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ZANGERLIA TESTUDINIMORPHA N. GEN., N. SP., A PRIMITIVE LAND TORTOISE FROM THE UPPER CRETACEOUS OF MONGOLIA

(Plate XXVIII)

Abstract. — *Zangerlia testudinimorpha* n. gen., n. sp., assigned to the Dermatemydidae, has been described on the basis of the material collected in 1970 in the Lower Nemegt Beds from the localities of Nemegt and Khulsan (GRADZIŃSKI & JERZYKIEWICZ, 1972). It has been found on the basis of morphological characters that these were tortoises adapted to the terrestrial mode of life, which, at the same time, preserved all features of primitive aquatic Dermatemydidae. In addition, the systematic position and ecological conditions have been discussed and remarks on the Mesozoic land tortoises presented.

INTRODUCTION

In 1970, the remains of shells of two large tortoises were found by the Polish-Mongolian Palaeontological Expedition (KIELAN-JAWOROWSKA & BARSBOLD, 1972) in the Nemegt and Khulsan outcrops located in the Nemegt Basin (GRADZIŃSKI & JERZYKIEWICZ, 1972). They come from the Lower Nemegt Beds. On the basis of the multituberculate fauna, the age of these beds has tentatively been recognized by KIELAN-JAWOROWSKA (*in* KIELAN-JAWOROWSKA & BARSBOLD, 1972) as Campanian. The remains of the tortoises were found in fine-grained and poorly cemented sandstones. Although GRADZIŃSKI (1970) mentions that the Lower Nemegt Beds are probably deposits of the lacustrine or fluvial origin, his studies conducted in 1970 (Dr. R. GRADZIŃSKI's personal communication) seem to indicate that most of these beds were deposited in a terrestrial environment. However, it will be only after the completion of geological studies in the locality discussed, that the data will be obtained which will enable a more accurate determination of the sedimentological conditions of the beds under study.

DESCRIPTIONS

Suborder **METACHELYDIA** ZANGERL, 1969
Family DERMATEMYDIDAE, GRAY, 1870
Genus **ZANGERLIA** nov.

Monotypic species: Zangerlia testudinimorpha n. sp.
Derivation of the name: in honour of Dr. RAINER ZANGERL, from the Field Museum of Natural History, Chicago.

Occurrence. — Known only from the Upper Cretaceous (Lower Nemegt Beds) of the localities of Nemegt and Khulsan in the Nemegt Basin, Gobi Desert, Mongolia.

Diagnosis. — The genus is monotypic, the generic characters being those of the type species.

Zangerlia testudinimorpha n. sp.

(Plate XXVIII; Text-figs. 1-2)

Holotype: A 24 cm long part of shell damaged anteriorly, together with fragmentary bones of shoulders girdle and toes of the right fronts, limb; Z.Pal.No.MgCh/72.

Type horizon and locality: Upper Cretaceous, Lower Nemegt Beds (probably Campanian), Southern Monadnocks, Nemegt Basin, Gobi Desert (see GRADZIŃSKI & JERZYKIEWICZ, 1972, Text-figs. 3).

Derivation of the name: Testudo – most common genus of land tortoises, Gr. *morphe* — shape.

Diagnosis. — A large land tortoise with characters indicative of degree of terrestrial specialization and the features of primitive aquatic forms preserved.

Shell strongly ossified, massive, without fontanels. Carapace convex, with an even, non-serrate peripheral margin. A poorly visible medial keel running along a characteristic, gutterlike depression. Eight neurals and two distinct metaneurals are probably present. Plastron massive, cross-shaped, considerably smaller than the inner aperture of carapace. Plastral bridge very wide and massive, only slightly narrower than the length of the entire plastron. Limbs with considerably and distinctly shortened phalanxes characteristic of land tortoises. Sculpture of all shell plates characteristically pock-marked, furrows of dermal shields very distinct and deep.

Material. — In addition to the holotype the specimen Z.Pal.No.MgCh/73 — an internal mould, about 55 cm long, with fragmentary plates of carapace and with the remains of a plastron in the Lower Nemegt Beds, found at Khulsan, Nemegt Basin, Gobi Desert.

Description. — Shell massive, convex, oval in outline; carapace steeply deflected in the pygal region. Peripheral margin even, without any traces of serration. Surface of plates strongly ornamented with a simultaneous preservation of distinct impressions of shields. The furrows of these shields are very clearly visible and deep. Distinctly visible are also the sutures of dermal plates, although in many cases the rifts on shell run along them. A not very large but clearly visible medial keel runs along the body axis of symmetry on the surface of neurals. It terminates on neural VIII. On the other hand, in the pygal part of carapace, a sharp bend of shell, visible as a node, occurs in both specimens. The medial keel is situated in a shallow trough. In the holotype, the carapace has been subject to a slight, dorsoventral compression, but its convexity was surely much more conspicuous.

Proneural plate is preserved only fragmentarily. It may be supposed on the basis of its small fragments that it was not very large, trapezoidal and similar to corresponding plates of other Dermatemydidae. Since a rift corresponding to its lateral outlines has been preserved on the right side of the specimen, the shape of this plate may be reconstructed. All neurals preserved. They formed one, uninterrupted row. In many places, their sutures are fairly indistinct, since they were covered with a thick, fossilized dermal layer dammaged mechanically in several places. Nevertheless, the shape of all the nine neurals may be distinctly reconstructed. Plate N-I is slightly larger than the rest of them and has almost parallel lateral margine; N-II is much smaller than N-I and has slightly convex lateral ridges. It is marked by a characteristic shape of the first neural of many tortoises. All other neurals, N-III through N-VII, are hexagonal, elongate and extended anteriorly, that is, having longer posterolateral ridges. N-VIII is conspicuously shortened, N-IV – trapezoidal. Metaneural I is as if slightly wedged into Met.-II. A suture connecting both plates is bent in the place of the bend of the pygal part of carapace. This characteristically steep bending is visible in both specimens, and, in this connection, the writer does not believe it to be any morphological irregularity. Pygal plate small, rectangular.

Pleurals fairly wide, their long ridges parallel to each other. The largest of them is, as usually, Pl-I, while Pl-VII is disproportionally small as compared with the rest of the plates. None of the peripherals, well-preserved in the case of holotype, distinguishes by any special characters. They form a compact, even ridge of carapace devoid of any traces of serration. The sutures connecting them with pleurals run very near the sulcus or in the sulcus itself which separates laterals from marginals. This feature is characteristic of land tortoises having a fairly strongly convex carapace. Peripherals are somewhat higher than marginals only in the pygal part.

All dermal shields, except for the praecentrale, may be easily reconstructed. Centrals (c-1 to c-5) are elongate and slightly longer than their width. Laterals (l-1 to l-4) are wide and very massive. Furrows of a strongly thickened dermal layer which excellently emphasize areoles are very well visible on their surface. At the same time, their surface — as in other shields — is strongly incrusted with a „tretosternoid" sculpture. There occur two postcentrals which do not differ in size from marginals. The sulcus separating them from each other, together with the sulcus which separates them from central 5, are situated on the surface of a pygal plate, the same as in the Recent Batagurinae.

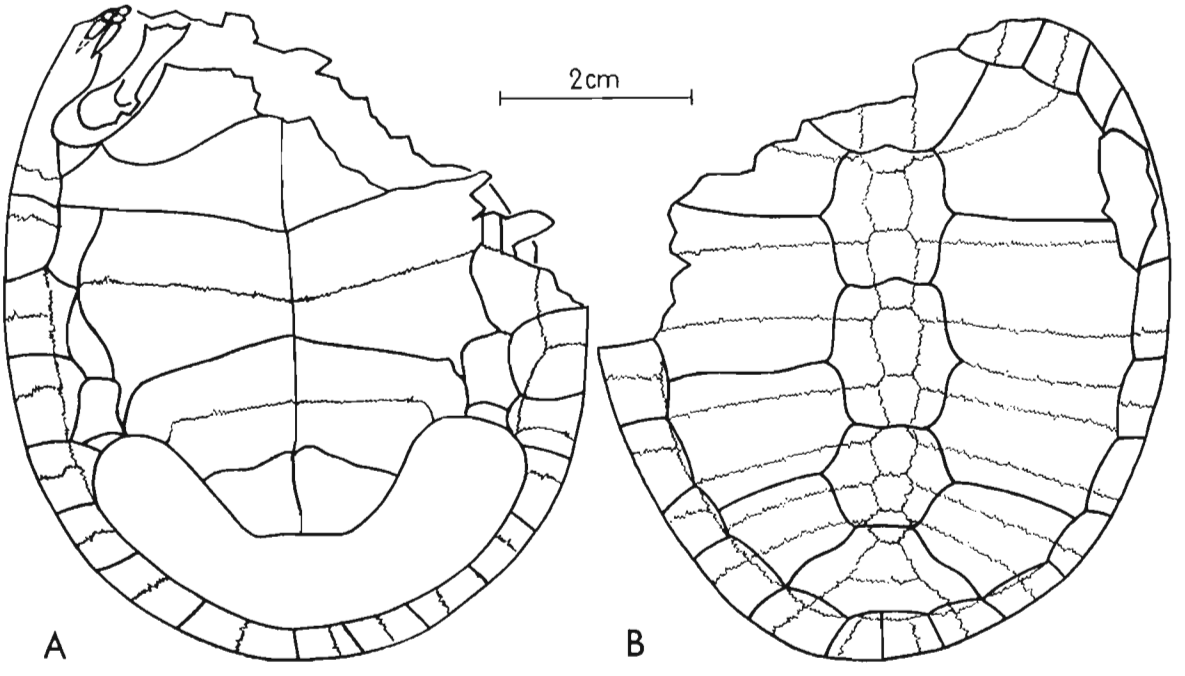

Fig. 1

Zangerlia testudinimorpha n. gen., n. sp., *a* - - the carapace, *b* — the plastron (see also Pl. XXVIII); Upper Cretaceous, Lower Nemegt Beds, Southern Monadnocks, Nemegt, Nemegt Basin, Gobi Desert (Z.Pal.No.MgCh/72).

In the specimen Z.Pal.No.MgCh/72, the plastron of *Zangerlia testudinimorpha* n. sp. is well-preserved although its ridges are in some places broken away. No epiplastra have also been preserved.

Plastron cross-shaped. Its lobes have nonrounded, straight gular and caudal ridges. A fairly extensive depression, which may suggest that these are the remains of a male, occurs

in the central part of plastron. Plastral bridge very wide, its width being only slightly smaller than the length of the entire plastron. All plastral plates are very closely connected with each other by sutures. In this connection, no mobility was observed in any of the lobes.

Although no epiplastral plates have been preserved since the break-off took place along the epiplastral suture, it may be found that the epiplastra were small, narrow and slightly connected with hyoplastra by a relatively straight suture. The entoplastron was also bound to be very small. The hyoplastron ridge preserved suggests that it was elongate, triangular and similar to entoplastron of the younger specimens of *Mongolemys elegans* KHOSATZKY & MŁYNARSKI. It was shifted further anteriorly. The hyo- and hypoplastra are large, massive and more or less of the same size. The suture which connects these groups of plates is delicate and not very well visible on the surface. Relatively clearly visible is, on the other hand, a characteristic suture which connects them with xiphiplastra. Its shape is the same as that in *Mongolemys elegans*. The dermal shields of plastron are in many places more difficult to reconstruct than the dermal shields of carapace. For instance, no traces have been preserved of the gulars but we may judge that they were wide and not elongate as well as small and similar to epiplastral plates. Humerals, much the same as pectorals are wide. The humeropectoral sulcus is situated far below the entoplastron. Pectoral shields extend towards the medial sulcus. Abdominals are the widest and largest of them. Femorals are considerably wider than pectorals, while anals are almost as wide as humerals.

Inframarginal shields are in the state of atrophy. Very strongly developed are inguinals which are so large that over a considerable stretch they separate marginals from plastral shields. In the specimen Z.Pal.No.MgCh/72, sulci of subsequent, probably three, inframarginals are clearly visible on the left side of plastron. They are, however, irregular in shape and asymmetric to the shields of the opposite part of the plastral bridge. Inframarginals 2 and 3 do not occur on the right side, which enables the contact of marginals and the shields of plastron. This is a specimen with an abnormal structure of inframarginals, but we may judge that a visible reduction in these shields here takes place with a simultaneous preservation and even hypertrophy of axillars and inguinals.

All plates of the shell are covered with deep pits which make up an incrustation much more distinct than that in other Mongolian Dermatemydidae. A similar type of sculpture occurs in this family only in the European representatives of the genus *Tretosternon* OWEN (LYDEKKER, 1889, p. 139; BORSUK-BIAŁYNICKA & MŁYNARSKI, 1968). This sculpture gives evidence of a strong fusion of the epidermal layer with the surface of plates and is characteristic of the forms which are associated with the water. At the same time, a very strong development of all shields may be observed, along with the hypertrophy of the epidermal layer mentioned above and which is manifested by the formation of areoles. This is one more feature characteristic of true land tortoises. It is difficult to decide whether the epidermal elements in our species were already hard and corneous or still preserved the nature of a soft, elastic epidermis. It is also not unlikely that there occurred the callosities of some parts of the shell and the callosities resulting from an animal's ageing. In this connection, the writer refrains from using the term corneous to designate the shields in *Zangerlia testudinimorpha*, replacing it with a less definite „dermal". The sculpture of the shell is one of the most important characters of *Zangerlia testudinimorpha* which allows one to distinguish this species from all other Asian Dermatemydidae.

The specimen Z.Pal.No.MgCh/72 has some bones of the schoulder girdle well preserved, of which particularly important are phalanxes II and III of the right front leg. The bones of these toes, only slightly shifted, could be properly prepared. In this case, characteristic is

a considerable reduction in phalanxes I and II, while the last phalanx, that is, phalanx III is strongly elongate and preserves the nature of a claw, which is sharp, slightly deflected and arcuate in transverse section. Phalanx II is in both toes considerably shortened. Its articular surface is flat which enabled a free bending of the toes. Analogous is Ph-I, clearly visible in the third toe. In regard to the second toe, it seems that its phalanx was fused with a corresponding

Fig. 2
Zangerlia testudinimorpha n. gen., n. sp., fragment of the right front limb; Upper Cretaceous, Lower Nemegt Beds, Southern Monadnocks, Nemegt, Nemegt Basin, Gobi Desert (Z.Pal.No.MgCh/72); × 1.

metacarpal. A slightly larger bone, occurring above the elements of the second toe mentioned above, is probably a radial which, in this place, may be also fused with metacarpal. It would be, therefore, the B type of fusion of more distal elements (AUFFENBERG, 1966, p. 166, Fig. 2) characteristic of the tortoises which are adapted to the terrestrial mode of life. The metacarpal of the third toe is somewhat more massive but narrower than the previous elements. Their arrangement is visible in the illustration enclosed (Text-fig. 2).

The humerus, preserved on the right side, is slightly S-shaped and represents the type of structure of the Recent snapping turtles. Processus deltopectoideus is shifted far from processus medialis and the head of the sholder bone. The humeral bone-head was large and enabled a considerable articulation also is lateral planes of the forelimb. The proximal part of humerus has not been preserved.

An entire scapula, marked by a strong structure, has been preserved on the left side. Processus acromialis is longer and more strongly developed than processus scapularis. An angle between these processes amounts to about 80°, that is, less than in the Recent species *Chelydra serpentina* (LINNAEUS) and the more so in marine turtles (see BRÄM, 1965, p. 51, Fig. 13). This angle is also much larger in the Recent land tortoises.

Zangerlia testudinimorpha had both its shoulder girdle itself and limbs built quite differently than those in the Dermatemydidae known thus far. Maintaining the features of the original structure characteristic of this group of tortoises, it developed characters indicative of its specialization and adaptation to the life on land.

Discussion. — The genus *Zangerlia* nov. is assigned to the Dermatemydidae on the basis of the following characters: (1) The dermal sculpture of the surface of plates the same as in the representatives of this family and related forms. (2) The presence of inframarginal shields which, although being subject to reduction; separate plastral from marginal shields. The tendency to reduce the inframarginal shields occurs also in a few other fossil Dermatemydidae, e. g., in *Lindholmemys elegans* RIABININ from the Upper Cretaceous of Uzbekistan (RIABININ, 1935; SUKHANOV, 1964).

In the genus *Zangerlia*, no characters are recorded which might be indicative of its assignement to another family. Although it is a form markedly different from all the Dermate-

mydidae known thus far, it displays at the same time certain characters of similarity to the Mongolian representatives of this family. This primarily concerns the tendency to reduce the epiplastra and to diminish entoplastron which is observed in *Mongolemys elegans*. Like the rest of the Mongolian representatives of the Dermatemydidae. *Zangerlia* has a primitive, strongly shortened, cross-shaped plastron and it does not display the tendency to the reduction in neurals characteristic of the Dermatemydidae from other continents, including their only Recent representative *Dermatemys mawii* GRAY.

Zangerlia testudinimorpha n. sp. represents a mixture of characters, both archaic and progressive. The former include the cross-shaped plastron characteristic of the oldest Mesozoic tortoises. A nearly straight humerus is also an archaic character although it is usually related to the adaptation to the aquatic mode of life. In progressive forms, such as, for instance, Neochelydia (ZANGERL, 1969) it is always pronouncedly S-shaped. The presence of inframarginals and the tretosternoid type of the structure of dermal shields are also primitive characters in *Zangerlia*.

Progressive characters are primarily represented by the modification of phalanxes and entire limbs adapted to the terrestrial mode of life. A similar shortening of phalanxes is also observed in the Recent land tortoises. This character was first found in the Dermatemydidae and it gives evidence of their considerably advanced land adaptation. The convexity of carapace is also indicative of the adaptation to this environment. Although SCHUBERT-SOLDERN (1962) maintains that the convexity of carapace alone cannot be evidence of either an aquatic or terrestrial mode of life, in the case under study it is, however, one of a few characters which do indicate a land adaptation. Likewise, a strong development of dermal shields and the formation of areoles on them, the same as in the Recent land tortoises, speak much of the terrestrial adaptation.

ECOLOGICAL REMARKS

Taking into account several characters of adaptation to the life on land in *Zangerlia testudinimorpha* mentioned above, we may assume that this tortoise lived in a dry, xerothermic environment. Those were steppes or, here and there, they might be steppe-desert areas. The strong, but long and sharp claws indicate that this tortoise lived in a fairly soft terrain, devoid of rocks and larger stones. The small, although massive and strong plastron and shoulder girdle similar to that of the Recent snapping turtles are indicative of a specific locomotive adaptation. The lack of a bend in humerus is, in the case under study, made up for by a small size of the anterior lobe of plastron, which thus leaves much space for the movements of limbs. Due to this fact, the tortoise understudy could, in the case of escape, stand up on straight legs with its shell raised over the ground. Its movements were probably considerably more similar to those of the Recent American species *Gopherus polyphemus* (DAUDIN) than to the manner of moving of the well-known Greek tortoises (*Testudo hermanni* GMELIN, see AUFFENBERG, 1966, p. 184, Fig. 9).

Owing to the preservation of an typical, „aquatic" shoulder girdle with a simultaneous strong adaptation of the carpal region, the tortoise under study was capable of performing lateral movements not only in an almost horizontal plane, but also of raising limbs slightly. On the basis of this fact, the present writer supposes that the tortoise did not use its fore limbs for digging hollows but for pushing the sand sidewards. The supposition may also be expressed that *Zangerlia testudinimorpha* did not hide its head behind its bent shoulders as is the case

in many land tortoises but at the moment of danger it tried to dig itself quickly and to camouflage itself by covering its shell with earth or sand. A similar burying reaction is observed in many Recent turtles on the bottom of water reservoirs. This is particularly distinct in, for instance, soft-shelled turtles, but such defensive reactions occur even in the representatives of the Emydidae (e. g., *Mauremys caspica caspica* (GMELIN)). The areas of old river shoals or simply dried water reservoirs were a convenient place for using such a defensive tactics, the habit of which may be considered as a heritage after the ancestors. Burying themselves and throwing sand or earth in all directions, the tortoises might actively and easily scars away their real or supposed enemies.

REMARKS ON THE EVOLUTION OF LAND TORTOISES

The oldest chelonians and their unknown ancestors were land animals. All Proganochelyidae display essential characters indicative of their terrestrial mode of life. These characters are not, however, as distinct as those in the land tortoises proper and it is quite possible to find in them the presence of characters which one can safely call „aquatic" ones. Among them, the most strongly vaulted shell is that of *Proterochersis robusta* FRAAS which in those times might replace the testudinids in a purely terrestrial environment. The remaining forms, including *Triassochelys dux* (JAEKEL), were brushwood animals, which lived near waters and marshes. Characteristically, no forms pronouncedly terrestrial are met with in the Jurassic. It is only in the Upper Cretaceous that the forms reappear which are adapted to the life in this environment. These are the Argentine representatives of the Meiolaniidae (*Niolamia argentina* AMEGHINO) and here described *Zangerlia testudinimorpha*. A distinct development of terrestrial forms begins in the Tertiary. Species of the Recent genus *Geochelone* GRAY, having their counterparts in the Recent fauna, are known as early as the Eocene. Land tortoises are much more numerous in the Miocene and their largest development on all continents is recorded in the Pliocene.

The mixture of characters in *Zangerlia testudinimorpha* is indicative of a very quick adaptation to extremely changing ecological conditions. The unknown ancestors of *Zangerlia* were certainly aquatic animals, which might even live in rivers with a fairly rapid current. In the areas in which the terrain they inhabited began to dry up, the turtles remained in their environment and adapted themselves to its changed conditions. What seems strange enough is a distinctly reduced plastron which under land conditions always increases. This might be to a certain extent explained by the relatively soft substratum. Undoubtedly, *Zangerlia testudinimorpha* forms a specialized side-lineage of the Dermatemydidae which did not survive a longer period.

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PLATES

PLATE XXVIII

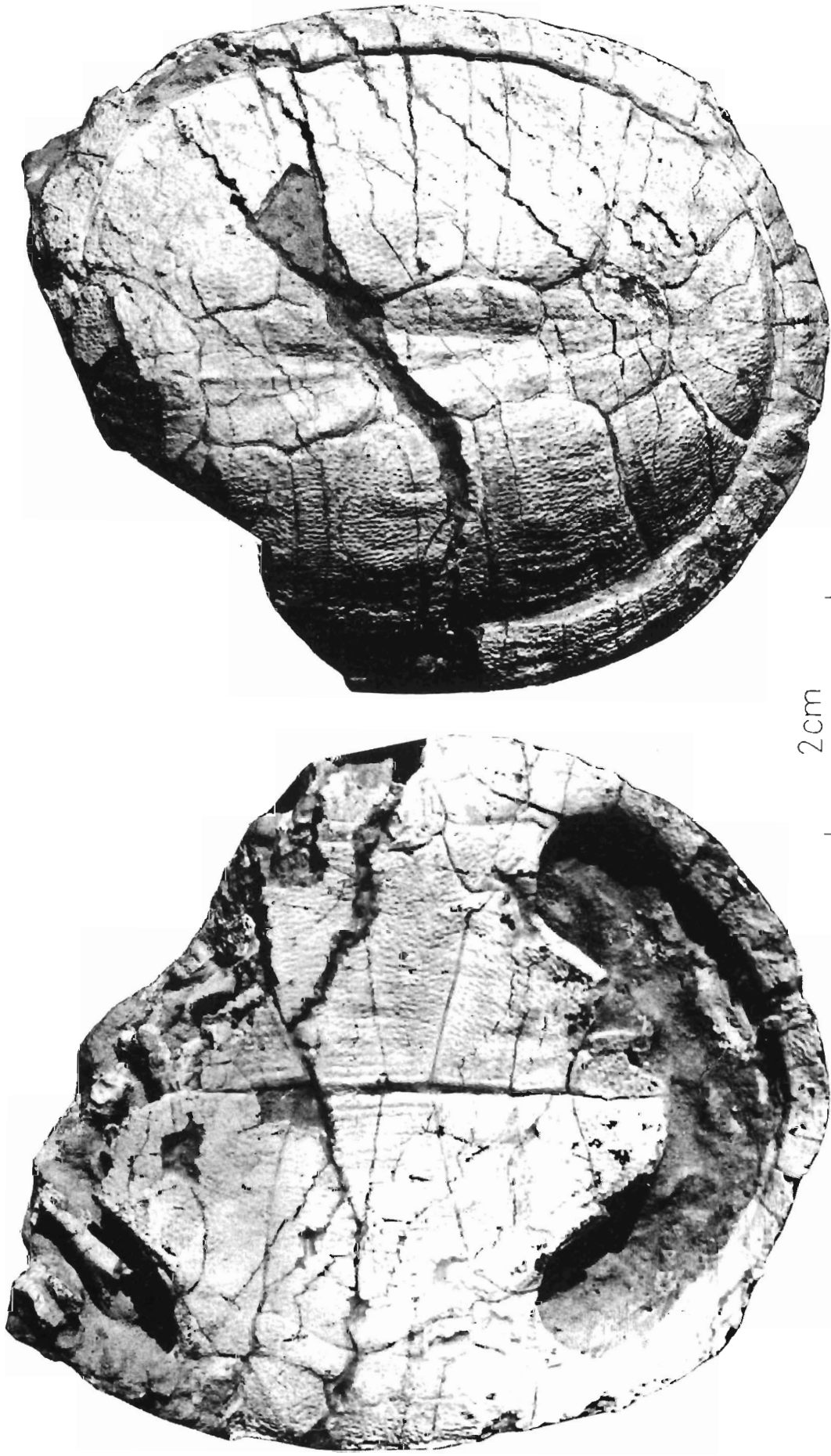
Page

Zangerlia testudinimorpha n. gen., n. sp. 86

Upper Cretaceous, Lower Nemegt Beds, Southern Monadnocks, Nemegt, Nemegt Basin, Gobi Desert

Fig. A. The carapace (Z.Pal.No.MgCh/72).
Fig. B. The plastron of the same specimen.

Photo: L. Sych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