

Chelonians (Reptilia: Testudines) from the Lower Miocene locality Dolnice (Bohemia, Czechoslovakia)

**Želvy (Reptilia: Testudines)
ze spodnomiocenní lokality Dolnice
(Czech summary)**

(3 text-figs, 2 plates)

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Chelonian remains from the Lower Miocene (Ottangian) of Dolnice (western Bohemia, Czechoslovakia) have been described. Most of the bony fragments have been recognized as belonging to the Miocene genus *Ptychogaster* (Emydidae: Emydinae), one of prevailing reptiles at this site. The remaining infrequent remnants belonged to the terrestrial tortoises (Testudinidae), presumably to two different forms (*Testudo* sp. large form and *Testudo* sp. small form). Moreover, presence of unidentified emydids (Emydidae indet.) in the material is presumed. In the systematic part of the paper methods and difficulties concerning identification of chelonian shell fragments as well as taxonomic position of recognized taxa are described. The final part of the paper contains considerations on adaptation of particular taxa to various kinds of habitat together with their significance for increasing our knowledge of faunistic and ecological analysis of the locality Dolnice. The text is supplemented with a complete list of amphibians and reptiles described up to the present from this classical European locality.

Introduction

Remains of chelonian shells described here are only a small part of rich material collected in Dolnice by Dr. O. Fejfar of the Geological Survey, Prague, and one of the authors (Z. R.). The material is a property of the Department of Paleontology, Faculty of Sciences, Charles University, Prague (DP FNŠP). Unfortunately, the whole material consists exclusively of tiny (though well preserved) shell fragments and disarticulated plates of carapace and plastron. These remains belong to at

least 40 specimens of various size, both adults and juveniles. Identifying of taxa has been based on bony fragments having high taxonomic importance, according to the method of significance of particular shell regions (Młynarski 1980a). However, identification based on the material available is somewhat problematic. Altogether, 3 or 4 taxa (species?) belonging to two different families (Emydidae and Testudinidae) have been recognized in the material. The greatest part of the remains belonged to *Ptychogaster*, a distinctive turtle of the European Miocene. The most characteristic bony fragments of particular forms are shown in illustrations.

The importance of turtles for reconstructing paleoecology is widely known and taken into account in paleontological investigations. For this reason the present article, although considered to be only a preliminary record, essentially contributes to previous studies of the faunistic composition and ecological character of the Dolnice herpetofauna.

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Systematic paleontology

We follow here the systematic subdivision accepted by Młynarski (1976), including modifications recently introduced by Młynarski (1978, 1980a), de Broin (1977), and others.

Order *Testudines* Batsch, 1788

Suborder *Cryptodira* Cope, 1870

Family *Emydidae* Gray, 1825

Subfamily *Emydinae* Gray, 1825

Tribe *Ptychogastrini* De Stefano, 1917

Genus *Ptychogaster* Pomel, 1847

Type-species: *Ptychogaster emydoides* Pomel, 1847

Type locality and horizon: Saint-Gérard-le-Puy, France; Aquitanian.

Note: There is a good deal of presumed species described as belonging to the genus *Ptychogaster*; most of them are probably synonyms of the type-species.

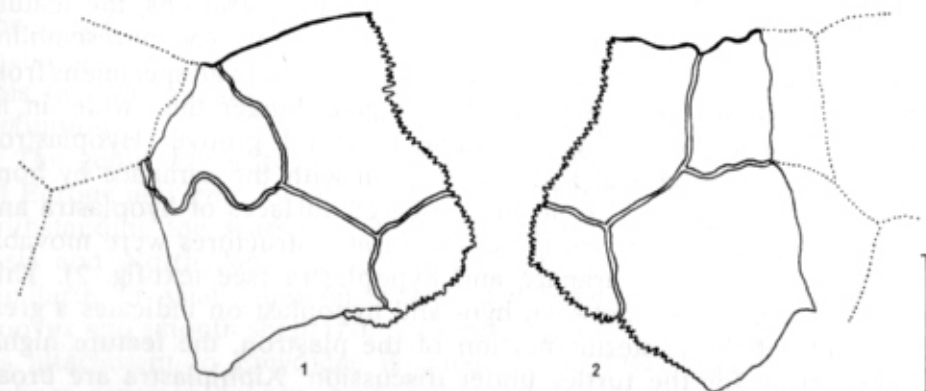
Ptychogaster cf. *emydoides* Pomel, 1847

Material: 1. Anterior margin of plastron consisting of fragmentary epiplastra and fragmentary entoplastron, belonging to a large specimen (DP FNSP 1661). 2. Right epiplastron of a small though adult specimen (DP FNSP 1942). 3. Nuchal with an impression of cervical of a large specimen (DP FNSP 1947). 4. Right hypoplastron of a large specimen (DP FNSP 1621). 5. Right incomplete hypoplastron with typical

sternal bridge, belonging to a large specimen (DP FNSP 1882). 6. Right xiphiplastron of a small juvenile specimen (DP FNSP 1887). 7. Pygal of a small specimen (DP FNSP 1812). 9. Left epiplastron of a large specimen (DP FNSP 1901). 10. Right xiphiplastron of a juvenile specimen (DP FNSP 1892). 11. Pygal of a juvenile specimen (DP FNSP 2113). 12. Left hypoplastron with characteristic bridge surface (DP FNSP 1773). 13. Fragmentary nuchal of very large size with an impression of wide cervical (DP FNSP 1771). 14. Fragmentary nuchal of similar size as the previous one, together with cervical, the latter somewhat distorted, though characteristic for the genus (DP FNSP 1772). 15. Pygal of a large specimen (DP FNSP 1755). 16. Cranial fragment of carapace with fused N-I and PL-I (DP FNSP 1704). 17. Left hypoplastron (DP FNSP 1692). 18. Nuchal (DP FNSP 1651). 19. Neural N-V of a large specimen (DP FNSP 2131). 20. Fragmentary right hypoplastron of large size with preserved fragment of movable hyo-hypoplastral connection (DP FNSP 2924). 21. Fragmentary left sternal bridge including strongly fused pleurals, peripherals with fragmentary hypoplastron fused with carapace and well preserved buttress of a large specimen (DP FNSP 2922). 22. Fragmentary left peripheral Pr-VII of a large size with fragmentarily preserved surface of detached bridge connection of carapace (DP FNSP 2921).

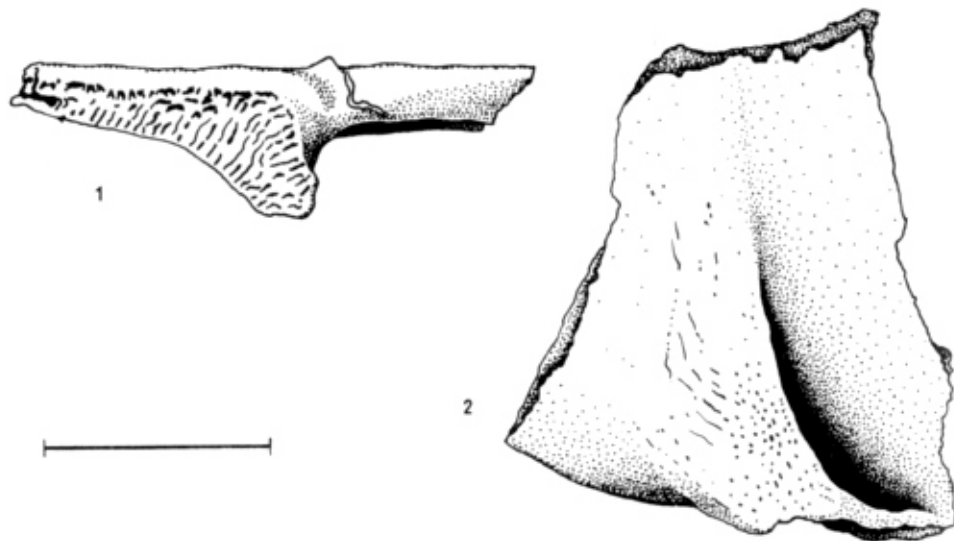
Note: The above list contains only material of high taxonomic importance.

Description: The above-mentioned shell fragments for the most part belonged to relatively small specimens of the shell length not exceeding 15 cm. Only few among them somewhat exceeded 20 cm. Pleurals, peripherals and neurals preserved in the material indicate that the carapace was convex and vaulted. There are no signs of the presence of either distinct medial keel (neurals) or lateral keels (pleurals). Impressions of a wide, pear-shaped cervical, characteristic for large forms of the genus *Ptychogaster*, are seen on the massive nuchal. Hexagonal neurals are comparatively wide, wider in their anterior portion, typical of emydids. Pleurals, despite distinct convexity of the carapace, are also provided with emydoid-like, lateral margins, parallel to each other. Peripherals form a uniform and uninterrupted margin in both cranial and caudal parts of the carapace. Impressions of the marginals indicate that they



1. *Ptychogaster*. 1. Nuchal (DP FNSP 1772) in dorsal view. 2. Nuchal (DP FNSP 1976) in dorsal view. (Scale equals 2 cm)

were higher than peripherals. Lateral peripherals are high; as can be seen from the remnants, their anterior parts indicate solid connection between the plastron and carapace, whereas the posterior parts indicate movable cartilaginous connection. The pygal part of carapace that can be reconstructed on the basis of preserved plates shows a form typical of Emydidae (sensu McDowell 1964). All mentioned pygal plates contain on their external surface impressed furrows of the margins of paired postcentrals.



2. *Ptychogaster*. 1. Right hypoplastron with sternal bridge (DP FNSP 1882) in lateral view. 2. Left peripheral Pr-VII with the surface of detached bridge connection of the carapace (DP FNSP 2921) in ventral view. Scale equals 2 cm

Plastron is broad, massive and rasher-like. All preserved epiplastra have distinctly thickened and well marked epiplastral lips, the feature very characteristic for the genus under discussion, somewhat resembling homologous structures of *Geoemyda* (Batagurinae). In all specimens from Dolnice entoplastron was distinctly elongate, longer than wide, in its posterior part crossed by the humeropectoral groove. Hyoplastron has preserved vestiges of solid connection with the carapace by bony raphes. As can be seen from the preserved surfaces of hyoplastra and peripheral plates of the carapace, the former structures were movably connected with both carapace and hypoplastra (see text-fig. 2). Thin and weak connection between hyo- and hypoplastron indicates a great movability at the posterior portion of the plastron, the feature highly characteristic for the turtles under discussion. Xiphiplastra are broad and somewhat resembling those of *Emys orbicularis*; the structures do not possess a distinct anal notch and the grooves of the anal (femoro-anal)

plate are distinctly shifted to the anterior margin of the xiphiplastra (the character of Emydidae; cf. Mlynarski 1980b: 15, fig. 9). Surfaces of these plates are always distinctly marked with the grooves of epidermal shield. As in most representatives of the genus *Ptychogaster*, epidermal layer was presumably not too thick and weakly sculptured. Shields are of typical shape of the genus, especially centrals; pear-shaped cervicals, postcentrals and anals have been discussed earlier.

Discussion: Identifying the above mentioned remnants as belonging to the genus *Ptychogaster* is quite easy. We based the determination on the shape and structure of the plastron, especially its characteristic connection with the carapace. Also the features of nuchal and pygal are of high importance. Another important feature of ptychogastrines is a common (also in our material) distinct anchylosis of raphes leading to the obliteration of the shape of particular plates as well as cracking of the shell, the process discordant with the disposition of the plates.

Identification of the species is much more complicated and always controversial in the case of *Ptychogaster*. Undoubtedly, it was a turtle very common throughout European Miocene but its remains from particular localities differ from one another to a small degree. Therefore, many of presumed species of the genus (cf. e.g. Kuhn 1964) are probably synonyms, for the most part of the type-species, *P. emydoides* (de Broin 1977 is also of similar opinion). Considering these small morphological differences resembling those between populations of living species, one might recognize the presumed species as paleontological subspecies. The latter term corresponds with the term subspecies or geographical race used for living animals. In the cases discussed the particular sites were distant from one another not only "in space", but often also "in time". The controversial problem of the definition of fossil subspecies is more complicated and needs to be discussed separately.

Identifying the turtle as belonging to *Ptychogaster emydoides* is based on the size of the largest specimens, morphology of epiplastral lips, and the shape of cervical. Since we have at our disposal only fragmentary material we treat our determination as provisional. In order to stress this fact we use the abbreviation "cf." according to Sanchíz's (1977) definition.

The genus *Ptychogaster* is a typical component of Neogene faunas of Europe and even almost a key fossil of the European Miocene. Notwithstanding the search for this genus at paleontological localities in Asia and North America, it has not been found outside Europe. Its similarity to Asiatic and American emydids characterized by a strongly convex and smooth shell, is only superficial, maybe convergent, although its attachment to Emydidae is unequivocal. Ptychogastrines form an extinct separate lineage, presumably having no equivalent in Recent fauna, though resembling *Emys* and Emydoidea to a certain degree.

Family *Testudinidae* Gray, 1822Genus *Testudo* Linnaeus, 1758

Type-species: *Testudo graeca* Linnaeus, 1758.

Terra typica: see Wermuth and Mertens (1977: 85); fossil distribution in Europe, Asia, North America, since the Miocene to Recent (Auffenberg 1974: 194).

Testudo sp. (large form)

Material: 1. Left peripheral Pr-VIII of a large adult specimen (DP FNSP 1984). 2. Right xiphiplastron of a medium size (DP FNSP 1643). 3. Pygal of a large specimen (DP FNSP 1762). 4. Damaged right xiphiplastron of a very large specimen (DP FNSP 1671). 5. Peripheral from the lateral bridge portion of carapace (DP FNSP 1791). 6. Right peripheral Pr-XI belonging to the same large specimen as pygal N° DP FNSP 1762 (DP FNSP 1721). 7. Neural N-III or V (DP FNSP 1849). 8. Peripheral Pr-II or III with considerably damaged margins, belonging to a large specimen (DP FNSP 1572). 9. Nuchal of a large specimen (DP FNSP 1891).

Description: The above mentioned fragments belonged to a dozen or so specimens of a shell length reaching even above 25 cm, therefore corresponding to the biggest living specimens of *Testudo graeca*. The plates show morphological patterns typical of testudinids in the number of tetragonal-shaped neurals, high and "testudinoid-like" peripherals (cf. Młynarski 1980b: 14, fig. 7d) as well as wedge-shaped pleurals. The fossils have been identified as belonging to the genus *Testudo* on the basis of the nuchal provided with well preserved, comparatively large and distinct cervical. Also massive xiphiplastra with distinct triangular anal notch are typical of the genus. Pygal plate of a large specimen is solid, strongly convex and devoid of a furrow of postcentral horny shields. It is indicative of the occurrence of a single broad postcentral characteristic for the most fossil and extant members of the genus.



3. 1. Nuchal of *Testudo* sp. (large form) (DP FNSP 1891) in dorsal view. 2. Nuchal of *Testudo* sp. (small form) (DP FNSP 1912) in dorsal view. Scale equals 2 cm

Shell fragments of large specimens display a rather weakly developed sculpture of epidermal layer.

Basing on the above-mentioned fragments we can assume that they belonged to a terrestrial tortoise of rather strongly convex and relatively smooth carapace with a uniform (i.e. not notched) peripheral margin. The presence of one postcentral shield and a large cervical one, as well as the size of the animal and its habitus, all these features recall the Recent tortoise *Testudo graeca*. However, this resemblance can be completely apparent: thus far, a lot of species have been described from the Miocene of Europe and some of them show identical features with the living *Testudo*, known since the Pliocene. Identical morphology shows e.g. *Testudo steinheimensis* Staesche, 1931, originating from a classical, though much younger locality Steinheim in Württemberg. Remains of similar morphology are also common at other sites, e.g. in Przeworno in Poland (Młynarski 1978). Owing to the fragmentary state of the fossil, precise determination is so far impossible.

Testudo sp. (small form)

Material: 1. Well preserved nuchal with impressions of furrows of epidermal shields (DP FNSP 1912). 2. Nuchal of a specimen of similar habitus (DP FNSP 1847). 3. Right peripheral Pr-XI (DP FNSP 1691). 4. Left peripheral Pr-VIII (DP FNSP 1601).

Description: All above mentioned fragments belonged to much smaller specimens, also characterized by more expressive sculpture and horny shields; the latter feature is especially well observable in peripherals. The shell length of these chelonians did not exceed 18 cm. The bony fragments are highly characteristic for the members of the genus *Testudo*, resembling homological shell fragments of medium-sized *T. graeca* and *T. hermanni*. It should be stressed that numerous though practically indeterminable fragments with heavy sculpture probably also belonged to the form discussed.

Discussion: Presence of the above mentioned fossils suggests the occurrence of another species of the genus *Testudo* in Dolnice. These remains do not show juvenile features. On the other hand, it is not unlikely that they represent younger specimens of the former form. At the same time, it is possible that in Dolnice, similarly as at the present, two species of testudinids of overlapping ecological areas, were present.

Emydidae indet.

Material: 1. Left hyoplastron (DP FNSP 1881). 2. Elongate entoplastron of a large specimen (DP FNSP 1662). 3. Neural N-V? (DP FNSP 2060). 4. Fragmentary nuchal of a large specimen (DP FNSP 1855). 5. Fragmentary pleural with distinct sculpture (DP FNSP 1952). 6. Neural N-I (DP FNSP 2073). 7. Neural N-II (DP FNSP 2078). 8. Neural N-VIII (DP FNSP 2071). 9. Left xiphiplastron of a small adult specimen (*Geoemyda*?) (DP FNSP 1718).

Discussion: The fossils display features of various emydids, of both the prevailing genus *Ptychogaster* and another unidentified form. Elongate and very massive entoplastron, crossed posteriorly by the humeropectoral furrow, is worthy of special attention. Entoplastron of *Ptychogaster* is usually more oval, wider and more similar to that of *Emys*. Nevertheless, such trends can be observed in members of this genus, too, especially in young specimens. Pleurals are sculptured similarly to *Geoemyda* and *Ocadia*, however, also these fossils could belong to *Ptychogaster*. Neurals, broad and tapering posteriorly, are typical of most the emydids; therefore, these plates are of small taxonomic importance. An incomplete nuchal belonging to a very large specimen is more conspicuous; its external surface preserved a trace of sulci of very broad and convex (barrel-shaped?) cervical. The structure of this plate corresponds to those found in plates of the largest specimens of the genus *Ptychogaster* belonging to the species-group *P. emydoides* (large forms), but it is not unlikely that the fossil represented another genus.

Discussion

The turtles described here supplement a long list of the hitherto known Dolnice herpetofauna. Judging by the abundance of the collected material, turtles were very common and numerous in this locality. *Ptychogaster* cf. *emydoides* was the dominant species, not only among turtles but most likely also among remaining reptiles. Terrestrial tortoises of the genus *Testudo* were much rarer; the presence of other chelonians is so far uncertain and needs to be confirmed.

Ptychogastrines, although they are members of the family including water turtles (Emydidae), were not typical aquatic animals. Considering the form of their shell and its external similarity to the shell of *Terrapene* and *Cuora*, they were rather terrestrial animals (de Broin 1977, Mlynarski 1978). Schleich (1981) suggests that juveniles and adults of *Ptychogaster* could have inhabited different environments, the condition known in some living emydids. Adaptation to a given habitat depends on the kind of required food. In the case of *Ptychogaster* we can suspect an analogy with *Terrapene*, as the skull of the former form was described accurately by de Broin (1977). Morphology of the alveolar surface of its jaws does not indicate an unequivocal specialization as is the case of e.g. *Clemmydopsis* (Mlynarski 1980a). Therefore, *Ptychogaster* was presumably an omniphagous, similarly to many living turtles, being at the same time herbivorous and carnivorous animals. In Dolnice, like at other Miocene localities, turtles belonging to this genus presumably inhabited forest borders, in the area of damp scrub near water reservoirs. Presence of such an environment is confirmed by the occurrence of

Table 1

List of amphibians and reptiles from the Lower Miocene of Dolnice

Taxa recognized	Frequency of occurrence	Type of environment
Amphibia		
1. <i>Latonia fejfari</i>	*	xerothermic area
Reptilia		
2. <i>Ptychogaster</i> cf. <i>emydoides</i>	****	scrub
3. <i>Testudo</i> sp. (large form)	**	xerothermic area
4. <i>Testudo</i> sp. (small form)	*	xerothermic area
5. <i>Chamaeleo caroliquarti</i>	*	scrub
6. <i>Palaeocordylus bohemicus</i>	**	xerothermic area
7. <i>Lacerta</i> sp.	****	xerothermic area
8. <i>Miolacerta tenuis</i>	*	xerothermic area
9. <i>Amblyolacerta dolnicensis</i>	**	xerothermic area
10. <i>Ophisaurus</i> cf. <i>spinari</i>	**	xerothermic area
11. <i>Ophisaurus</i> sp. I	*	xerothermic area
12. <i>Ophisaurus</i> sp. II	*	xerothermic area
13. <i>Pseudopus</i> sp.	*	xerothermic area
14. cf. <i>Xestops</i> sp.	**	xerothermic area
15. <i>Omoityphlops gracilis</i>	*	xerothermic area
16. <i>Dolniceophis lehmani</i>	*	scrub

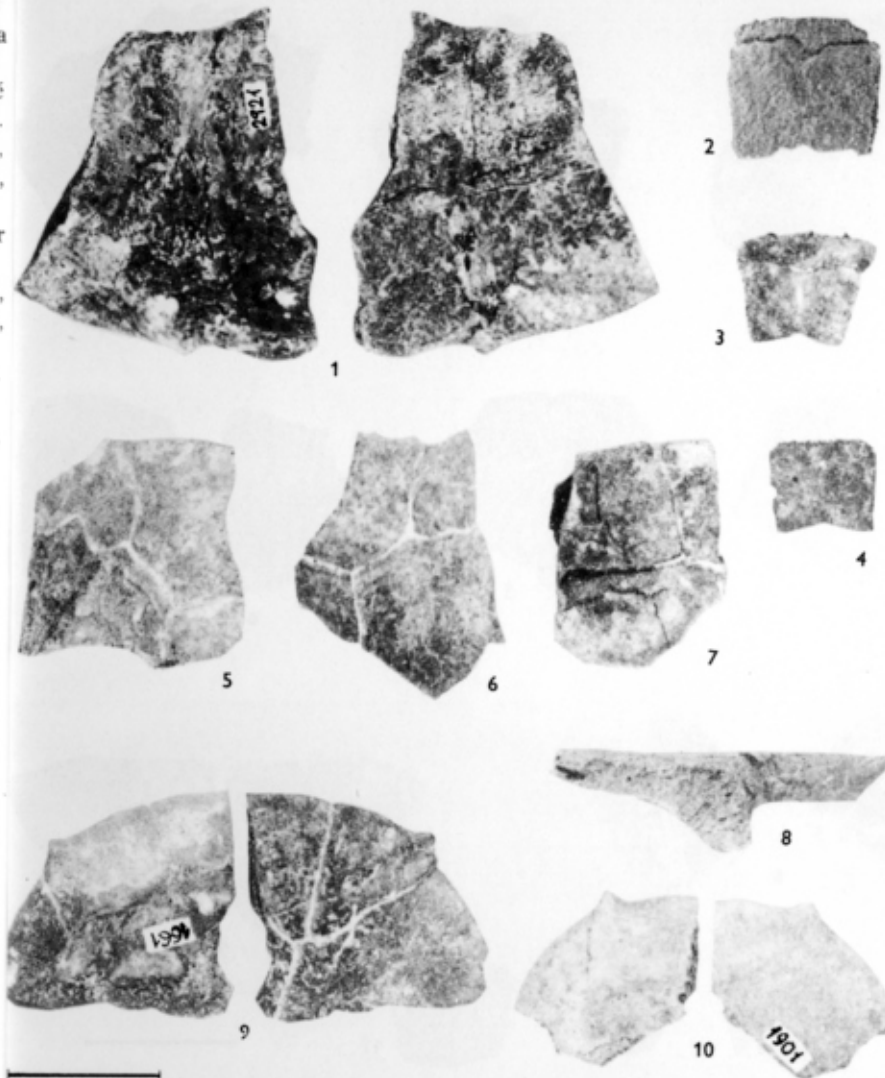
**** — very common, *** — common, ** — rare, * — occasional

chameleons (Moody - Roček 1980), as well as some snakes (Rage - Roček 1983), mammals (Fefjar 1972, 1974) and birds (Švec 1980, 1981, 1982). Moreover, similarly as is the case with many other Miocene sites, e.g. Steinheim and Przeworno, there are indicators suggesting the presence of dry, xerothermic areas in Dolnice. This standpoint can be confirmed by the occurrence of terrestrial tortoises (*Testudo* sp.) as well as various lizards (Roček 1984), mostly Anguidae (Roček, op. cit., Klembara 1979, 1981).

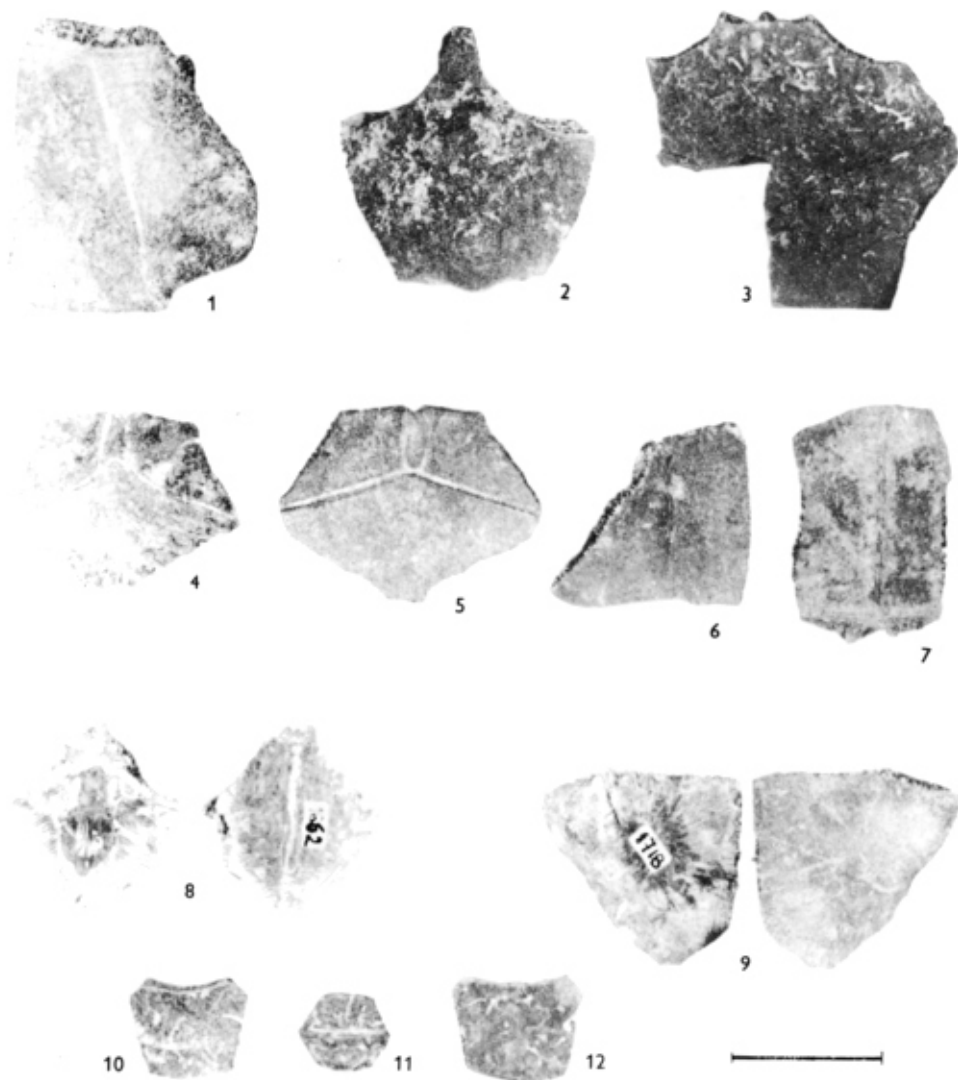
Both these kinds of environment, dry and damp (scrub), overlapped each other to a certain degree. Such conditions making the replacement of habitats possible were especially favourable to *Ptychogaster*, as is demonstrated by the large amount of their remnants. Migration between the areas afforded possibilities for changing the food and searching for favourable mating and breeding places. However, it should be stressed that drawing conclusions as to the biology and ecology of *Ptychogaster* by analogy with the living species is somewhat hazardous. After all, they are entirely an extinct group.

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Ptychogaster cf. *emydoidea* (scale equals 2 cm). 1. Left peripheral Pr-VII (DP FNSP 2921) in ventral and dorsal views. 2. Pygal (DP FNSP 1735) in dorsal view. 3. Neural N-V (DP FNSP 2131) in dorsal view. 4. Pygal (DP FNSP 1890) in dorsal view. 5. Nuchal and cervical (DP FNSP 1772) in dorsal view. 6. Nuchal and cervical (DP FNSP 1976) in ventral and dorsal views. 10. Left epiplastron (DP FNSP 1901) in ventral and dorsal views. 9. Epiplastra and entoplastron (DP FNSP 1661) in ventral and dorsal views. 10. Left epiplastron (DP FNSP 1901) in ventral and dorsal views



Testudo sp. (large form). 1. Left peripheral Pr-VIII (DP FNSP 1584) in dorsal view. 2. Pygal (DP FNSP 1762) in dorsal view. 3. Nuchal (DP FNSP 1891) in dorsal view. *Testudo* sp. (small form). 4. Nuchal (DP FNSP 1847) in dorsal view. 5. Nuchal (DP FNSP 1912) in dorsal view. 6. Right peripheral Pr-XI (DP FNSP 1691) in dorsal view. 7. Left peripheral Pr-VIII (DP FNSP 1891) in dorsal view. (Scale equals 2 cm). Emydidae indet. 8. Entoplastron (DP FNSP 1662) in dorsal and ventral views. 9. Left xiphiplastron (DP FNSP 1718) in dorsal and ventral views. 10. Neural (DP FNSP 2068) in dorsal view. 11. Neural N-VIII (DP FNSP 2071) in dorsal view. 12. Neural N-II (DP FNSP 2078) in dorsal view. (Scale equals 2 cm)