amphibians and reptiles of Poland carried out up to the present time, completed with some new, unpublished data regarding the old and the new localities. The introductory part presents the characteristics of the localities under study: Weże I, Weże II, Podlesice, Rębielice Królewskie, Kamyk and Kadzielnia and of the amphibians and reptiles occurring in them. The systematic part comprises the review of the forms and systematic groups so far recognized with special respect to turtles and lizards. The note on the occurrence of Lacerta (Podarcis) ef. sicula Rafinesque, the survey of the fossil remains of Anguis Linnaeus and the determination of the systematic position of Testudo szalaii Meynarski deserve here particular attention. The character of the "preglacial" herpetofauna of this country and its comparison with the amphibian and reptilian fauna from the Pliocene and early Pleistocene of the localities in Czechoslovakia, Austria, Hungary and Roumania are the subject of the general part. The problem of the origin of the contemporary European land tortoises and their ancestors is also discussed.

INTRODUCTION

In the last ten years several Pliocene and early Pleistocene localities abounding in the remains of amphibians and reptiles were found in Poland. Most of them have been already worked out in detail; those discovered recently will be worked out in the nearest future. Even now the knowledge of the herpetofauna of all the localities mentioned in this paper, based on the new, unpublished

material, permits us to make some general conclusions as to the origin, character and relationships of these preglacial amphibians and reptiles. The new finds at Weże and systematic inquiry into the old material render it possible to revise and complete the opinions so far published by me and, moreover, they suggest a necessity to do so.

LOCALITIES

All the localities from which the amphibian and reptilian remains are derived lie in the region of the Kraków—Wieluń Jurassic Mountains except for the hill of Kadzielnia, which is in Kielce. The remains were found together with many other bones of the Vertebrata in crevices and rock pockets left after old caves and karst funnels. The remains of vertebrates appear in them in the form of a breccia, cemented by calcite or mixed up with the clay material of weathering. The colour of the material is dark-red, characteristic of terra rossa and indicating its accumulation in warm and hot periods. Uncluckily, most of the remains are very fragmentary, which makes accurate identification impossible in many cases.

1. Podlesice

This locality is situated near Olkusz, NW of Kraków. This is a remnant of an old cave with sediments abounding in bones of bats. The remains of other vertebrates, including those of amphibians and reptiles, are here comparatively scarce. At first the assemblage was regarded as coming from the Pleistocene (K. Kowalski 1956), but then it was dated by Dr K. Kowalski (personal information) as Pliocene, though older than the collection from Węże I.

Small snakes of the subfamily Colubrinae, a small lizard of the genus Lacerta Linnaeus, a slow-worm Anguis cf. fragilis Linnaeus and Ophisaurus sp., probably O. pannonicus Kormos, were found at Podlesice.

2. Węże I

This is the oldest and, probably, most abundant Pliocene locality in this country. It was discovered in 1934 and described by J. Samsonowicz in 1934. It is situated on the Jurassic hill Zelce near the village of Weże on the river Warta, NW of Częstochowa. The chink in this hill was filled up with a typical, strongly crystallized in places, bone breccia. The study on the vertebrate fauna of Weże I was started in 1950 by the workers of the former Museum of Natural History in Kraków directed by Prof. J. Stach (the first publication issued in 1951). So far, 18 studies on the fauna of this locality have been published,

6 of which are entirely or partially devoted to the Amphibia and Reptilia (M. MŁYNARSKI 1953, 1955, 1956a, 1956b, 1961a and 1961b).

It has been generally determined on the basis of the remains of small and large mammals that the bone breccia of Weże I originated from the Pliocene (J. Stach 1951, A. Sulimski 1959, K. Kowalski 1960). The abundant material collected up to 1939 was put in disorder in the wartime, which made it impossible to demarcate the horizons exactly. Two periods might be distinguished owing to the present investigations: in the first of them, probably the first older one, the steppe fauna predominated, while the forest or the steppe-forest species appeared in the second.

The amphibian and reptilian fauna of this locality is terrestrial and thermophil in character. Here, the numerous *Pelobatidae* and *Bufonidae* attract our attention, of which *Bufo tarloi* MŁYNARSKI, the only form coming close to the fauna from Roussillon, and the primitive fossil toad *Pliobatrachus langhae* FEJÉRVÁRY, described from the Pliocene locality at Episcopia Biharuli (Püspökfürdö) in Roumania, deserve to be mentioned. The collection abounds also in the remains of a small frog resembling the contemporary *Rana latastei* Boulenger, and the vertebrae of the *Caudata* of the family *Salamandridae* occur rather frequently.

The commonest remains of reptiles at Weże I are the shell fragments of turtles of the families Emydidae and Testudinidae. At least 6 different forms were distinguished and it was possible to identify three of them exactly. Emys wermuthi Młynarski is the characteristic turtle of Węże. It is a small emydid with a strongly domed carapace, much resembling the American turtles of the genus Terrapene Merrem and Testudo szalaii Meynarski in appearance. The latter tortoise comes near the contemporary "European Greek Tortoise" Testudo hermanni Gmelin. The lizards are represented, first of all, by Ophisaurus pannonicus Kormos (Anguidae), the species common in the European "preglacial". The remains of this lizards are abundant and well preserved, which permits the accurate identification of species. The presence of the membres of the genus Anguis Linnaeus, the form identical with the contemporary slowworm Anguis fragilis LINNAEUS, has been recently found to be undubitable. The Lacertidae are represented by a small form showing close agreement with the Recent Mediterranean lizard Lacerta sicula Rafinesque. However, there are no unquestionable finds of forms closely related to the South and Central European species L. agilis Linnaeus and L. viridis Laurenti. Although the vast material of remains was examined, no fragments of geckoes or agamas were found in it, contrary to what I suggested in my study on lizards (M. MŁY-NARSKI 1956a). This permits me to regard them as absent from this material. Snakes are pretty numerous at Weże I. They are mostly members of the subfamily Colubrinae resembling the Recent snakes of the genus Coluber LINNAEUS. Small specimens of "aquatic snakes" of the subfamily Natricinae are here considerably less frequent and the vertebrae of small vipers (Viperidae s. lat.) are encountered only occasionally:

This locality is situated at a distance of about 200 metres from the old karst funnel referred above to as Weże I. It lies in the north slope of the hill Zelce, in a nearly vertical rock crevice filled up with dark-red weathering clay mixed with many vertebrate remains. The locality was discovered by Mgr Andrezej Sulimski in 1958, who also worked out a preliminary report on it (A. Sulimski, in the press). At Weże II the layers of material were taken off separately one after another, which ought to make the determination of the particular horizons possible. The material is in preparation now and next it will be carefully worked out. The finds date back to the Pliocene.

The search for amphibians at Weze II has failed as yet. As to the reptiles, the fragments of turtle-shells are the most numerous in the collection with the evident predomination of the *Emydidae* over the *Testudinidae*. So far the presence of *Emys wermuthi* Meynarski and some testudinid (*Testudo* sp.) has been demonstrated. The lizards are represented by *Lacerta* sp., the form approaching to that from Weże I and to *Anguis* cf. *fragilis* Linnaeus. The locality is also rich in the remains of *Ophisaurus pannonicus* Kormos, among which the jaw fragments of juvenile individuals deserve special attention.

4. Rębielice Królewskie

This Pliocene locality was discovered and described by Z. Mosoczy (1959). It is situated in a quarry in the village of Rebielice Królewskie near Kłobuck, NW of Częstochowa. The remains of vertebrates are here obviously less frequent than at Węże and they are embedded in dark-red weathering clay just as those at Węże II are. The age of the locality was determined on the basis of the fauna of small mammals by K. Kowalski (1960b). The accumulation was derived from the Pliocene, though it was possibly a little younger than that of Węże I. Also here the intermixture of the material made it impossible to distinguish any defined horizons.

The amphibian and reptilian fauna of Rebielice Królewskie was described in detail in three studies (M. MLYNARSKI 1959, 1960, 1961a). The reptiles are represented by the numerous remnants of turtles of the family Emydidae. They are almost exclusively the shell fragments of the species Geoemyda eureia (Wegner), the form known in Poland since the Upper Miocene and occuring in very different environments (R. N. Wegner 1913). The remains of the genus Clemmys Ridgen appear here very rarely, and those of testudinids have not yet been found at all. The lizards are represented by pretty abundant remains of Ophisaurus pannonicus Kormos, Anguis cf. fragilis Linnaeus and Lacerta (Podarcis) sp. resembling the Recent L. muralis Laurenti. The snakes occur in relatively large numbers and mostly belong to the subfamily Colubrinae, probably standing close to the genus Elaphe Fitzinger in Wagler. The Natricinae are, however, very scarce in the collection. The amphibians are represen-

ted at Rebielice Królewskie by the remmants of big frogs similar to the contemporary Rana arvalis Nilsson, the Pelobatidae and Bufonidae. At this locality the remains of the primitive fossil toad Pliobatrachus langhae Fejérváry were found for the first time in Poland.

Generally speaking, the amphibian and reptilian fauna from Rebielice shows a large number of wood forms associated with wet environment, the typical water forms being, however, rare.

5. Kadzielnia

This locality lies in the reserve on the hill Kadzielnia in Kielce. The fauna of Kadzielnia has been worked out by K. Kowalski (1958), who determined its origin in the Günz-Mindel interglacial on the basis of the remains of small mammals.

The amphibian and reptilian fauna of Kadzielnia is considerably richer than that of Kamyk, which will be discussed below (K. Kowalski op. cit., M. Meynarski 1961a). While the amphibians of Kadzielnia are not very numerous and are limited to the remains of frogs (Rana sp.) and toads (Bufonidae), the reptiles are represented by Ophisaurus cf. pannonicus Kormos, few remains of Lacerta sp. and abundant and large remains of the snakes of the subfamily Colubrinae, which were forms larger than the Aesculapian Snake now living in Poland. It is also supposed that the turtles occurred in this locality, but two shell fragments, the only ones found as yet, cannot be identified quite accurately.

6. Kamyk

This locality is situated in an old quarry by the road at Kamyk near Kłobuck, NW of Częstochowa. It was found and described by Z. Mossoczy (1959). According to K. Kowalski (1960c) the fauna of small mammals of this locality indicates that it took origin in the early Pleistocene, in the Günz-Mindel interglacial. The remains of vertebrates are not very numerous here. The amphibian and reptilian fauna from Kamyk was described in two papers (K. Kowalski 1960c, M. Młynarski 1961a).

The amphibians are represented by the bones of the Ranidae and Bufonidae. The reptilian remains found at Kamyk are not very numerous osteoderms of the genus Ophisaurus Daudin, probably O. pannonicus Kormos, small fragments of little lizards of the genus Lacerta Linnaeus and vertebrae of the snakes of the families Colubridae and Viperidae. All the bony fragments are greatly damaged and their surfaces (e. g. those of snake vertebrae) are mechanically polished owing to the action of water currents.

Amphibians and Reptiles of the Polish Pliocene and Early Pleistocene

	Podle- sice	Węże I	Węże II	Rębie- lice Kr.	Kadziel- nia	Ka- myk
Discoglossus sp.		1+				
Eopelobates sp.		+				
Pelobates cf. fuscus (Laurenti)		+++		++ "		
Pliobatrachus langhae Fejérváry		++		+		
Bufo tarloi Meynarski		+++				
Bufo sp.		++++		++	+	+
Rana sp. (little form)		++++				
Rana sp. (large form)				++	+	+
Salamandridae gen. non det.		++				
Testudo szalaii Meynarski		+++	+?			
Testudo antiqua noviciensis Depéret		++				
Testudo sp. (large form)		+				
Emys wermuthi MŁYNARSKI		++++	++			
Emys orbicularis (Linnaeus)		++?				
Geoemyda eureia (Wegner)	, ,	+		++++		
Clemmys sp.		+		+	100	
Ophisaurus pannonicus Kormos	+	++++	++	+++	++	+
Anguis cf. fragilis LINNAEUS	+	++	++		+	
Lacerta cf. sicula Rafinesque		+++		++		
Lacerta sp.	+	+?		+	+	+
Coluber cf. viridiflavus Lacépède		+++				
Elaphe sp.	+	?		+++	+++	+
Natricinae gen non det.		++		+		
Viperidae gen. non det.		1+				+

++++- very common, +++- common, ++- rare, +- very rare.

SYSTEMATIC SURVEY

Amphibians

The remains of amphibians are scanty in this material except for those from Weze I and Rebielice Królewskie, which have been recently worked out in detail, and so I confine myself to a short survey of the forms (see M. Meynarski, 1960, 1961b).

The *Discoglossidae* have been so far known only from Weże I and represented by a large form of *Discoglossus* sp., similar to the Miocene species *Discoglossus giganteus* Wettstein-Westerheimb. The occurrence of some specimens of the genus *Alytes* Otth. is also possible at this locality.

The *Pelobatidae* are common at Weże and Rębielice Królewskie. They are all forms much resembling the Recent *Pelobates fuscus* (LAURENTI), from which they do not differ either in morphology or in size. The genus *Eopelobates* PARKER, which has been found present at Weże I, is also a form standing close

to *Pelobates fuscus* (Laurenti) (proportions, size) and it may have been described by H. W. Parker (1929) on the basis of atypical, "pathologic", adult specimens in which, as in juveniles, the urostyles were not fused with the sacrum.

The Bufonidae are numerous in the localities in question. Special attention should be given to Bufo tarloi Meynarski from Weże I, which may have occurred in Rębielice Królewskie, as the analysis of long bones suggests. This toad is similar to the Pliocene species Bufo (Diploplecturus) ruscinensis Depéret from Roussillon. Several very well preserved specimens of Pliobatrachus langhae Fejérváry were found in our collections, which permits the foundation of this primitive fossil species upon the strong ground. In my latest study (1961b) I discussed this species described by G. J. Fejérváry (1917) on the basis of the sacrum and primitive urostyle.

The Ranidae are represented in our preglacial fauna by two forms. One of them resembles the Recent Mediterranean Rana latastei Boulenger in size and morphology; the other, larger, is similar to the contemporary Polish species Rana esculenta Linnaeus, R. temporaria Linnaeus and R. arvalis Nilsson.

The Salamandridae have not been identified exactly yet. Judging from the material so far available (vertebrae, long bones, fragments of girdles and phalanges) they may be either tritons (*Triturus* Rafinesque) or salamanders. These remains have been known only from Węże.

Reptiles

The remains of turtles are relatively well known as compared with other reptiles of the collection. They occur in only three of the localities here discussed, but in these they constitute a large and even very large (e. g. at Węże) percentage of all the vertebrate remains.

The turtle fauna has been discussed in detail in 5 studies (M. MŁYNARSKI 1953, 1955, 1956b, 1959, 1960). The following species deserve special attention:

Testudo szalaii MLYNARSKI* was described from Węże I on the basis of a large fragment of the pygal part of a carapace and xiphiplastra (holotype) in 1955. Several years later a well-preserved fragment of the pygal part of the carapace of a young male (very strongly convex pygals) was found, which I reckon among the paratypes (Pl. XIV, Fig. 4).

T. szalaii Młynarski is a typical representative of the so-called "antiquagraeca" group (M. Glaessner 1933, T. Szalai 1934) characterized, as a rule, by the presence of one suprapygal (= metaneural, K. Staesche 1961) plate with the exception of "pathologic" individuals. This is one of the few fossil

^{*} Derivatio nominis: szalaii — after the name of the Hungarian geologist and chenologist, Prof. Tibor Szalai from Budapest.

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turtles that have two distinct supracaudal shields like those in the Recent T. hermanni GMELIN. At the discussion of the species in question, a similar Pliocene form, T. globosa Portis described from Valdarno Superiore in Italy (A. Portis 1890), was omitted. As can be seen from the illustration (op. cit., Pl. I), this tortoise also had 2 well-developed supracaudal shields, but the author compared his specimen only with T. graeca Linnaeus without mentioning this essential fact. Basing oneself on the description only, it is difficult to realize whether he meant T. hermanni GMELIN according to the then binding herpetological nomenclature. T. globosa Portis is undoubtedly a form very similar and related to T. szalaii Meynarski from our collection. I do not exclude the possibility of recognizing this testudinid from Weże as a synonym or race of the species coming from Valdarno in the future, which is, however, impossible now, on account of the fragmentary state of our material, which we failed to reconstruct exactly.

Testudo antiqua noviciensis Depéret occurs in abundance at Węże I. This form stands very close to or perhaps it is identical with the Recent T. graeca ibera Pallas. Considered by M. Glaessner (1926) to be a variation of T. antiqua Bronn, it is very common in the Upper Tertiary of Europe. Using now the subspecific name in accordance with the principles of the zoological nomenclature, we cannot treat this form strictly as a race, however, for our knowledge of the distribution of T. antiqua Bronn is very fragmentary. N. Macarovici & St. Vancea (1960) have recently described a new testudinid form from the Pliocene of Moldavia in Roumania under the name of Testudo praegraeca ibera Macarovici et Vancea. Judging from the description and illustrations this form is intermediate between T. graeca Linnaeus and T. hermanni Gmelin and doubtless it belongs to the same "antiqua-graeca" group.

Emys wermuthi Meynarski described from Węże I (M. Meynarski 1956b) has been recently found at Węże II. This emydid is characterized by the smooth, very strongly domed carapace. At the first glance its shell resembles the shells of the American turtles of the genus Terrapene Merrem. However, its structure is typical of the genus Emys Duméril. Thus the likeness between this turtle and the terrapins is a pure convergence, which was not stated strongly enough in the previous study. The similitude of the turtles here considered is due to their adaptation to the land conditions of living. E. wermuthi Meynarski is the youngest member of the genus Emys Duméril with a strongly domed shell similar to that in the Swiss Miocene species E. herri (Portis).

Geoemyda eureia (Wegner) described from the Upper Miocene of Opole (R. N. Wegner 1913) was found at Weże I and Rebielice Królewskie. I discussed this species in detail in 1959 and compared it with the European geomyds so far known and with the Recent species *. G. eureia (Wegner) is a species oc-

^{*} Discussing the ecologic adaptation of the geoemyds I reckoned G. annulata (Gray) and G. punctularia (Daudin) among the strictly terrestrial forms erroneously. These species have not the same "ecologic potency"; while the first one is really terrestrial, the other often stays

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curring in various environments but avoiding those typically xerothermic. The strongly domed carapace evidently shows its adaptation to land conditions.

Emys orbicularis (LINNAEUS), whose occurrence at Weże I was reported in my studies of 1953 and 1955 and called in question in that of 1956b, was, however, probably present in the Pliocene of Poland. In the material of Weże I there is a large number of shell fragments and several interior moulds of carapaces, which are obviously weakly domed and show a great similarity to the above-mentioned, now existing species. The presence of E. orbicularis (LINNAEUS) in the Hungarian and Slovakian Pliocene has been shown to be beyond a doubt (T. SZALAI 1934). Unluckily, in our fragmentary material there are two forms so similar to each other that the occurrence of the European Pond Turtle cannot be regarded as quite certain.

In 1955 I described the fragments of shells of big land tortoises, larger than the corresponding fragments of T. szalaii Meynarski or T. antiqua noviciensis Depéret. No new, large fragments have been found since then to make exact identification possible. These remains may have belonged to a species similar to or identical with the large Pliocene testudinids of Hungary and Roumania, such as T. grandis Macarovici & Vancea from Moldavia.

The remains of the turtles identified as *Clemmys* sp. were found at Weże I and Rebielice Królewskie. In both cases the remains differ from each other, which, however, may result from individual variations.

Two species of the genus Clemmys Ridgen have been recently described from the European Pliocene. The first of them, C. ukoi Bachmayer, comes from the Upper Pannonian freshwater layers of Austria (Bachmayer 1957), and the other, C. malustensis Macarovici & Vancea, form the land layers of Moldavia. In the latter case, as might be inferred from the description and illustrations, we rather have to do with the genus Geoemyda Gray.

The lizards are represented in our collection by the members of the families *Anguidae* and *Lacertidae*. Their remains were found in all the localities investigated up to now.

Ophisaurus pannonicus Kormos is a very common species in the Pliocene and, probably, early Pleistocene of this country. Particularly well-preserved remains of this species were found at Węże I (M. MŁYNARSKI 1956a). O. pannonicus Kormos is remarkably common in the Pliocene and Pleistocene localities of Czechoslovakia, Austria, Hungary and Roumania. This species is extremely similar to the contemporary Glass Lizard O. apodus (Pallas). The only essential differences that can be pointed out between these forms at present are those in size. Similar, though probably less prominent, differences are to be noticed also in the contemporary specimens of O. apodus (Pallas) from Bulgaria and Palestine (Israel). Hence it is not impossible that already at the close of the Tertiary and in the Pleistocene the contemporary Glass Lizard lived in Europe and O. pannonicus Kormos was its north race, which extingushed in the Pleistocene.

in water, though it is no longer an aquatic species sensu stricto. Also G. spinosa (GRAY), considered to be one of the exceptional, strictly aquatic forms, is in fact more terrestrial than G. trijuga (Schweigger). I thank Dr. G. Krefft for these remarks.

Phylogenesis of the European Glass Lizards

Holocene	Ophisaurus apodus (Pallas)
Pleistocene	*Ophisaurus pannonicus Kormos
Pliocene	Ophisaurus pannonicus Kormos
Miocene	Ophisaurus moguntinus (Boettger)
Early Tertiary	Anguidae from Geiseltal

According to R. Hoffstetter (1955) the ancestors of the European Glass Lizards should be looked for among the Eocene anguids with still pretty well-preserved extremities, described by O. Kuhn (1940) from Geiseltal in Saxony. On the other hand, the proper Glass Lizards appeared in the Miocene and were abundant throughout Europe at once. The oldest representatives are O. moguntinus (BOETTGER) and O. (Propseudopus) fraasi (HILGENDORF), which according to M. Fejérváry-Langh (1923) is synonymous with the former species. This opinion has not been supported by many authors probably because the description presented by O. Boettger (1877, p. 197) is very laconic and may refer to any Glass Lizard. These being two identical forms, the priority of O. moguntinus (Boettger) should be recognized in accordance with the rules of nomenclature. After M. Fejérváry-Langh (1923) I placed the species Propseudopus cayluxi Stefano from the phosphorites of Quercy among the synonyms of O. moguntinus (Boettger) in my study of 1956a. As has been shown in the studies of R. HOFFSTETTER (1955) this is a form of the genus Placosaurus Filhol (Anguidae nec Scincidae). O. moguntinus (Boettger) is closely related to O. pannonicus Kormos and may be still considered to be its ancestor. The only differences that can be pointed out are the presence of several rows of prevomeral teeth and the distinct supraangular margin in the first species (demonstrated on the material from Sansan in France) and they are of little importance.

Anguis cf. fragilis (LINNAEUS) has been recorded from several of our localities. The remains are jaw fragments, small osteoderms and vertebrae. The fragments differ in no essential detail from the corresponding fragments of the Recent Slow Worm. The members of the genus Anguis LINNAEUS appear in large numbers in the Miocene and similarly to Ophisaurus do not differ from the contemporary species in anything particular.

Slow Worms are especially numerous in the Miocene and Pliocene of France. Many species have been recorded in. a. from Sansan, but most of them, described by E. Lartet (1851) and M. Gervais (1848/1852) under the names of Anguis bibronianus. Laret, A. laurillardi Lartet (acc. to O. Kuhn, 1939, nomina nuda) and A. acutidentatus Gervais are synonymous with Ophisaurus moguntinus (Boettger) and were described on the basis of the remains of young individuals of Glass Lizards. Also A. polgardensis Bolkay from the Hungarian Pliocene is synonymous with O. pannonicus Kormos and has been described from juveniles. From the Riss-Würm interglacial of Upper Frankonia G. Brunner (1954) described the species A. stammeri Brunner on the basis of the fragments of the jaws of a markedly large specimen with robust teeth, larger than the contemporary Slow Worms. Similar bony fragments are in the French collection from St. Gèrand. The crowns of the teeth of these animals are distincly sharp, somewhat bent backward. The comparative material being poor, it is impossible to state as yet whether in both cases we have to do with the genus Anguis Linnaeus or Ophisaurus Daudin. We know the remains of a Recent Slow Worm dating back to the Pliocene (Episcopia Bihurali in Roumania), and this reptile was common throughout the Pleistocene.

The remains of the *Lacertidae* (*Lacerta* sp.) were recorded from all our localities. They all belonged to fairly small forms corresponding to. *L. agilis*

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LINNAEUS as far as their size was concerned. Owing to the examination of rich material I was able to show the presence of a form similar to the Recent Mediterranean species L. sicula RAFINESQUE at Węże I. Similar lizards occur at Rębielice Królewskie and, probably, at Węże II.

Lacerta (subgenus Podarcis) cf. sicula Rafinesque has been identified from a well preserved parietal bone, the structure of which was typical of a big male (cf. K. Klemmer 1957, T. 8, Fig. 27) and numerous maxillaries and dentaries from Weże I* and Rebielice Królewskie. K. Klemmer (op. cit., p. 25) is of opinion that it is impossible to identify a species exactly from a parietal bone only, as it was done, for instance, by G. Brunner (1954, pp. 106—107). However he does not exclude the fact that still in the Riss-Würm interglacial the species in question may have been distributed considerably farther to the north than it is now. This suggestion is supported by the later studies of G. Brunner (1957, 1958), in which he reports L. sicula RAFINESQUE from other Pleistocene localities of Upper Frankonia. On account of the relatively poor comparative material and the lack of other parietal bones preserved and taking into consideration some difference in the shape of the parietal shields, which might be here an individual character, I ascertain the presence of a form only very similar to L. sicula Rafinesque. Fragments of maxillaries with the distinct prints of the frenoocular osteoderms are also characteristic of the structure of the subgenus Podarcis Wagler (species typica: L. muralis Laurenti). Such osteoderms do not occur, or they appear only exceptionally in the members of the subgenus Lacerta Linnaeus (species typica: L. agilis Linnaeus). I realized this fact when comparing the remains of lizards from Rebielice Królewskie with the contemporary L. muralis nigriventris (LAURENTI) (1960).

The genus Lacerta Linnaeus appears in Europe as late as the Miocene. Consequently, all the earlier forms included in this genus should be accepted with all reserve. The members of the Lacertidae were unfrequent in the early Tertiary (Eolacerta Nöth from the Eocene of Geiseltal, Plesiolacerta Hoffstetter, Dracaenosaurus Filhol from the phosphorites of Quercy and Pseudoeumeces Hoffstetter from the Oligocene). Lacerta mucronata Filhol and L. lamandini Filhol (Filhol 1877, pp. 421—423) are members of the family Cordylidae (= Zonuridae) as has been pointed out by R. Hoffstetter (1942). Also L. crassidens Gervais and L. rottensis H. v. Meyer, which in my previous study (1956a) were specified in the list of the fossil members of the Lacertidea, in fact belong to the Anguidae (see F. Nopcsa 1908, p. 37).

The genus Lacerta Linnaeus is represented in large numbers at Sansan. M. Lartet (1851) records its three species derived from this locality. The species L. sansanensis Gervais (nec Lartet) mentioned by this author is regarded by O. Kuhn (1939, p. 27) as nomen nudum. In fact, this form was already described by P. M. Gervais in the first edition of the Zoologie et Paléontologie française etc. (1848/1852) on page 258 (Pl. I, Fig. 13). This species as well as the other forms from Sansan are already very closely related to the modern species. J. Bolkay (1913/1915) records the Recent L. viridis Laurenti from the Pliocene of Hungary and Roumania (Polgardi, Episcopia Biharuli).

^{*} On page 137 (Fig. 1) of my work (1956a) on lizards I gave a wrongly executed reconstruction of a mandible of *Lacerta* sp. from Weże I. The fault consists in using the fragments of individuals of different sizes for reconstruction and marking a crack as if it were a suture in the articulation part of the bone.

Snakes occur in all the localities of this country. Unluckily, their remains consist mostly of vertebrae, from which it is difficult to determine their systematic position exactly. The remains of the members of the subfamily Colubrinae are particularly abundant. Two forms resembling the contemporary genera Elaphe Fitzinger in Wagler and Coluber Linnaeus can be distinguished among them on the basis of the fragments of the articularies. The remains of the Natricinae coming near the genus Natrix Linnaeus (skull fragments from Węże I) and the Viperidae are evidently less frequent. The detailed data concerning the material from Węże I, Rębielice Królewskie, Kadzielnia and Kamyk have been given in the special paper (1961a).

Faunistic and ecological characteristics

Nearly whole "preglacial" herpetofauna so far known from this country is definitely thermophil. Most of the forms are typical of dry xerothermic environment (testudinids, Ophisaurus, Lacerta subgenus Podarcis, Colubrinae). The forms living in parklands are less numerous (?Emys wermuthi Meynarski, Elaphe sp., Natricinae), and so are the silvan forms (Anguis). A comparatively large proportion of animals is periodically or loosely associated with water (all amphibians including elements typical of xerothermic environment, Geoemyda eureia (Wegner), Natricinae, Emys orbicularis (Linnaeus)), while the decidedly aquatic forms constitute a very small proportion (Clemmys sp.).

Most of the species and genera occurring in the "preglacial" material under study have their counterparts in the modern Ponto-Mediterranean fauna (Testudo szalaii Młynarski, T. antiqua noviciensis Depéret, Clemmys sp., Ophisaurus pannonicus Kormos, Lacerta ef. sicula Rafinesque, Discoglossus sp., Rana sp. from Weże I, Coluber cf. viridiflavus Lacépède). A small number of forms has persisted or returned to this territory and contributes to the composition of the contemporary herpetofauna (Anguis cf. fragilis Linnaeus, Pelobates cf. fuscus (LAURENTI), Natricinae, Elephe sp.). Extinct forms are represented by four species (Geoemyda eureia (Wegner), Emys wermuthi Młynarski, Pliobatrachus langhae Fejérváry and Buto tarloi Meynarski), E. wermuthi MŁYNARSKI being so far confined to Weże only. The only "tropical" form in this collection is Geoemuda eureia (WEGNER) belonging to the genus, which did not outlive the Pleistocene in Europe. No such thermophil forms as Trionychidae (Malusteni in Moldavia and Pécs in Hungary), Varanidae (Villany in Hungary) or Aniliidae (?) (Brun-Voesendorf in Austria) have been found in the Pliocene fauna of Poland. The enormous land tortoises typical of many Pliocene localities (Pikermi, Roussillon) do not occur in the collections of this country. either. The early Pleistocene fauna of Poland, however, resembles the numerous faunae of this period in Hungary and Czechoslovakia (see below). It is characterized by the lack of turtles and the presence of forest forms. Nevertheless. Ophisaurus still occurs in it.

Out of the related faunae those of Hajnáčka and Ivanovce in Slovakia (Pliocene) probably come nearest the Polish fauna. A large number of turtles (Testudo sp., Emys orbicularis (LINNAEUS)), Ophisaurus sp. and the Salientia were found there. The material recently collected in these old localities is now being worked out and it will be soon possible to identify it exactly (A. Kormos 1917, T. Szalai 1934, O. Fejfar 1961).

Out of the Hungarian localities I may mention Polgárdi on Lake Balaton, from where O. pannonicus Kormos was described for the first time. Moreover, this locality has a similar fauna of snakes (Coluber, Elaphe) (J. Bolkay 1913/1915, J. Szunyoghy 1932), frogs, slow-worms and toads. T. kalksburgensis Toula has not been recorded from our material, but it may be simply a developmentally irregular form of T. antiqua Bronn.

Special attention should be given to the South Hungarian localities at Villany, Csarnota and Beremend * in the Baranya district (M. Kretzoi 1956). Almost all the amphibians and reptiles there occurring have their counterparts in the Polish Pliocene fauna. A small turtle Testudo lambrechti Szalai described from these localities on the basis of long bones is a form resembling T. hermanni GMELIN, as T. szalaii MLYNARSKI does. Snakes are represented by the numerous Colubrinae and lizards by Ophisaurus pannonicus Kormos (Fejérváry-Langh 1923), whose synonyms are O. intermedius Bolkay described from Beremend and Varanus deserticolus Bolkay (?) (Fejérváry-Langer op. cit., p. 179). The Varanidae, the occurrence of which was demonstrated by G. J. Fejérváry (1918) and confirmed by the new finds of jaw fragments personal communication from Prof. M. Kretzoi as well as a number of primitive amphibians such as Baranophrys discoglossoides Kretzoi (Discoglossidae, a form resembling Ascaphus of Liopelmidae) and, similar to it, Spondylophryne villanyensis Kretzoi are the elements of those localities unknown to Poland. The presence of Pliobatrachus langhae Fejérváry was shown in the same formations of Villany 6, very rich in amphibian and reptilian remains. Out of the frogs the new species Rana villanyensis Kretzoi is noteworthy.

Episcopia Biharuli (Püspökfürdö) (*Pliobatrachus, Bufo* sp., *Discoglossidae, Ophisaurus pannonicus* Kormos, *Anguis fragilis* Linnaeus) and Maluşteni in Moldavia (*Testudinidae, Emydidae*) are similar localities in Roumania.

Taking into consideration the faunistic composition of the amphibians and reptilians, characterized by an abundance of Glass Lizards, lizards of the subgenus *Podarcis*, testudinids and land emydids, as well as the topography of the region, I believe that in the Pliocene and early Pleistocene the conditions in the Polish Jurassic Mountains resembled those existing in the karst regions in the Balkan Peninsula at the present time. Caves and crevices, numerous in that period, were not only a hiding-place for many amphibians and reptiles but often became traps for them. This is how I tried to explain the great assemblage of bones at Weże I (1955). Turtles are particularly ready to fall into the crevices

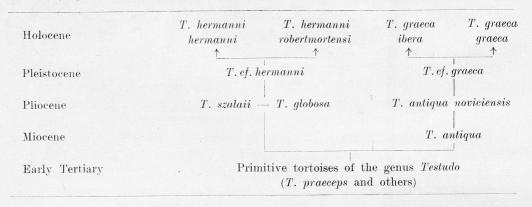
^{*} By mistake cited as Roumanian in the study of 1961a (p. 24).

or pitfalls and then perish in them unable to get out. The opinion held by certain workers in this country that there lived some predatory mammals feeding on turtles must be refuted, because, however carefully the abundant material was examined, no remains of these amphibians bearing marks of biting were found.

Ancestors of modern European land tortoises

In the General Part of my study of 1955 I suggested that T. szalaii MLY-NARSKI, originating from the Miocene T. antiqua Bronn, may have been the ancestor of the Recent T. hermanni GMELIN. As I am now acquainted with more chenological material, I wish to revise this suggestion a little. In comparison with T. graeca LINNAEUS and T. antiqua Bronn, T. hermanni GMELIN and the Pliocene turtles closely related to it have distinctly different, possibly more primitive, features of structure (paired supracaudal and broad pactoral shield). Thus, we cannot regard T. antiqua Bronn as the ancestor of T. szalaii MLYNARSKI or T. globosa Portis, the more so because in the Pliocene it still occurred in abundance. Since all the turtles mentioned above belong to one group, "antiqua-graeca", characterized by having a single suprapygal, they may have had the common ancestor. This should be looked for among the oldest, primitive, European (Eurasian?) land tortoises which still preserved "emydoidal

Phylogenesis of the European Land Tortoises of the "antiqua-graeca"" Group



characters" and showed some similarities with the American genus Stylemys Leidy (e. g. T. praeceps Haberlandt). It is from them that the two evolutionary lines branched off and are now represented by T. graeca Linnaeus and T. hermanni Gmelin, often inhabiting the same region. It is possible that both these species appeared as early as the late Tertiary, for most of the characteristics used to describe plenty of species of the Tertiary testudinids are obviously individual variations and can be demonstrated in some modern specimens. In the mild, favourable climate of the Pliocene they lived in the large area of Central Europe. As the climate deteriorated in the Pleistocene,

they had to move southwards, where owing to the isolation caused by the mountainous barriers new East and West European races originated. The supposed process of the evolution is shown in the diagram recently revised.

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STRESZCZENIE

Powyższa publikacja jest podsumowaniem badań nad szczątkami plioceńskich i wczesnoplejstoceńskich płazów i gadów opisanych dotychczas z Polski. Dotychczasowe dane zostały uzupełnione na podstawie przebadania nowych materiałów pochodzących ze znanych już lub nowo odkrytych stanowisk. W części wstępnej podano charakterystykę stanowisk położonych na terenie Jury Krakowsko-Wieluńskiej (Podlesice, Węże I, Węże II, Rębielice Królewskie, Kamyk) oraz Kadzielni w Kielcach. W części systematycznej podano przegląd dotychczas stwierdzonych płazów i gadów ze szczególnym uwzględnieniem żółwii i jaszczurek. Na uwagę zasługuje tu dyskusja gatunku Testudo szalaii MŁY-NARSKI pochodzącego ze stanowiska Węże I, stwierdzenie występowania jaszczurek typowych dla fauny śródziemnomorskiej (Lacerta (Podarcis) cf. sicula RAFINESQUE) oraz dyskusja poświęcona kopalnym jaszczurkom (Lacertidae) i padaleom (Anguidae).

W części ogólnej przedstawiono charakterystykę faunistyczną i ekologiczną naszej plioceńskiej i wczesnoplejstoceńskiej fauny płazów i gadów. Polską "preglacjalną" herpetofaunę porównano następnie z herpetofauną stanowisk czechosłowackich, węgierskich i rumuńskich pochodzących z tych samych okresów i wykazujących do niej widoczne podobieństwo. Stwierdzono również, że wbrew początkowym przypuszczeniom, niewielkie jest podobieństwo naszej herpetofauny do herpetofauny z Roussillon czy Pikermi. W ostatniej części omówiono pochodzenie współczesnych gatunków i ras żyjących w Europie żółwi lądowych (Testudinidae) i ich trzeciorzędowych przodków.

РЕЗЮМЕ

Данная публикация является итогом исследований описанных до сих пор остатков амфибий и рептилий из плиоцена и раннего плейстоцена Польши. Известные до сих пор данные дополнены здесь на основании новых материалов походящих с известных уже, а также вновь открытых местоположений. Во вступительной части работы дана характеристика местоположений находящихся в области Краковско-велюньской Юры (Подлесице, Вэнже I, Вэнже II, Ренбелице Крулевские, Камык), а также Кадзельни в Кельцах. В систематической части работы дан обзор отмеченных до сих пор амфибий и рептилий с особым учетом черепах и ящериц. Заслуживают здесь на внимание: дискуссия над видом Testudo szalaii Мехнаков найденным в Вэнже I, установление наличия ящериц типичных для средиземноморской фауны (Lacerta (Podaris) cf. sicula Rafinesque), дискуссия посвященная ископаемым ящерицам (Lacertidae) и веретеницам (Anguidae).

В общей части работы рассмотрен фаунистический и экологический характер нашей плиоценской и раннеплейстоценской фауны амфибий и рептилий. Польская

"преглациальная" герпетофауна сравнена с герпетофауной чешскословацких, венгерских и румынских местоположений, которые происходят с тех же периодов и проявляют явное сходство. Констатировано также, вопреки предыдущим предположениям, что сходство нашей герпетофауны с герпетофауной из Русилон (Roussillon) и Пикерми (Рікекмі) является незначительным. В последней части работы рассмотрен вопрос происхождения нынешних видов и рас выступающих в Европе сухопутных черепах (Testudinidae) и их третичных предков.

PLATE

Plate XIV

- Fig. 1. Parietale of Lacerta (Podarcis) sp. from Weże I.
- Fig. 2. Maxillare-fragment of Lacerta (Podarcis) sp. from Weże I.
- Fig. 3. Dentale of Anguis cf. fragilis (LINNAEUS) from Weże I.
- Fig. 4. Young Testudo szalaii Meynarski (paratype). Pygal part of carapace.

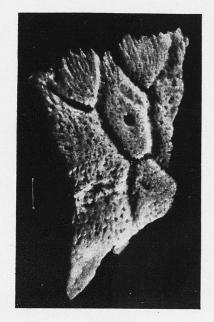


Fig. 1

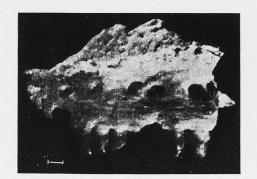


Fig. 2



Fig. 3

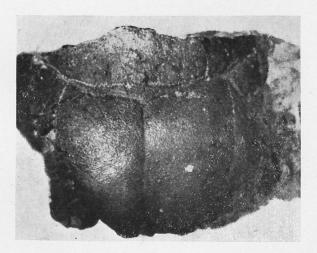


Fig. 4

Phot. L. Sych M. Mlynarski

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