

Introduction to zoogeography and subspecific differentiation in *Emys orbicularis* (LINNAEUS, 1758)

UWE FRITZ

Abstract

A summary and discussion of the present knowledge of subspecific differentiation, distribution, fossil history, and zoogeography of the European pond turtle, *Emys orbicularis*, is presented. Special emphasis is given to Holocene range fluctuations. *E. orbicularis* ranges from the Maghreb region in North Africa over the Iberian peninsula and most parts of South and Central Europe and Asia Minor to the Aral Sea. This taxon is highly polytypic, and 13 subspecies are now distinguished. However, most probably some additional populations deserve subspecific rank. The highest subspecific diversity is found in the southern areas of the species' range, reflecting the Pleistocene extinctions and recolonisations of the more northern areas from only few glacial refugia. *E. orbicularis* is the sole Old World representative of the Emydinae, an otherwise exclusively Nearctic turtle subfamily. Most probably, the ancestors of *E. orbicularis* reached the Palearctis during the Middle or Upper Tertiary over the Bering Bridge. This implies an Old World radiation of *Emys* from East Asia to the West. In accordance with this assumption, the oldest known *Emys* fossils are from the Middle Miocene from the area of the former Turgai Strait in Central Asia which separated Europe from East Asia until the Oligocene. With the exception of the problematical *Emys wermuthi* MLYNARSKI, 1956 from Poland, all fossil taxa represent chronospecies, leading to the recent *E. orbicularis*. In the Mediterranean, the fossil record is quite incomplete, the oldest findings dating only back to the Villafranca. The Holocene distribution pattern of *E. orbicularis* is much influenced by man, especially in Central Europe. The northern distribution limit is not a natural one. Instead, it reflects impacts over the course of thousands of years in a heavily disturbed environment.

Key words: Testudines: Emydidae: *Emys orbicularis*; zoogeography.

Zusammenfassung

Der derzeitige Kenntnisstand hinsichtlich subspezifischer Differenzierung, Verbreitung, Fossilgeschichte und Zoogeographie der Europäischen Sumpfschildkröte, *Emys orbicularis*, wird zusammengefaßt und diskutiert, wobei die holozänen Arealfluktuationen besondere Beachtung finden. Das Verbreitungsgebiet von *E. orbicularis* erstreckt sich von der nordafrikanischen Maghreb-Region über die Iberische Halbinsel und den größten Teil von Süd- und Mitteleuropa sowie Kleinasien bis zum Aralsee. Es handelt sich bei dieser Art um ein hochgradig polytypisches Taxon mit derzeit 13 anerkannten Unterarten. Wahrscheinlich werden in naher Zukunft einige weitere hinzukommen. Die größte Subspezies-Diversität findet sich in den südlichen Arealteilen, was bis heute die pleistozänen Auslösungen und Rekolonisationen von nur wenigen Glazialrefugien widerspiegelt. *E. orbicularis* ist die einzige altweltliche Form der ansonsten rein nearktischen Sumpfschildkröten-Unterfamilie Emydinae. Höchstwahrscheinlich erreichten die Vorfahren von *E. orbicularis* die Paläarktis im mittleren bis oberen Tertiär über die Bering-Brücke, was eine altweltliche Ausbreitung von Ostasien nach Westen impliziert. Tatsächlich stammen die ältesten bekannten *Emys*-Fossilien aus dem Gebiet der ehemaligen zentralasiatischen Turgaj-Straße (mittleres Miozän), die bis zum Oligozän Ostasien von Europa trennte. Mit Ausnahme der problematischen *Emys wermuthi* MLYNARSKI, 1956 aus Polen stellen alle fossilen *Emys*-Taxa Chronospezies dar, die zur rezenten Art *E. orbicularis* führen. Im Mittelmeergebiet ist der Fossilbericht ziemlich lückenhaft. Die ältesten Funde stammen erst aus dem

Villafranca. Das holozäne Verbreitungsgebiet von *E. orbicularis* wurde durch den Menschen stark beeinflusst, vor allem in Mitteleuropa. So stellt die heutige nördliche Verbreitungsgrenze keinesfalls einen natürlichen Zustand dar, sondern vielmehr das Resultat eines seit Jahrtausenden massiv gestörten Lebensraumes.

Schlagwörter: Testudines: Emydidae: *Emys orbicularis*; Zoogeographie.

Introduction

Until 1989 the European pond turtle, *Emys orbicularis* (LINNAEUS, 1758), was considered a text book example of a wide ranging, monotypic species (e.g. WERMUTH & MERTENS 1961, 1977, BANNIKOV et al. 1977, PRITCHARD 1979). With the description of a very distinctive subspecies at that time (*Emys orbicularis luteofusca* FRITZ, 1989) I started a series of articles reporting the results of my morphological research, now based on more than 1,600 preserved and living specimens of *E. orbicularis*. I found out that in its vast range a great number of distinctive subspecies occurs, exhibiting a complicated distribution pattern (FRITZ 1989, 1992, 1993a, b, 1994, 1995a, 1996, FRITZ & OBST 1995, FRITZ et al. 1996). Here I present a review of published results on taxonomy, try to incorporate palaeontological data and to formulate a brief zoogeographical interpretation of the detected distribution patterns. Thereby, special emphasis is given to the Holocene range fluctuations in Central and North Europe.

Distribution

The European pond turtle inhabits one of the largest distribution areas among the turtles of the world, comparable only to *Chelydra serpentina* and *Trachemys scripta* sensu lato (cf. ERNST 1990). *E. orbicularis* ranges from North Africa north of the Atlas Mountains over the Iberian peninsula and most of Europe and Asia Minor to the Aral Sea in Central Asia. All southern European peninsulas are inhabited as well as Corsica, Sardinia, Sicily, the Balearic Islands Majorca and Menorca, and lots of islands in the East Mediterranean (FRITZ 1995a, 1996). In Central Asia the easternmost populations were known from the Aral Sea, with an outpost near the settlement Julek on the lower course of the River Syrdariya (Kazakhstan, PARASKIV 1956). It is suspected that these populations are nowadays entirely extinct, due to the human mediated deterioration and aridisation of the whole Aral Sea region.

Subspecies and Subspecies Groups – an Overview

Currently, 13 subspecies are recognized (see below), and this count already includes *E. o. eiselti* to be described later in this volume by FRITZ et al. (1998). Probably a few additional ones will be named in future using the results of modern molecular techniques (cf. LENK et al. 1998), among them are some populations which were treated earlier as morphological intermediates (intergrades) between other subspecies. The individual subspecies as defined so far differ in size, shell and head proportions, several colour and pattern characters of shell, soft parts, and the iris colouration of males (FRITZ 1989, 1992, 1993a, b, 1994, 1995a, 1996, FRITZ & OBST 1995, FRITZ et al. 1996). I do not concur with ZUFFI & BALLASINA (1998) that colouration is much influenced by environmental factors. During my former, six-year employment at the Zoological Garden "Wilhelma", Stuttgart, about 300 *E. orbicularis* of different subspecies and populations were captive bred and reared

under differing indoor and outdoor conditions. All developed the same colour and pattern characteristics typical of the subspecies and/or population of their parents. However, colder reared specimens attain the adult colouration at a smaller size, a fact apparently mistaken by ZUFFI & BALLASINA.

Due to morphological similarities I grouped the 13 subspecies into several infraspecific categories, namely into five subspecies groups and divided these into a western and an eastern line (FRITZ 1996). Figure 1 shows the distribution of these subspecies groups. The western line was defined for the *occidentalis* and *galloitalica* subspecies groups, sharing the same principal plastral pattern of dark blotches along the distal seams of the scutes and a rectangular nuchal. Their close relationship is well corroborated by molecular methods (LENK et al. 1998). However, molecular systematics links with this group *E. o. hellenica*, too. Because

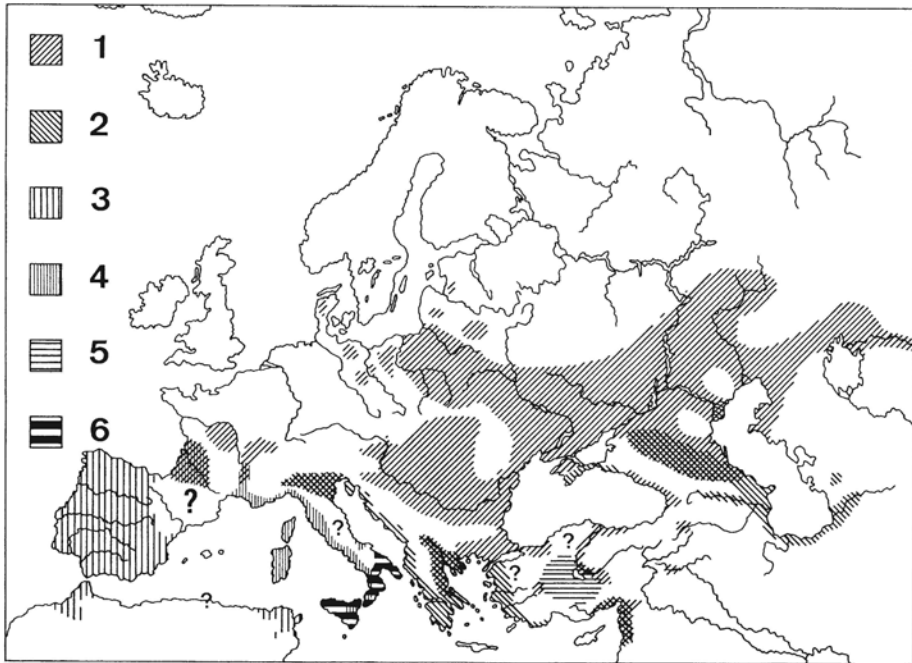


Fig. 1. Distribution of the subspecies groups of *Emys orbicularis*, modified from FRITZ (1996) with new distribution records (PUPINA & PUPINŠ 1996, BRINGSØE 1997) and results by FRITZ et al. (1998) and LENK et al. (1998). According to LENK et al., the southern Italian/Sicilian population represents a distinct evolutionary lineage. 1: *orbicularis* group, 2: *hellenica* group, 3: *occidentalis* group, 4: *galloitalica* group, 5: *luteofusca* group, 6: South Italian taxon. Cross hatching: intergradation zones.

Verbreitung der Unterartengruppen von *Emys orbicularis* verändert nach FRITZ (1996) unter Berücksichtigung neuer Verbreitungsdaten (PUPINA & PUPINŠ 1996, BRINGSØE 1997) und der Ergebnisse von FRITZ et al. (1998) und LENK et al. (1998). Die süditalienisch-sizilianische Population stellt nach LENK et al. eine eigene Evolutionslinie dar. 1: *orbicularis*-Gruppe, 2: *hellenica*-Gruppe, 3: *occidentalis*-Gruppe, 4: *galloitalica*-Gruppe, 5: *luteofusca*-Gruppe, 6: Süditalienisches Taxon. Sich überlagernde Schraffuren: Intergradationszonen.

of the different trapezoid shape of the nuchal I attributed this and two related Transcaucasian subspecies (*iberica*, *persica* = *hellenica* group) to the eastern line (FRITZ 1996), which was defined as an unit for the *hellenica*, *orbicularis*, and *luteofusca* subspecies groups. Interestingly, the males of *hellenica* share with the western *occidentalis* and *galloitalica* groups the yellow or whitish iris colouration. It would be interesting to know more on the molecular affinities of the above mentioned easternmost representatives of the *hellenica* group.

The westernmost *occidentalis* subspecies group exhibits an Ibero-Maghrebine distribution pattern. The West Mediterranean *galloitalica* group occurs in and around the Tyrrhenian Sea (Corsica, Sardinia, tyrrhenian coast of southern France and Italy). The *hellenica* group shows a highly disjunct Eastern Mediterranean distribution pattern found in lots of other herp taxa (FRITZ 1996). The *orbicularis* subspecies group, as redefined here with the new results of LENK et al. (1998), has a Balkanic-Pontic range, and the enigmatic *luteofusca* group, represented by a single subspecies, is endemic to the internally drained central basin of Anatolia, a situation echoed by other aquatic biota in Asia Minor (e.g. BĂNĂRESCU 1992). We have to add in future at least one additional, distinctive lineage, occurring on the southern Italian peninsula and Sicily (LENK et al. 1998). The populations from there are characterized by a close morphological similarity to *E. o. hellenica* (FRITZ 1995a).

However, this picture of higher infraspecific taxa can easily change if more subspecies will be used for cladogram construction.

What is sure, reflected by traditional morphology and molecular systematics, is that several clear cut evolutionary units exist within *E. orbicularis*. They would be called full species by advocates of the phylogenetic species concept such as CRACRAFT (1992). However, I adopt the biological species concept as defined e.g. by MAYR (1963). By using this, there is no doubt that all taxa belong to the same species, with the possible exception of the parapatric *occidentalis* group, because we know of intergradation zones (FRITZ 1992, 1995a, 1996, FRITZ & OBST 1995, LENK et al. 1998). A review of the different subspecies and subspecies groups follows (cf. pls. 1-2).

***occidentalis* subspecies group** (medium sized, large headed pond turtles with very long intergular seams and a vermiform yellowish head pattern. Both sexes same sized. Males with yellowish, white or seldom brownish iris):

E. o. occidentalis FRITZ, 1993, maximum shell length around 15 cm, is distributed in the Maghreb region of North Africa and occurs in Mediterranean and semiarid locations near sea level as well as up to 1,600 m in the Middle Atlas. A generally dark coloured subspecies with mainly black plastron in most younger individuals, often bleaching in older ones. Nuchal scute trapezoid or with parallel seams.

E. o. hispanica FRITZ, KELLER & BUDDE, 1996, maximum shell length 17 cm, described from the Doñana region of Andalusia (southwestern Spain). Probably most or all of the pond turtles in the Atlantic drainage systems of the Iberian peninsula belong to this subspecies. It is similar to the North African subspecies, but lighter coloured and has a mainly yellow plastron with dark blotches along the distal seams and a clearly shorter interhumeral seam compared with *E. o. occidentalis*. Nuchal scute distinctly larger and with parallel seams.

E. o. fritzjuergenobsti FRITZ, 1993, maximum shell length 15 cm, is known from the Mediterranean coastal area in eastern Spain. Closely related with *E. o. hispanica* but with narrower carapace and a lighter colouration, plastron often uniform yellow. Interfemoral seam longer than in *E. o. hispanica*.

galloitalica subspecies group (small to medium sized pond turtles with narrow nuchal scutes with parallel side seams. Males smaller than females and with yellowish or white iris):

This subspecies group includes three taxa originally described within the framework of one megasubspecies (*E. orbicularis galloitalica* FRITZ, 1995). This classification is congruent with the greater morphological similarity of these three taxa to one another as compared with other subspecies. LENK et al. (1998) found no sequence differences in the mitochondrial DNA fragment analysed in contrast to the other studied subspecies. Both point to a younger differentiation age than in the other taxa. However, the clear morphological and ecological differences justify and reinforce the further treatment of *galloitalica*, *lanzai*, and *capolongoi* as "microsubspecies" (for a discussion of the megasubspecies category see AMADON & SHORT 1976, 1992, BÖHME 1982).

Interestingly, unequivocal fossils of *E. orbicularis* are known from the Tyrrhenian interglacial of Sardinia (CALOI et al. 1981), which leads to the speculation that a period longer than 130,000 years is necessary to develop at least slight mitochondrial DNA sequence differences in *E. orbicularis* (if, as supposed, the DNA evolution rate is indeed the same). LANZA (1983) suggests that *Emys* reached Corsosardinia during the Cassian regression (Middle Pleistocene), which would support a very slow evolution rate.

E. o. (g.) galloitalica FRITZ, 1995, maximum shell length 16.5 cm (record size), normally below 15 cm, is distributed from southern France along the Mediterranean coast to the area of the Gulf of Policastro in southern Italy. It is a polymorphic subspecies with light and dark coloured individuals in the same local populations. However, the plastron usually is yellow, if a dark pattern is present, it resembles the distal blotched pattern of *hispanica* or *fritzjuergenobsti*. It occurs in standing waters as well as in fast moving streams.

E. o. (g.) lanzai FRITZ, 1995 attains a maximum shell length of at least 15 cm, however, as a general rule the specimens grow on the average to a slightly larger size than in *galloitalica* or *capolongoi*. This subspecies has a larger head than the two other members of this group and is usually dark coloured. Specimens with a mainly black plastral pattern occur. It is an inhabitant of still bodies of water on Corsica, and avoids streams.

E. o. (g.) capolongoi FRITZ, 1995, is the Sardinian counterpart to *E. o. (g.) lanzai*. Its maximum shell length is 14.5 cm. It is a light coloured form with predominantly yellow plastra with or without dark blotches near the distal seams. Like the mainland *E. o. (g.) galloitalica*, it lives in ponds, creeks, and streams.

hellenica subspecies group (small to medium sized pond turtles with yellow throats, often broad headed, and generally with a trapezoid nuchal scute. Males with reticulate, females with spotted head pattern. Males are in this subspecies group generally smaller than females):

E. o. hellenica (VALENCIENNES, 1832) has a maximum shell length of about 17 cm, in the drainage system of the Dalmatian Neretva River, 19 cm may be reached.

However, most specimens are below 14 or 15 cm, and dwarfed local populations with maximum shell lengths of 12 cm are known. Plastra mainly yellow, a faded dark pattern may be present especially on the hind lobe. Males with yellowish or white iris. This subspecies is distributed from the coastal area of the Po Plain southwards over Istria and Dalmatia to the Peloponnese and Voiotia. Possibly the pond turtles of western Asia Minor and of the Crimea belong to *E. o. hellenica* or to a closely related taxon.

E. o. iberica EICHWALD, 1831 (*E. o. kurae* FRITZ, 1994 is a junior synonym of this name). Maximum shell length 18 cm, but normally below 16 cm, it is mainly restricted to the drainage system of the central Caucasian Kura River. It is not known from the Araxes River, but extends northwards to Daghestan. It closely resembles *E. o. persica*, but the forelegs have more yellow. In the course of their lives, most specimens change the colour of the carapace from dark to light. Plastra yellow. Males with reddish iris.

E. o. persica EICHWALD, 1831 (*E. o. orientalis* FRITZ, 1994 is a junior synonym of this name). Maximum shell length 18 cm, but normally between 10 and 15 cm. This subspecies occurs along the southern coast of the Caspian Sea in northern Iran and adjacent Turkmenia. It is similar to *E. o. iberica*, but most specimens retain their dark carapace, often with lots of tiny yellow dots, during life, and sporadically specimens with heavily dark patterned or entirely black plastra occur. Gular scutes smaller than in all other subspecies, with the exception of *E. o. eiselti*. Males with reddish (PRITCHARD 1966) and/or yellowish iris?

In his "Zoologia specialis" EICHWALD (1831: 196) was already aware of the distinctiveness of Transcaucasian pond turtles. He created for these populations two new names, accompanied with short Latin descriptions. For his var. *iberica* the exact locality of occurrence was not given, though EICHWALD and contemporary researchers called the central Caucasian area corresponding to the central Kura River valley "Iberia" (cf. EICHWALD 1841: 47), a name which goes back to an ancient people living there. The second population, from "Masanderan", was named var. *persica* by EICHWALD (1831). Both names were printed in italics, but not published in juxtaposition with a generic name. Therefore they were overlooked by subsequent authors like NIKOLSKY (1915), WERMUTH & MERTENS (1961, 1977) and consequently by FRITZ (1994). However, it can be interpreted from the Latin text that *iberica* and *persica* are combined with the generic name *Emys* in the sense of varieties of *Emys europaea*. Hence, *Emys europaea* var. *iberica* EICHWALD, 1831 and *Emys europaea* var. *persica* EICHWALD, 1831 are available (International Code of Zoological Nomenclature 1985: article 11, iii, 2) and senior synonyms of *E. o. kurae* FRITZ, 1994 and of *E. o. orientalis* FRITZ, 1994, respectively.

Later, EICHWALD (1841) even specified the distribution of both taxa. He gave for *iberica* the marshy valleys of Iberia and all tributaries of the Kura River, and extended the range of *persica* to the "warm springs of Ghilan". However, in contrast to EICHWALD (1831) the quite exact description of *iberica* in the 1841 book is seemingly in error, fitting much better the nominate subspecies which is treated immediately before.

orbicularis subspecies group: In this subspecies group several cryptic taxa are hidden, as it turned out by the molecular research by PETER LENK (cf. LENK et al. 1998). Some of the populations formerly thought to represent intergrades with *E. o. hellenica* (FRITZ 1992, 1996, FRITZ & OBST 1995) from the Danube area and the

eastern Balkans proved to possess discrete, unique mitochondrial haplotypes, pointing to a long separate evolutionary history. The southern representatives from Bulgaria and adjacent areas, presently lacking a name, are quite small specimens, in contrast to the medium sized to large turtles from the Danube and more northern and eastern areas. As originally defined by FRITZ (1995a), the *orbicularis* group comprises populations with dark coloured pond turtles, generally with a trapezoid nuchal scute. The plastra are often predominantly black, in males frequently with a highly distinctive speckled light-dark pattern. Males possess a reddish iris and are smaller than females in the mean. The following subspecies are presently recognized:

E. o. orbicularis (LINNAEUS, 1758), maximum shell length around 23 cm (but see SZCZERBAK 1998), is distributed from Central Europe far to the East. FRITZ (1995a, 1996) attributed to this subspecies all populations from Germany east to the Aral Sea. As it is shown by LENK et al. (1998), some populations within the western part of this area share the same principle mitochondrial haplotype with the Danube population, which is morphologically clearly distinct from the northern conspecifics (FRITZ 1992, FRITZ & OBST 1995, FARKAS et al. 1998). Further research is needed to understand these findings better. If in future the Danube population will be given subspecific rank, the name *Emys europaea* var. *sparsa* DÜRIGEN, 1897 is available (FRITZ 1992).

E. o. colchica FRITZ, 1994, is a highly problematic taxon (cf. FRITZ et al. 1998 and LENK et al. 1998). It was described from the Colchis area of the east Black Sea coast, East Turkey, and the Turkish Black Sea coast. In fact, in this subspecies most local populations of eastern Asia Minor and the western Transcaucasus were lumped together (with the exception of *E. o. eiselti*) which closely resemble each other, being too small and too light coloured for *E. o. orbicularis*. Taking the plentiful physiogeographic barriers of the Caucasian and eastern Turkish area into account, *E. o. colchica* easily could be composed of several evolutionary units (cf. FRITZ et al. 1998).

E. o. eiselti FRITZ, BARAN, BUDAK & AMTHAUER, 1998, is described in this volume and the details on distribution and characters are given there.

***luteofusca* subspecies group:** Only a single taxon, *E. o. luteofusca* from the internally drained Central Basin of Anatolia, belongs to this distinctive subspecies group. New data on *E. o. luteofusca* are given in FRITZ et al. (1998) and TAŞKAVAK & REIMANN (1998). The populations of *E. o. luteofusca* are light coloured and small headed. Depending on environmental conditions, the local populations show a considerable degree of variation in shell length. Besides dwarfed populations, under better environmental conditions fair sized individuals may be found, reaching about 20 cm shell length. Males are red-eyed.

The Genus *Emys* in the Old World: an Outpost of a Nearctic Family

E. orbicularis is the sole recent member of the Emydidae (sensu GAFFNEY & MEYLAN 1988), an otherwise exclusively New World turtle family (fig. 2). It is generally accepted that the nearctic genera *Emydoidea*, *Terrapene*, and *Clemmys* are the closest relatives of *Emys*. *Emys*, *Emydoidea*, *Terrapene*, and *Clemmys* form together the subfamily Emydinae, the sister group of the Deirochelyinae, the latter consisting of the genera *Chrysemys*, *Deirochelys*, *Graptemys*, *Malaclemys*, *Pseudemys*, and *Trachemys* (GAFFNEY & MEYLAN 1988, BURKE et al. 1996).

However, the status of the exact sister group relations within the Emydinae remain unclear (cf. GAFFNEY & MEYLAN 1988, BICKHAM et al. 1996, BURKE et al. 1996). The most specialized genus *Terrapene* is known together with the primitive *Emydoidea hutchisoni* since the Barstovian (Middle Miocene) of Nebraska (HUTCHISON 1981, HOLMAN & CORNER 1985, HOLMAN 1987, 1995). Hence, it may be taken for sure that *Emys* reached the Old World from North America.

Fossil Record and Zoogeography

Fossil Taxa

A quite exhaustive discussion of fossil taxa is given in FRITZ (1995b, see also FRITZ & FARKAS 1996). During the 19th century lots of fossil taxa were described originally as members of the genus *Emys* or *Clemmys* sensu lato (cf. KUHN 1964). However, in former times these genera were often used simply for lumping together fossil aquatic turtles of unclear relationships. MLYNARSKI (1969) was already aware of this problem, but he still included in the genus *Emys* "about eight fossil species", among them the North American forms now recognized as members of the genus *Emydoidea*. A few years later the same author restricted *Emys* to only two fossil species, *Emys wermuthi* MLYNARSKI, 1956 from the Pliocene of Poland and the still extant *E. orbicularis*, known since the Villafranca (MLYNARSKI 1976). Today, three or four fossil taxa are regarded as valid within



Fig. 2. Distribution of the extant Emydidae and of *Emys orbicularis* (combined from ERNST 1990, ZUG 1993, FRITZ 1995b and data presented in this study). The range of *E. orbicularis* represents the Old World distribution part of the Emydidae.

Verbreitung der rezenten Vertreter der Familie Emydidae und von *Emys orbicularis* (kombiniert nach ERNST 1990, ZUG 1993, FRITZ 1995b und Angaben aus der vorliegenden Arbeit). Das Areal von *E. orbicularis* stellt den altweltlichen Verbreitungsteil der Emydidae dar.

Emys: *E. tarashchuki* (CHKHIKVADZE, 1980): Middle to early Upper Miocene of Kazakhstan, *E. sukhanovi* CHKHIKVADZE, 1983: Upper Miocene of East Europe, *E. orbicularis antiqua* KHOSATZKY, 1956: Middle Pliocene to Villafranca of East and Central Europe, and *E. wermuthi*: Middle Pliocene of Poland. With *E. o. antiqua* closely related, contemporary forms are known from Georgia, Italy, and perhaps Israel and Tunisia (HAAS 1966, FRITZ 1995b). With the exception of the doubtful *E. wermuthi*, which could be no more than an individual aberration, all represent most probably chronotaxa (fig. 3), leading to the recent *E. orbicularis*, which is known from the Pleistocene onwards.

Figure 4 depicts the geographic distribution of the fossil findings. However, it has to be stressed that this map clearly reflects areas of intensive excavation activities (e.g. Central Europe or mining areas in the former USSR). On the other

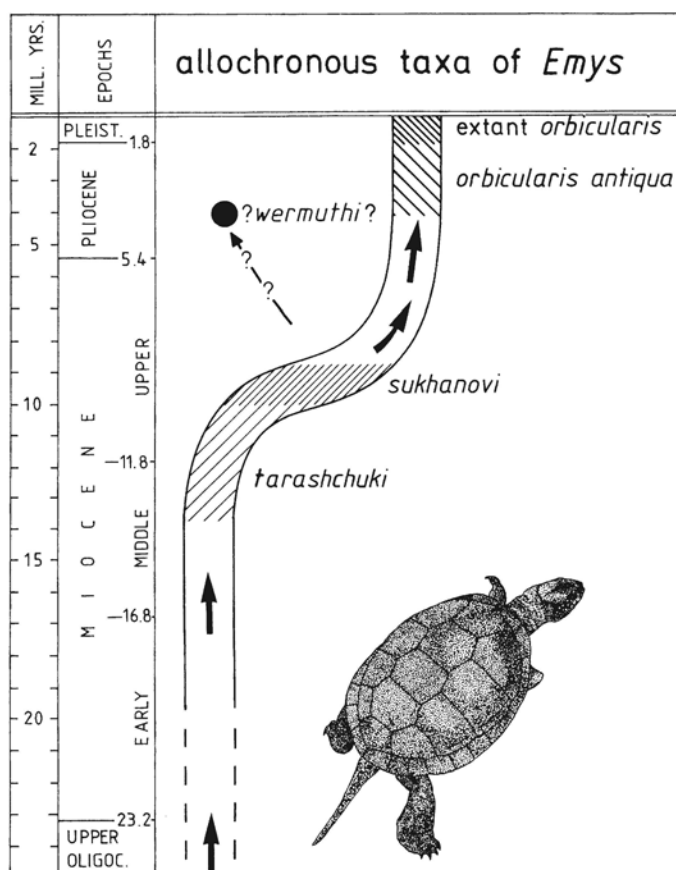


Fig. 3. Stratigraphical distribution of the chronotaxa leading to the extant *Emys orbicularis* and of *Emys wermuthi* (modified from FRITZ 1995b).

Stratigraphische Verbreitung der zur heutigen *Emys orbicularis* führenden Chronotaxa und von *Emys wermuthi* (verändert aus FRITZ 1995b).

side of the picture, areas with few or none fossil records are not necessarily congruent with sparsely colonized areas or areas free of pond turtles at a certain time. The lack of findings could be simply due to bad preservation conditions, a lack of "appropriate", contemporary layers, or even to a lack of excavations there. Anyway, it is obvious, the oldest findings were made far in the East, whereas only quite young fossils are known from the Mediterranean and Central Europe, dating at best to the Pliocene or to the Plio-Pleistocene border (Villafranca).

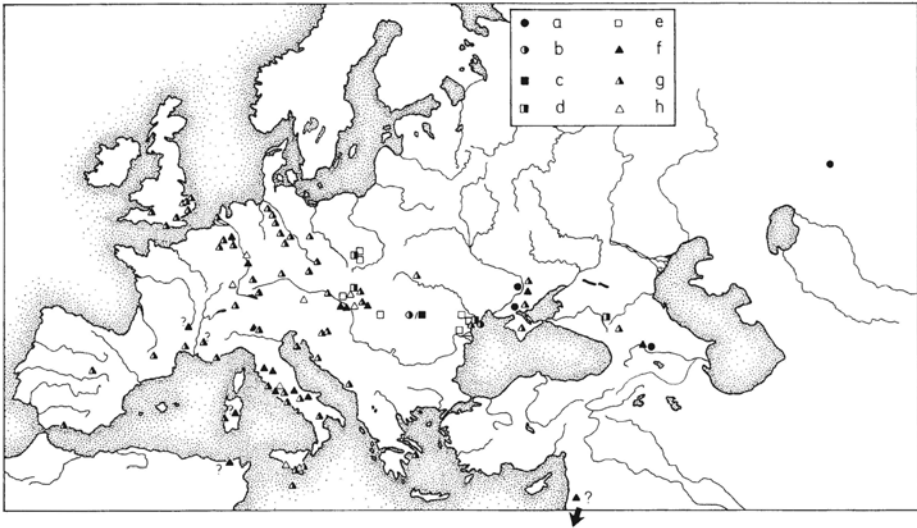


Fig. 4. Geographical distribution and age of fossil records of the genus *Emys*. Modified from FRITZ (1995b). The Villafrancan locality in the South, indicated with an arrow, is 'Ubeidiya in the Jordan Valley (HAAS 1966). Further additional localities are from the following sources (in alphabetical order): Croatia: HOLMAN (1998); France: CHEYLAN (1998); Germany: HOLMAN (1998); Great Britain: HOLMAN (1998); Italy: BONIFIGLIO & INSACCO (1992), CONATO et al. (1980), DELFINO (1994/95), KOTSAKIS (1982, 1996), SALA (1996); Yugoslavia (Montenegro): HOLMAN (1998).

(a): Medial Miocene, (b): Upper Miocene, (c): Lower Pliocene, (d): Medial Pliocene, (e): Upper Pliocene, (f): Plio-/Pleistocene border (Villafranca/Villanyium), (g): Pleistocene except Villafranca/Villanyium, (h): Pleistocene without exact dating. Due to different reliabilities of sources and differences in the dating systems used inconsistencies in the datings are possible.

Geographische Verteilung und Alter fossiler Funde der Gattung *Emys*. Verändert aus FRITZ (1995b). Bei dem Fund aus dem Villafranca, auf den im Süden mit einem Pfeil hingewiesen wird, handelt es sich um 'Ubeidiya im Jordantal (HAAS 1966). Weitere zusätzliche Fundorte sind folgenden Quellen entnommen (in alphabetischer Reihenfolge): Deutschland: HOLMAN (1998); England: HOLMAN (1998); Frankreich: CHEYLAN (1998); Italien: BONIFIGLIO & INSACCO (1992), CONATO et al. (1980), DELFINO (1994/95), KOTSAKIS (1982, 1996), SALA (1996); Jugoslawien (Montenegro): HOLMAN (1998); Kroatien: HOLMAN (1998).

(a): mittleres Miozän, (b): oberes Miozän, (c): unteres Pliozän, (d): mittleres Pliozän, (e): oberes Pliozän, (f): Grenze Plio-/Pleistozän (Villafranca/Villanyium), (g): Pleistozän mit Ausnahme vom Villafranca/Villanyium, (h): Pleistozän ohne genaue Datierung. Aufgrund der verschiedenen Verlässlichkeit der Quellen und Unterschieden bei den Datierungssystemen sind Unstimmigkeiten bei den Altersangaben nicht auszuschließen.

Originally several of the fossil taxa treated here as members of the genus *Emys* (partially now regarded as synonyms, cf. FRITZ 1995b) were described as or taken for *Emydoidea* species (CHKHIKVADZE 1980, 1983, 1989). However, as demonstrated in FRITZ (1995b), there are no valid arguments for putting these taxa into *Emydoidea*. All synapomorphies which are used for defining the extant genus *Emydoidea* (cf. MCCOY 1973, BRAMBLE 1974, GAFFNEY & MEYLAN 1988, BURKE et al. 1996) are not preserved in any Old World fossils.

It may be noted that there is no proof that any other emydid with the exception of the chronotaxa of *Emys* ever reached the Old World at all. The famous Georgian palaeoherpetologist CHKHIKVADZE (1983, 1984, 1987, 1989, 1990) regarded numerous Palaearctic Tertiary fossils as Emydidae, belonging to the genera *Pseudochrysemys*, *Zaisanemys*, and *Chrysemys* sensu lato. However, the "*Chrysemys* species" from Kazakhstan and Siberia possess in sharp contrast to the recent North American "congeners" musk gland ducts (CHKHIKVADZE 1989) like batagurids. In addition, the reduction of the bony bridge in "*Chrysemys*" from Kazakhstan and Siberia (CHKHIKVADZE 1989) does not speak for a close relationship with the recent (and fossil) Emydidae from the New World. The same is true for the conspicuous sculpturing of the bony shell in *Zaisanemys* (CHKHIKVADZE 1989). Based mainly on the above mentioned differences from the New World species, KHOSATZKY (in KHOSATZKY & CHKHIKVADZE 1993) erected the new genus *Baicalemys* for the Central Asian "*Chrysemys*". The relationships of *Pseudochrysemys* remain unclear at all. CHKHIKVADZE (1987) assumed that this genus from the Palaeocene of

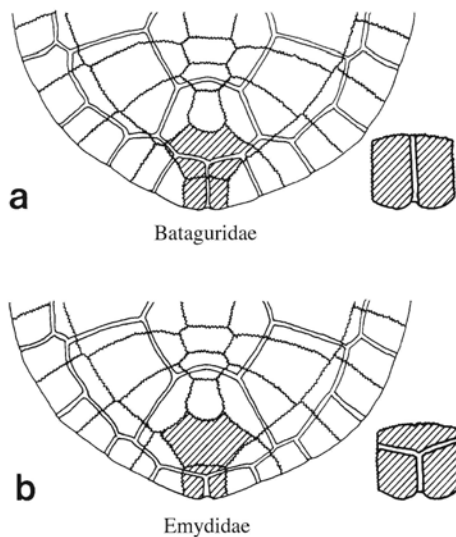


Fig. 5. Position of the seam between the last vertebral and the supracaudal scutes on the pygal and metaneural bones in batagurids (a) and emydids (b). Elements of the bony shell are indicated by zig-zag lines, of the horny shell by double straight lines. The pygal and the second metaneural bone are hatched and the pygal on the right enlarged. Note that the vertebral-supracaudal seam is on the second metaneural in batagurids. The pygal bears therefore only a longitudinal seam groove. In emydids the vertebral-supracaudal seam is positioned on the pygal. This results in a T-shaped seam groove on the latter (modified from MLYNARSKI 1976).

Lage der Naht zwischen dem letzten Vertebrale und den Supracaudalia auf dem Pygal- und dem zweiten Metaneural-Knochen bei Bataguriden (a) und

Emydiden (b). Elemente des Knochenpanzers sind durch Zickzacklinien dargestellt, die des Hornpanzers durch gerade Doppellinien. Das Pygale und das zweite Metaneurale sind schraffiert und das Pygale rechts vergrößert dargestellt. Beachte, daß bei Bataguriden die Naht zwischen dem Vertebrale und den Supracaudalia auf dem zweiten Metaneurale liegt. Der Pygal-Knochen trägt hier nur eine longitudinale Nahtlinie. Bei den Emydiden liegt dagegen auch die Vertebral-Supracaudal-Naht auf dem Pygale, wodurch dort eine T-förmige Nahtlinie entsteht (verändert nach MLYNARSKI 1976).

Mongolia is "perhaps" the ancestor of all emydids. The main argument for CHKHIKVADZE's allocation of all these turtles to the Emydidae is the position of the horny seams on the bony pygal scute. In most cases, emydids and batagurids can be diagnosed by the different positions of the seams (fig. 5, cf. MLYNARSKI 1969, 1976). However, there are exceptions, like the *Chinemys reevesii* (Bataguridae) figured in MLYNARSKI (1976) with an "emydid seam position". Moreover, these characters occur in other chelonian families, too (cf. the figures in MLYNARSKI 1976), so that an "emydid seam position" does not argue necessarily for belonging to this family.

In addition to these examples, it becomes more and more obvious that the generic allocation of the so called "*Chrysemys* species" from the Palaeogene and Neogene of Central and West Europe is not appropriate. For example, *Chrysemys astrei* BERGOUNIOUX, *Ch. lachati* (SAUVAGE), *Ch. iberica* BERGOUNIOUX and *Ch. elegans* BERGOUNIOUX belong all to the batagurid (?) genus *Palaeochelys*, and represent most probably not more than a single taxon (DE BROIN 1977, JIMENÉZ FUENTES & MARTÍN DE JESÚS 1991). According to DE BROIN (1977), *Ch. germanica* (HUMMEL) from the Eocene of Germany as well as the contemporary *Ch. testudiniformis* (OWEN) and *Ch. bicarinata* (OWEN & BELL) from England are *Palaeochelys*, too, and for *Ch. bisbalensis* BERGOUNIOUX it was shown by JIMENÉZ FUENTES & MARTÍN DE JESÚS (1991) that this taxon is a *Mauremys* (Bataguridae). The same generic allocations may probably be proven for the remaining fossil European "*Chrysemys*" in future.

Palaeogeography

The only unequivocal Old World emydids are hence the above mentioned *Emys* species. The oldest known fossil is a nuchal bone of *Emys tarashchuki* from Kentyubek in central Kazakhstan (Middle Miocene, probably early Sarmatian, described as *Emydoidea tasbaka* by CHKHIKVADZE 1989). Slightly younger fossils of *E. tarashchuki* (upper Sarmatian) were found at the famous Ukrainian fossil site Krivoi Rog and in the Caucasian republic of Georgia.

There is no reason to assume an earlier invasion of the Palaearctis by *Emys* than in Middle or Upper Tertiary, what means that neither the Thule nor the De Geer passage over the North Atlantic could have been used. In other terms: Because the North Atlantic land connections did not exist so long (DIETZ & HOLDEN 1970), *Emys* must have reached Eurasia from the East via the Bering Bridge. If CHKHIKVADZE's (1989) opinion is correct that the Kentyubek fossil belongs to the so called Praehipparion fauna, the pond turtle entered Eurasia even a little bit earlier than the well known three toed horse *Hipparion*. Probably, the little piece of a carapace from Kentyubek testifies to a westwards directed range shift of *Emys* after the Oligocene subsidence of the Turgai Sea which separated East Asia from Europe after the Cretaceous (RUSSEL 1975). The pond turtle was forced at that time to spread north of the Paratethys Sea, which covered a large area of the western Palaearctis (fig. 6). Asia Minor was not connected with the Asian mainland until the end of the Oligocene (RÖGL & STEININGER 1983, STEININGER et al. 1985), and until now no old *Emys* fossils from there are known, so that a route via Asia Minor, bypassing the Paratethys in the South, seems improbable. Obviously, *Emys* vanished from its former range in East Asia (as well as in the New World) soon. However, it is remarkable that the recently described fossil *Emydoidea hutchisoni* HOLMAN, 1995 from the Barstovian of Nebraska still exhibits some "primitive" characters reminiscent of *Emys*.

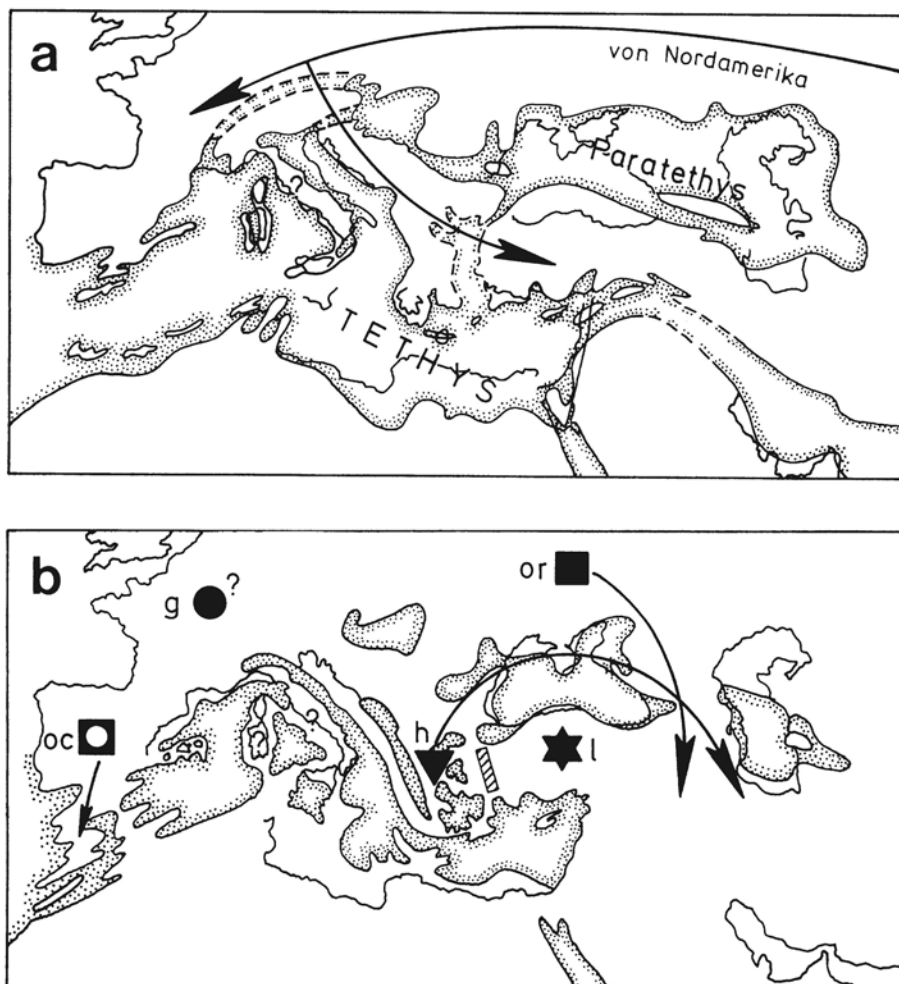


Fig. 6a. Hypothetical immigration of *Emys* to Europe in the Middle and Upper Tertiary. "Von Nordamerika" = "From North America".

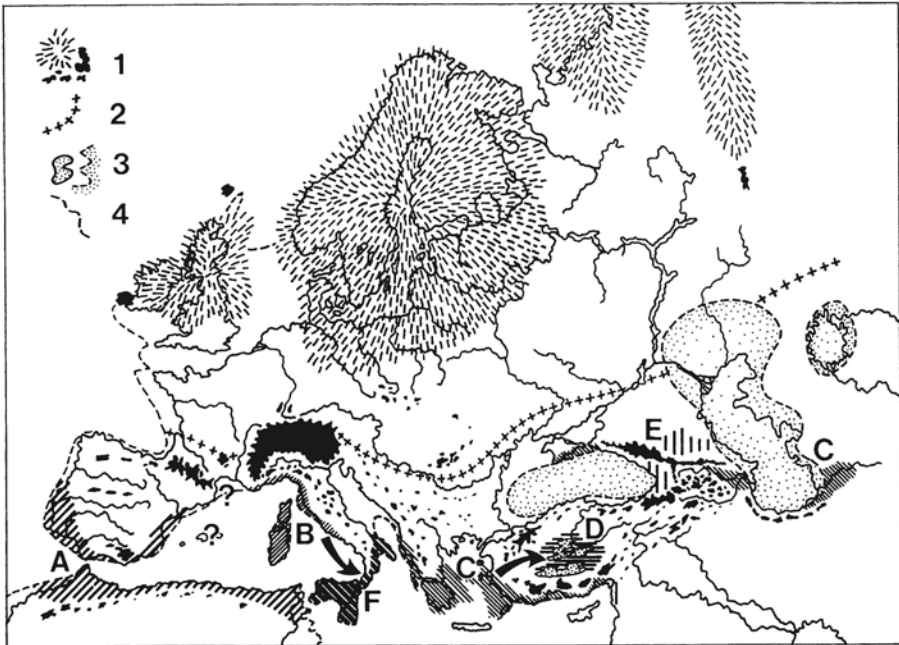
b. Radiation of the ancestors of the extant subspecies groups during the Messinian salinity crisis. oc = ancestor of the *occidentalis* subspecies group, g = ancestor of the *galloitalica* subspecies group, h = ancestor of the *hellenica* subspecies group, or = ancestor of the *orbicularis* subspecies group, l = ancestor of *Emys orbicularis luteofusca* (from FRITZ 1996).

a. Hypothetische Einwanderung von *Emys* nach Europa im mittleren und oberen Tertiär.

b. Radiation der Vorläufer der heutigen Unterartengruppen während der messinischen Salinitätskrise. oc = Vorläufer der *occidentalis*-Unterartengruppe, g = Vorläufer der *galloitalica*-Unterartengruppe, h = Vorläufer der *hellenica*-Unterartengruppe, or = Vorläufer der *orbicularis*-Unterartengruppe, l = Vorläufer von *Emys orbicularis luteofusca* (aus FRITZ 1996).

It is unknown when the more western parts of Eurasia were colonized by *Emys*. The age of the known fossils from Central Europe and the Mediterranean (fig. 4) seems to reflect the assumed westwards directed range shift. However, we cannot exclude that *Emys* occurred much earlier there as documented by fossils. We know that *Emys* was present in the Mediterranean region and in West Europe in the Villafranca already, what points to a colonization of this area near the end of the Tertiary. It is likely that several range expansions and restriction events occurred already during the climatic and sea level fluctuations in the Messinian and Pliocene. In FRITZ (1996) a model is elaborated that in this period the more western and southern regions were reached over the intermittent Messinian and Pliocene land bridges (fig. 6). In *E. orbicularis*, the general distribution pattern and higher taxonomic units, namely the subspecies groups, were probably formed already by the time the southern peninsulas were reached, as in other western Palaearctic amphibians and reptiles (cf. SZYNDLAR 1984 for snakes). These were later modified only by Pleistocene extinctions, range restrictions and expansions which resulted in the definite formation of the recent subspecies.

Pleistocene extinctions are of special importance in the more northerly regions. Taking the highly disjunct range of the *hellenica* subspecies group into account, echoed by lots of other East Mediterranean herps, one has to suspect that no later than the time of the first severe Pleistocene cooling the formation of the subspecies groups was finished, resulting in a disjunct, patchwork-like distribution pattern in these taxa (cf. fig. 1). However, in FRITZ (1996) arguments are given for an even slightly older separation of the North African subspecies *E. o. occidentalis*, a remarkable fact in light of the genetic similarity of this race compared with the



Iberian ones (LENK et al. 1998). Unfortunately we know nothing about the genetic similarity among the subspecies of the *hellenica* group.

At least in the Holocene, and the same is probably true for older Pleistocene thermal periods, most subspecies were not able to expand their glacial ranges extensively. They are still restricted mainly to their former, small southern refugia (fig. 7). Only the eastern *orbicularis* group colonized the more northern parts of Europe again, a result already verified by morphological investigations (FRITZ 1992, 1995a, 1996) and reinforced and refined by means of molecular genetics (LENK et al. 1998).

Fig. 7. Hypothetical glacial refugia of *Emys orbicularis* (modified from FRITZ 1996). Proglacial basins with short-lived lakes, meltwater drainage systems, deviating river courses, and the Pleistocene location of the Black Sea-Mediterranean connection ("Sakarya Bosphorus") not shown.

- 1: Ice sheets, glaciers or isolated areas with permafrost or long seasonal freezing
- 2: Southern boundary of continuous permafrost or long seasonal freezing
- 3: Pleistocene lakes and inland seas (1-3: maximum cooling of the last glaciation, about 20,000 to 18,000 yrs. BP)
- 4: Glacial coastline deviating from present day position

Refugia:

- A: Subspecies of the *occidentalis* group
- B: Subspecies of the *galloitalica* group
- C: Subspecies of the *hellenica* group
- D: *luteofusca* refugium
- E: Subspecies of the *orbicularis*-group
- F: Refugium of South Italian taxon

The arrows stand for a hypothetical intergradation during temperate and warm interglacial and interstadial phases. During Pleistocene cool phases, the East Mediterranean populations were connected over Aegean land bridges between Greece and Anatolia.

Hypothetische Glazialrefugien von *Emys orbicularis* (verändert nach FRITZ 1996). Gletscher- und Stauseen, Urströme, Änderungen von Flußläufen und die pleistozäne Lage des „Sakarya-Bosporus“ blieben unberücksichtigt.

- 1: Eisschilder, Gletscher oder Inseln mit Permafrost oder langer jahreszeitlicher Gefrorenis
- 2: Südgrenze von geschlossenem Permafrost oder langer jahreszeitlicher Gefrorenis
- 3: Pleistozäne Seen und Binnenmeere (1-3: letztglaziales Kältemaximum, vor etwa 20.000 bis 18.000 Jahren)
- 4: Vom heutigen Verlauf abweichende pleistozäne Küstenlinie

Refugien:

- A: Unterarten der *occidentalis*-Gruppe
- B: Unterarten der *galloitalica*-Gruppe
- C: Unterarten der *hellenica*-Gruppe
- D: *luteofusca*-Refugium
- E: Unterarten der *orbicularis*-Gruppe
- F: Refugium des süditalienischen Taxons

Die Pfeile symbolisieren eine hypothetische Intergradation während temperater und wärmer interglazialer und interstadialer Phasen. Die ostmediterranen Vorkommen waren in pleistozänen Kaltzeiten über ägäische Landbrücken zwischen Griechenland und Anatolien verbunden.

Holocene Range Fluctuations in Central and North Europe

Already the classic works by KURCK (1917), ISBERG (1929), PAAVER (1958), and DEGERBØL & KROG (1951) demonstrated that *E. orbicularis* reached its distributional maximum early in the Holocene with flourishing populations in Denmark, southern Sweden and Estonia in the Boreal, Atlantic, and Subboreal periods. In addition, the pond turtle is known from Flandrian deposits in East Wretham, Norfolk (Great Britain, STUART 1979, cf. fig. 8). These early authors attributed, like most later ones, the retreat of the species, starting at the latest with the beginning of the Subatlanticum, to climatic changes. Indeed, the picture is much more complicated,

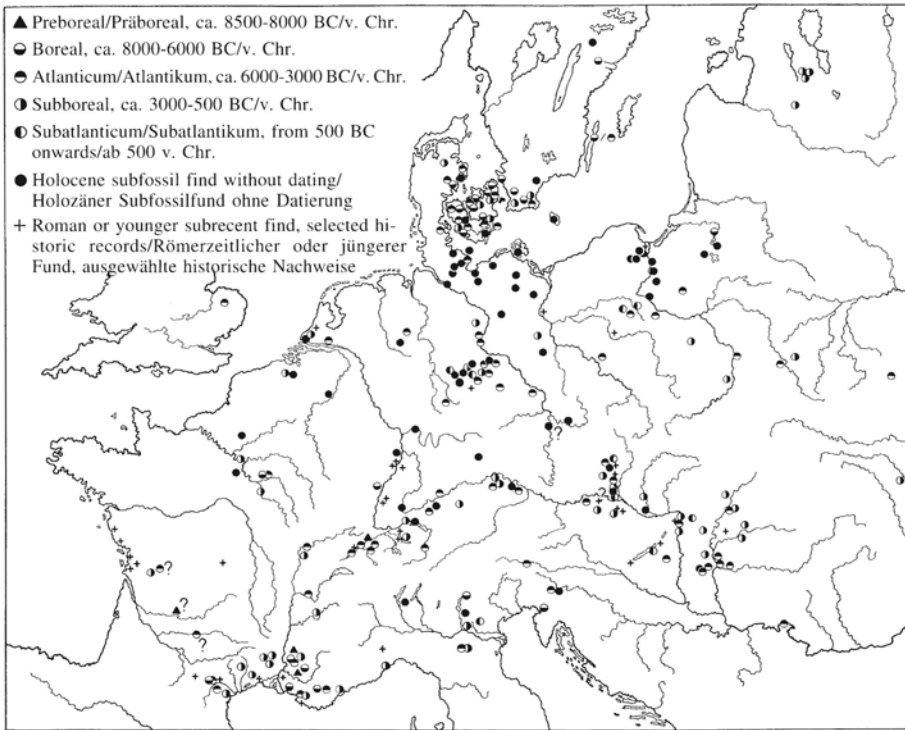


Fig. 8. Holocene subfossil finds of *Emys orbicularis* in Central Europe and adjacent areas (modified from FRITZ 1996, with new records in alphabetical order from the following sources: Austria: PUCHER in RÖSSLER 1998; Czech Republic: NEČAS et al. 1997; France: CHEYLAN 1998, MARNIVAL-VIGNE et al. 1989; Germany: COBLENZ & FRITZSCHE 1980, ELBURG 1994; Italy: AIMAR & DELFINO in press, BON et al. 1991, BOSCATO & SALA 1980, DE GROSSI MAZZORIN 1988, DORIA & SALVIDIO 1994, GUERRESCHI et al. 1986; Netherlands: VAN WIJNGAARDEN-BAKKER 1996; Sweden: PERSSON 1992).

Subfossile Funde von *Emys orbicularis* aus dem Holozän in Mitteleuropa und angrenzenden Gebieten (erweitert mit neuen Funden nach FRITZ 1996. Zusätzliche Quellen in alphabetischer Reihenfolge: Deutschland: COBLENZ & FRITZSCHE 1980, ELBURG 1994; Frankreich: CHEYLAN 1998, MARNIVAL-VIGNE et al. 1989; Italien: AIMAR & DELFINO im Druck, BON et al. 1991, BOSCATO & SALA 1980, DE GROSSI MAZZORIN 1988, DORIA & SALVIDIO 1994, GUERRESCHI et al. 1986; Niederlande: VAN WIJNGAARDEN-BAKKER 1996; Österreich: PUCHER in RÖSSLER 1998; Schweden: PERSSON 1992; Tschechische Republik: NEČAS et al. 1997).

as shown by FRITZ (1996). The Holocene climatic changes in Central Europe are by far not so impressive as thought by these early authors (FRENZEL 1978). After a quick warming phase, a quite stable climate developed, with no unidirectional temperature shift as earlier supposed (deterioration by a cooler, more oceanic climate). This is especially true for the last 2,000 years (FRENZEL et al. 1989), a period in which the pond turtle disappeared from large parts of its former range.

Hence, the range regressions in Central and North Europe have to be understood as a synergistic effect, caused by suboptimal environmental conditions and, more important, direct and indirect disturbances by man. The latter are known to exist to a considerable extent since Neolithic times in Central Europe (FRITZ 1996). Interestingly, CHEYLAN (1998) came to similar conclusions concerning the distributional situation in southern France, a region with a much more favourable climate for such a thermophilous chelonian.

Among the most important factors in Central and North Europe impacting the pond turtle's situation for the worse is surely the direct exploitation for food, which is known since Mesolithic and Neolithic times. Holocene pond turtle fossils are often found in trash of early man (e.g. TRINGHAM 1969, MURRAY 1970, BOGUCKI 1982, WILLMS 1986, CHEYLAN 1998), and this tradition of turtle eating was continued up to recent times (e.g. KINZELBACH 1988, FRITZ et al. 1993, FRITZ & GÜNTHER 1996, CHEYLAN 1998). However, an even more influential factor brought to attention quite recently is the succession of the plant cover (FRITZ 1996). The open, forest-steppe like vegetation in the early Holocene became the closed, shaded forests of today, dramatically diminishing the number of nesting places with suitable micro-climate. Together with a heavy human impact on the living habitats and especially breeding grounds from the Neolithic onwards, mainly in southern Germany and adjacent areas, the pond turtle disappeared much earlier from some regions with a still more favourable climate (southern Germany, Switzerland, Austria, the Bohemian Depression with the adjacent Upper Elbe region of Saxony) than from some areas sparsely populated by man where it is still present (e.g. Mecklenburg and Brandenburg in northeastern Germany, northern parts of Poland, Lithuania, even from Denmark and Latvia, from where BRINGSØE 1997 and PUPINA & PUPINŠ 1996 report recent sightings of probably native specimens).

Hence, one has to keep in mind that the current or historic northern distribution limit of *E. orbicularis* with its enigmatic distribution gap in western Central Europe (fig. 1) does not reflect a natural border line according to biological minimal climatic requirements of this species. Instead it reflects, as in lots of other European animal species, a state achieved over thousands of years in a heavily disturbed environment.

Acknowledgements

M. DELFINO (Romano Canavese) shared generously his data base on Pleistocene and Holocene amphibians and reptiles of Italy with me. M. RÖSSLER and E. PUCHER (Vienna) provided unpublished data on Holocene finds of *E. orbicularis* in Austria. Further I am indebted to the following persons for their help within the course of my investigations on *Emys*: N. ANANYEVA (St. Petersburg), C. ARDIZZONI (Viagrande), O. ARRIBAS (Barcelona), W. BÖHME (Bonn), R. BÖTTCHER (Stuttgart), H. BRINGSØE (Køge), M. BUDDE (Ulm), J. BUSKIRK (Oakland), D. CAPOLONGO (Naples), C. CORTI (Florence), R. DANDOVÁ (Prague), I. DAREVSKY (St. Petersburg), B. DEVAUX (Gonfaron), A. VON DEN DRIESCH (Munich), J. EISELT (Vienna), B. FARKAS (Budapest), B. FRENZEL (Stuttgart-Hohenheim), S. FRISENDA (Putignano), R.

GEMEL (Vienna), R. GÜNTHER (Berlin), M.S. HOOGMOED (Leiden), C. KELLER (Sevilla), B. LANZA (Florence), R. MASCORT (Barcelona), H. MARTENS (Frankfurt a. M.), M. and W. MATZANKE (Gäufelden), J. MAYOL (Palma de Mallorca), M. MLYNARSKI (Cracow), N. ORLOV (St. Petersburg), V. ORLOVA (Moscow), H.-J. PAEPKE (Berlin), I. and W. PAULER (Wachenheim), G. PETTERS (Alghero), H. PINTER (Enköping), R. PODLOUCKY (Isernhagen), P. PRITCHARD (Casselberry), J.F. SCHMIDTLER (Munich), A. SCHLÜTER (Stuttgart), N. SCHNEEWEISS (Zepernick), K. SCHNIEBS (Dresden), J. SERVAN (Paris), P. SURA (Cracow), F. TIEDEMANN (Vienna), S. TRIPEPI (Arcavacata di Rende), I. VERGNER (Zbyšov v Čechách), H. WERMUTH (Freiberg/N.), T. WISCHUF (Murr). Special thanks go to: R. BOUR (Paris), S. KUZMIN (Moscow), F.J. OBST (Dresden), O. PICARIELLO (Naples), H. RAHMANN (Stuttgart-Hohenheim), and H.-J. RUMMLER (Aichwald). H. BILLING (Rapperswil), M. BUDDE (Ulm), U. KOEPERNICK (Dresden), N. ORLOV (St. Petersburg), S. ROMER (Lublin), U. SATTLER (Waiblingen), and E. SNIESHKUS (Kaunas) contributed photos of specimens published here.

Literature Cited

- AIMAR, A. & M. DELFINO (in press): Analisi archeozoologica dei reperti faunistici provenienti dai siti Medievali di Santa Vittoria e "Via Gioberti", Alba (CN). – Atti del Secondo Convegno Nazionale di Archeozoologia.
- AMADON, D. & L.L. SHORT (1976): Treatment of subspecies approaching species status. – Syst. Zool., Washington, **25**: 161-167.
- & — (1992): Taxonomy of lower categories – suggested guidelines. – Bull. B.O.C. Centenary Suppl., **112A**: 11-38.
- BĂNĂRESCU, P. (1992): Zoogeography of Fresh Waters. Vol. 2, Distribution and Dispersal of Freshwater Animals in North America and Eurasia. – Wiesbaden (Aula), pp. 519-1091.
- BANNIKOV, A.G., I.S. DAREVSKY, W.G. ISHCENKO, A.K. RUSTAMOV & N.N. SZCZERBAK (1977): Opredelitel' zemnovodnykh i presmykayushchikhsya fauny SSSR. – Moscow (Prosveshcheniye), 414 pp.
- BICKHAM, J.W., T. LAMB, P. MINX, & J.C. PATTON (1996): Molecular systematics of the genus *Clemmys* and the intergeneric relationships of emydid turtles. – Herpetologica, Lawrence, **52**(1): 89-97.
- BOGUCKI, P.I. (1982): Early neolithic subsidence and settlement in the Polish Lowlands. – BAR Intern. Ser., Oxford, **150**: I-VIII, 1-166.
- BÖHME, W. (1982): Das Problem der Hierarchie innerartlicher Gruppierungen. – Vertebrata Hungarica, Budapest, **21**: 47-53.
- BON, M., G. PICCOLI & B. SALA (1991): I giacimenti quaternari di vertebrati fossili nell'Italia Nord-Orientale. – Mem. Sci. Geol., Rome, **43**: 185-231.
- BONIFIGLIO, L. & G. INSACCO (1992): Palaeoenvironmental, paleontologic and stratigraphic significance of vertebrate remains in Pleistocene limnic and alluvial deposits from southeastern Sicily. – Palaeogeogr., Palaeoclimatol., Palaeoecol., Amsterdam, **95**: 195-208.
- BOSCATO, P. & B. SALA (1980): Dati paleontologici, paleoecologici e cronologici di tre depositi epipaleolitici in Valle dell'Adige (Trento). – Preistoria Alpina, **16**: 45-61.
- BRAMBLE, D. (1974): Emydid shell kinesis: biomechanics and evolution. – Copeia, Washington, **1974**: 707-727.
- BRINGSØE, H. (1997): Forekomst af europæisk sumpskildpadde, *Emys orbicularis*, i Danmark. – Nordisk Herpetol. Foren., Køge, **40**(2): 57-64.
- DE BROIN, F. (1977): Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé supérieur et du Tertiaire de France. – Mém. Mus. nat. Hist. natur., Nouv. Sér., Sér. C, Paris, **38**: I-IX, 1-366, tabl. I-XXXVIII.

- BURKE, R.L., T.E. LEUTERITZ & A.J. WOLF (1996): Phylogenetic relationships of emydine turtles. – *Herpetologica*, Lawrence, **52**(4): 572-584.
- CALOI, L., T. KOTSAKIS, M.R. PALOMBO & C. PETRONIO (1981): Il giacimento a vertebrati del Pleistocene superiore di San Giovanni in Sinis (Sardegna occidentale). – *Rend. Accad. Naz. Lincei*, Ser. 8, Rome, **69**, 1980: 185-197.
- CHEYLAN, M. (1998): Evolution of the distribution of the European pond turtle in the French Mediterranean area since the post-glacial. – In: FRITZ, U. et al. (eds.): *Proceedings of the EMYS Symposium Dresden 96*. Mertensiella, Rheinbach, **10**: 47-65.
- CHKHIKVADZE, V.M. (1980): O sistematicheskom polozhenii presnovodnykh cherepakh neogena Moldavii, Ukrainy i nekotorykh stran Zentralnoi Evropy. – *Soobshch. AN GSSR*, Tbilisi, **99**(3): 721-724.
- (1983): Iskopaemye cherepakhi Kavkaza i Severnogo Prichernomorya. – Tbilisi (Metsniereba), 149 pp.
- (1984): Classification des tortues de la famille des Emydidae et leurs liens phylogénétiques avec d'autres familles. – *Studia Geol. Salmanticensia*, Salamanca, Vol. Esp. 1 (Studia Palaeocheloniol. 1): 105-113.
- (1987): Sur la classification et les caractères de certaines tortues fossiles d'Asie rares et peu étudiées. – *Studia Geol. Salmanticensia*, Salamanca, Vol. Esp. 2 (Studia Palaeocheloniol., 2, 3): 55-86.
- (1989): Neogenovye cherepakhi SSSR. – Tbilisi (Metsniereba), 102 pp.
- (1990): Paleogenovye cherepakhi SSSR. – Tbilisi (Metsniereba), 95 pp.
- COBLENZ, W. & C. FRITZSCHE (1980): Kleinkindbestattung in einer reich ausgestatteten Salzründer Grube. – *Ausgrabungen und Funde*, Berlin, **25**(1): 5-17.
- CONATO V., D. ESU, A. MALTESTA & F. ZARLENGA (1980): New data on the Pleistocene of Rome. – *Quaternaria*, Rome, **22**: 131-176.
- CRACRAFT, J. (1992): Species concepts and speciation analysis. – In: ERESHEFSKY, M. (ed.), *The Units of Evolution*. Cambridge, Mass. (The MIT Press), pp. 93-120.
- DEGERBØL, M. & H. KROG (1951): Den europæiske Sumpskildpadde (*Emys orbicularis* L.) i Danmark. – *Danmarks Geol. Undersøg.*, II. Række, Copenhagen, **78**: 5-130, 3 pls.
- DELFINO, M. (1994/95): *Erpetofauna Tardo Villafranchiana di Cava dell'Erba e Cava Pirro* (Foggia, Puglia, Italia). – Turin (unpublished dissertation thesis, Turin University), 194 pp.
- DIETZ, R.S. & J.C. HOLDEN (1970): Reconstruction of Pangaea: Breakup and dispersion of continents, Permian to Present. – *J. Geophys. Res.*, Washington, **75**(26): 4939-4956.
- DORIA, G. & S. SALVIDIO (1994): *Atlante degli anfibi e rettili della Liguria*. – Genova (Regione Liguria, cataloghi dei beni naturali), 151 pp.
- EICHWALD, E. (1831): *Zoologia specialis. Pars posterior*. – Vilna (Zawadzki), III, 404 pp.
- (1841): Fauna caspio-caucasia nonnullis observationibus novis. – *Petropolis*, 233, 2 pp., 40 pls.
- ELBURG, R. (1994): Dorf auf dem Lößlehm – eine Siedlung der ersten Bauern in Dresden-Cotta. – *Archäologie aktuell im Freistaat Sachsen*, Dresden, **1994**(2): 39-46.
- ERNST, C.H. (1990): Systematics, taxonomy, variation, and geographic distribution of the slider turtle. – In: GIBBONS, J.W. (ed.), *Life History and Ecology of the Slider Turtle*. Washington (Smithsonian Institution Press), pp. 57-67.
- FARKAS, B., U. FRITZ, N. JENDRETZKE & N. SCHNEEWEISS (1998): Morphological differences between pond turtles (*Emys orbicularis*) from the Hungarian Lowlands, eastern Poland, and northeastern Germany. – In: FRITZ, U. et al. (eds.): *Proceedings of the EMYS Symposium Dresden 96*. Mertensiella, Rheinbach, **10**: 89-94.

- FRENZEL, B. (1978): Landschaftsgeschichte und Landschaftsökologie des Kreises Freudenstadt. – In: Der Kreis Freudenstadt. Stuttgart (Theiss), pp. 52-76.
- FRENZEL, B., G. FURRER & W. LAUER (1989): Zur Paläoklimatologie der letzten 2500 Jahre in Mitteleuropa. – Festschr., Akad. Wiss. Lit. Mainz 1949-1989. Wiesbaden (Steiner), pp. 143-182.
- FRITZ, U. (1989): Zur innerartlichen Variabilität von *Emys orbicularis* (LINNAEUS, 1758). 1. Eine neue Unterart der Europäischen Sumpfschildkröte aus Kleinasien *Emys orbicularis luteofusca* subsp. nov. – Salamandra, Bonn, **25**(3/4): 143-168.
- (1992): Zur innerartlichen Variabilität von *Emys orbicularis* (LINNAEUS, 1758). 2. Variabilität in Osteuropa und Redefinition von *Emys orbicularis orbicularis* (LINNAEUS, 1758) und *E. o. hellenica* (VALENCIENNES, 1832). – Zool. Abh. Staatl. Mus. Tierkd. Dresden, **47**(5): 37-77.
- (1993a): Zur innerartlichen Variabilität von *Emys orbicularis* (LINNAEUS, 1758). 3. Zwei neue Unterarten von der Iberischen Halbinsel und aus Nordafrika, *Emys orbicularis fritzjuergenobsti* subsp. nov. und *E. o. occidentalis* subsp. nov. – Zool. Abh. Staatl. Mus. Tierkd. Dresden, **47**(11): 131-155.
- (1993b): Weitere Mitteilung zur innerartlichen Variabilität, Chorologie und Zoogeographie von *Emys orbicularis* (LINNAEUS, 1758) in Kleinasien. – Herpetozoa, Wien, **6**(1/2): 37-55.
- (1994): Zur innerartlichen Variabilität von *Emys orbicularis* (LINNAEUS, 1758). 4. Variabilität und Zoogeographie im pontokaspischen Gebiet mit Beschreibung von drei neuen Unterarten. – Zool. Abh. Staatl. Mus. Tierkd. Dresden, **48**(4): 53-93.
- (1995a): Zur innerartlichen Variabilität von *Emys orbicularis* (LINNAEUS, 1758). 5a. Taxonomie in Mittel-Westeuropa, auf Korsika, Sardinien, der Apenninen-Halbinsel und Sizilien und Unterartengruppen von *E. orbicularis*. – Zool. Abh. Staatl. Mus. Tierkd. Dresden, **48**(13): 185-242.
- (1995b): Kritische Übersicht der Fossilgeschichte der Sumpfschildkröten-Gattung *Emys* A. DUMÉRIL, 1806. – Zool. Abh. Staatl. Mus. Tierkd. Dresden, **48**(14): 243-264.
- (1996): Zur innerartlichen Variabilität von *Emys orbicularis* (LINNAEUS, 1758). 5b. Intraspezifische Hierarchie und Zoogeographie. – Zool. Abh. Staatl. Mus. Tierkd. Dresden, **49**(3): 31-71.
- FRITZ, U., O. PICARIELLO, R. GÜNTHER & F. MUTSCHMANN (1993): Zur Herpetofauna Süditaliens. Teil 1. Flußmündungen und Feuchtgebiete in Kalabrien, Lucanien und Südapulien. – herpetofauna, Weinstadt, **15**(84): 6-14.
- FRITZ, U., C. KELLER & M. BUDDE (1996): Eine neue Unterart der Europäischen Sumpfschildkröte aus Südwestspanien, *Emys orbicularis hispanica* subsp. nov. – Salamandra, Rheinbach, **32**(3): 129-152.
- FRITZ, U., İ. BARAN, A. BUDAK & E. AMTHAUER (1998): Some notes on the morphology of *Emys orbicularis* in Anatolia, especially on *E. o. luteofusca* and *E. o. colchica*, with the description of a new subspecies from southeastern Turkey. – In: FRITZ, U. et al. (eds.): Proceedings of the EMYS Symposium Dresden 96. Mertensiella, Rheinbach, **10**: 103-121.
- FRITZ, U. & B. FARKAS (1996): The proper generic allocation of *Clemmys mehelyi* KORMOS, 1911. – Fragm. Mineral. Palaeontol., Budapest, **18**: 103-105.
- FRITZ, U. & R. GÜNTHER (1996): Europäische Sumpfschildkröte – *Emys orbicularis* (LINNAEUS, 1758). – In: GÜNTHER, R. (ed.), Die Amphibien und Reptilien Deutschlands. Jena (Fischer), pp. 518-534.
- FRITZ, U. & F.J. OBST (1995): Morphologische Variabilität in den Intergradationszonen von *Emys orbicularis orbicularis* und *E. o. hellenica*. – Salamandra, Rheinbach, **31**(3): 157-180.

- GAFFNEY, E.S. & P.A. MEYLAN (1988): A phylogeny of turtles. – In: BENTON, M. J. (ed.), *The Phylogeny and Classification of the Tetrapods*, Vol. 1: Amphibians, Reptiles, Birds. Oxford (Syst. Ass. Spec. Vol., 35A), pp. 157-219.
- DE GROSSI MAZZORIN, J. (1988): Tabina Magreta: la terramara e i resti di età etrusca (campagne di scavo 1985-1986). Nota preliminare sulla fauna dell'insediamento della media età del Bronzo. – In: *Modena dalle origini all'anno Mille*, Studi di archeologia e storia. Vol. 1. Modena, pp. 225-229.
- GUERRESCHI, G., P. CATALANI & N. CESCHIN (1986): Belforte di Gazuolo (Mantova). Una stazione con vasi a bocca quadrata del Neolitico superiore. – *Preistoria Alpina*, **22**: 35-118.
- HAAS, G. (1966): On the Vertebrate Fauna of the Lower Pleistocene Site 'Ubeidiya. – *Jerusalem (Isr. Acad. Sci. Humanit.)*, 68 pp., 16 pls.
- HOLMAN, J.A. (1987): Herpetofauna of the Egelhoff Site (Miocene: Barstovian) of north-central Nebraska. – *J. Vertebr. Paleontol.*, Oklahoma City, **7**: 109-120.
- (1995): A new species of *Emydoidea* (Reptilia: Testudines) from the Late Barstovian (Medial Miocene) of Cherry County, Nebraska. – *J. Herpetol.*, Houston, **29**(4): 548-553.
- (1998): Pleistocene Amphibians and Reptiles in Britain and Europe. – Oxford (Oxford University Press, Oxford Monogr. Geol. Geophys.), x, 254 pp.
- HOLMAN, J.A. & R.G. CORNER (1985): A Miocene *Terrapene* (Testudines: Emydidae) and other Barstovian turtles from south-central Nebraska. – *Herpetologica*, Lawrence, **41**(1): 88-93.
- HUTCHISON, J.H. (1981): *Emydoidea* (Emydidae, Testudines) from the Barstovian (Miocene) of Nebraska. – *Paleo Bios*, Berkeley, **37**: 1-6.
- International Code of Zoological Nomenclature (1985) – London (Intern. Trust for Zool. Nomencl.), xx, 338 pp.
- ISBERG, O. (1929): Das ehemalige Vorkommen der Sumpfschildkröte (*Emys orbicularis* L.) in Schweden und damit zusammenhängende klimatische Erscheinungen. – *Ark. Zool.*, Stockholm, **21A**(3): 1-52, map.
- JIMÉNEZ FUENTES, E. & S. MARTÍN DE JESÚS (1991): Ejemplares-tipo de quelonios fósiles españoles. – *Rvta. Esp. Paleontol.*, **6**: 98-106.
- KHOSATZKY, L.I. & V.M. CHKHIKVADZE (1993): Novye dannye o miotsenovykh cherepakhkh roda *Baicalemys*. – *Soobshch. Akad. Nauk Gruzii*, Tbilisi, **148**(3): 155-160.
- KINZELBACH, R. (1988): Die Europäische Sumpfschildkröte (*Emys orbicularis*) im Einzugsbereich des Rheins. – *Zeitschr. Angew. Zool.*, Berlin, **75**(4): 385-419.
- KOTSAKIS, T. (1982): Les Amphibiens et les Reptiles du Villafranchien de l'Italie. – In: *Le Villafranchien Méditerranéen*. Lille, pp. 83-91.
- (1996): Anfibi e Rettili. – In: BASILE, B. & S. CHILARDI (eds.), *Siracusa, le ossa dei giganti: lo scavo paleontologico di Contrada Fusco. Regione Siciliana (Assessorato Beni Culturali ed Ambientali e Pubblica Istruzione)*, pp. 56-60.
- KUHN, O. (1964): *Fossilium Catalogus I: Animalia*. Pars 107, Testudines. – s'Gravenhage, 276 pp.
- KURCK, C. (1917): Den forntida utbredningen af kärrsköldpaddan, *Emys orbicularis* (Lin.), i Sverige, Danmark och angränsande länder. – *Lunds Univ. Årsskrift*, N.F., Avd. 2, **13**(9): 1-129, map.
- LANZA, B. (1983): Ipotesi sulle origini del popolamento erpetologico della Sardegna. – *Lavori Soc. Ital. Biogeografia*, N.S., **8**(1980): 723-744.

- LENK, P., U. JOGER, U. FRITZ, P. HEIDRICH & M. WINK (1998): Phylogeographic patterns in the mitochondrial cytochrome b gene of the European pond turtle (*Emys orbicularis*): first results. – In: FRITZ, U. et al. (eds.): Proceedings of the EMYS Symposium Dresden 96. Mertensiella, Rheinbach, **10**: 159-175.
- MARNIVAL-VIGNE, M.-C., D. MORDANT, G. AUBOIRE, A. AUGEREAU, S. BAILON, C. DAUPHIN, G. DELIBRIAS, V. KRIER, A.-S. LECLERC, C. LEROYER, P. MARNIVAL, C. MORDANT, P. RODRIGUEZ, P. VILLETTE & J.D. VIGNE (1989): Noyen-sur-Seine, site stratifié en milieu fluvial: une étude multidisciplinaire intégrée. – Bull. Soc. Prehist. Française, Paris, **86**(10-12): 370-379.
- MAYR, E. (1963): Animal Species and Evolution. – Cambridge, Mass. (Harvard Univ. Press), 797 pp.
- MCCOY, C. J. (1973): *Emydoidea*, *E. blandingii*. – Cat. Amer. Amph. Rept., New York, **136**: 1-4.
- MLYNARSKI, M. (1969): Fossile Schildkröten. – Wittenberg Lutherstadt (Ziemsen, Die Neue Brehm-Bücherei), 128 pp.
- (1976): Teil 7, Testudines. – In: O. KUHN (ed.), Handbuch der Paläoherpetologie. Stuttgart and New York (Fischer), VI, 130 pp.
- MURRAY, J. (1970): The First European Agriculture, a Study of Osteological and Botanical Evidence until 2000 BC. – Edinburgh (University Press), VIII, 380 pp.
- NEČAS, P., D. MODRÝ & V. ZAVADIL (1997, eds.): Czech Recent and Fossil Amphibians and Reptiles. – Frankfurt a.M. (Edition Chimaira,) 94 pp.
- NIKOLSKY, A.M. (1915): Faune de la Russie. Reptiles (Reptilia). Vol. I. Chelonia et Sauria. – Petrograd (Imperatorsk. Akad. Nauk), VI, III, **532**, 2 pp., IX pls.
- PAAVER, K.L. (1958): O nakhodkakh kostnykh ostatkov bolotnoi cherepakhi *Emys orbicularis* (L.) na posdneneoliticheskoi stoyanke Tamula (Yushnaya Estoniya). – Izvest. AN ESSR, Tallinn, **7**: 75-78.
- PARASKIV, K.P. (1956): Presmykayushchiesya Kazakhstana. – Alma-Ata (Izdatelstvo Akad. Nauk Kazakhsk. SSR), 228 pp.
- PERSSON, A. (1992): Den europeiska kärrsköldpaddan *Emys orbicularis* (LINNAEUS 1758) och dess forntida förekomst i Sverige. – Snoken, Lund, **22**(4): 12-23.
- PRITCHARD, P.C.H. (1966): Notes on Persian turtles. – Brit. J. Herpetol., London, **3**(11): 271-275.
- (1979): Encyclopedia of turtles. – Neptune, N.J. (t.f.h.), 895 pp.
- PUPIŃA, A. & M. PUPIŃS (1996): Żółw błotny (*Emys orbicularis* L.) na Łotwie. – Proc., IV Ogólnopolska Konferencja Herpetologiczna, Kraków, **1996**: 96d (3 pp.).
- RÖGL, F. & F.F. STEININGER (1983): Vom Zerfall der Tethys zu Mediterran und Paratethys. – Ann. Naturhist. Mus. Wien, **85/A**: 135-163, 14 pls.
- RÖSSLER, M. (1998): Populationsökologie und Habitatansprüche der Europäischen Sumpfschildkröte (*Emys orbicularis*) im Nationalpark Donau-Auen. Grundlage für Schutzmaßnahmen. – Wien, unpubl. (Jahresbericht des Schildkrötenprojekts 1997/1998), 97 pp.
- RUSSEL, D.E. (1975): Palaeoecology of the Palaeocene-Eocene transition in Europe. – Contr. Primatol., Basle, **5**: 28-61.
- SALA, B. (1996): Gli animali del giacimento di Isernia La Pineta. – In: PERETTO, C. (ed.), I reperti paleontologici del giacimento paleolitico di Isernia La Pineta, l'Uomo e l'ambiente. Istituto regionale per gli studi storici del Molise "V. Cuoco" (Cosmo Iannone Editore), pp. 25-49.

- STEININGER, F.F., G. RABEDER & F. RÖGL (1985): Land mammal distribution in the Mediterranean Neogene: a consequence of geokinematic and climatic events. – In: STANLEY, D.J. & F.-C. WEZEL (eds.), *Geological Evolution of the Mediterranean Basin*. New York (Springer), pp. 559-571.
- STUART, A.J. (1979): Pleistocene occurrences of the European pond tortoise (*Emys orbicularis* L.) in Britain. – *Boreas*, Oslo, **8**: 359-371.
- SZCZERBAK, N.N. (1998): The European pond turtle (*Emys orbicularis*) in Ukraine. – In: FRITZ, U. et al. (eds.): *Proceedings of the EMYS Symposium Dresden 96*. Mertensiella, Rheinbach, **10**: 259-266.
- SZYNDLAR, Z. (1984): Fossil snakes from Poland. – *Acta Zool. Cracov.*, Kraków, **28**(1): 1-156.
- TAŞKAVAK, E. & M. REIMANN (1998): The present status of *Emys orbicularis* (LINNAEUS, 1758) in southern Central Anatolia. – In: FRITZ, U. et al. (eds.): *Proceedings of the EMYS Symposium Dresden 96*. Mertensiella, Rheinbach, **10**: 267-278.
- TRINGHAM, R. (1969): Animal domestication in the neolithic cultures of the south-west part of European U.S.S.R. – In: UCKO, P.J. & G.W. DIMBLEBY (eds.), *The Domestication and Exploitation of Plants and Animals*. London (Duckworth), pp. 381-392.
- WERMUTH, H. & R. MERTENS (1961): Schildkröten, Krokodile, Brückenechsen. – Jena (Fischer), XXVI, 422 pp.
- & — (1977): Testudines, Crocodylia, Rhynchocephalia. – *Das Tierreich*, Berlin, **100**: I-XXVII, 1-174.
- VAN WIJNGAARDEN-BAKKER, L.H. (1996): A new find of a European pond tortoise, *Emys orbicularis* (L.) from the Netherlands: osteology and taphonomy. – *Intern. J. Osteoarcheol.*, New York, **6**: 443-453.
- WILLMS, C. (1986): Die europäische Sumpfschildkröte im neolithischen Nahrungssystem. – *Germania*, Mainz, **64**(2): 561-564.
- ZUFFI, M.A.L. & D.L.PH. BALLASINA (1998): Contribution to the knowledge of regional polymorphism of *Emys orbicularis* in Italy, and notes on the husbandry activities at the CARAPAX Centre. – In: FRITZ, U. et al. (eds.): *Proceedings of the EMYS Symposium Dresden 96*. Mertensiella, Rheinbach, **10**: 279-286.
- ZUG, G.R. (1993): *Herpetology. An Introductory Biology of Amphibians and Reptiles*. – San Diego (Academic Press), xv, 527 pp.

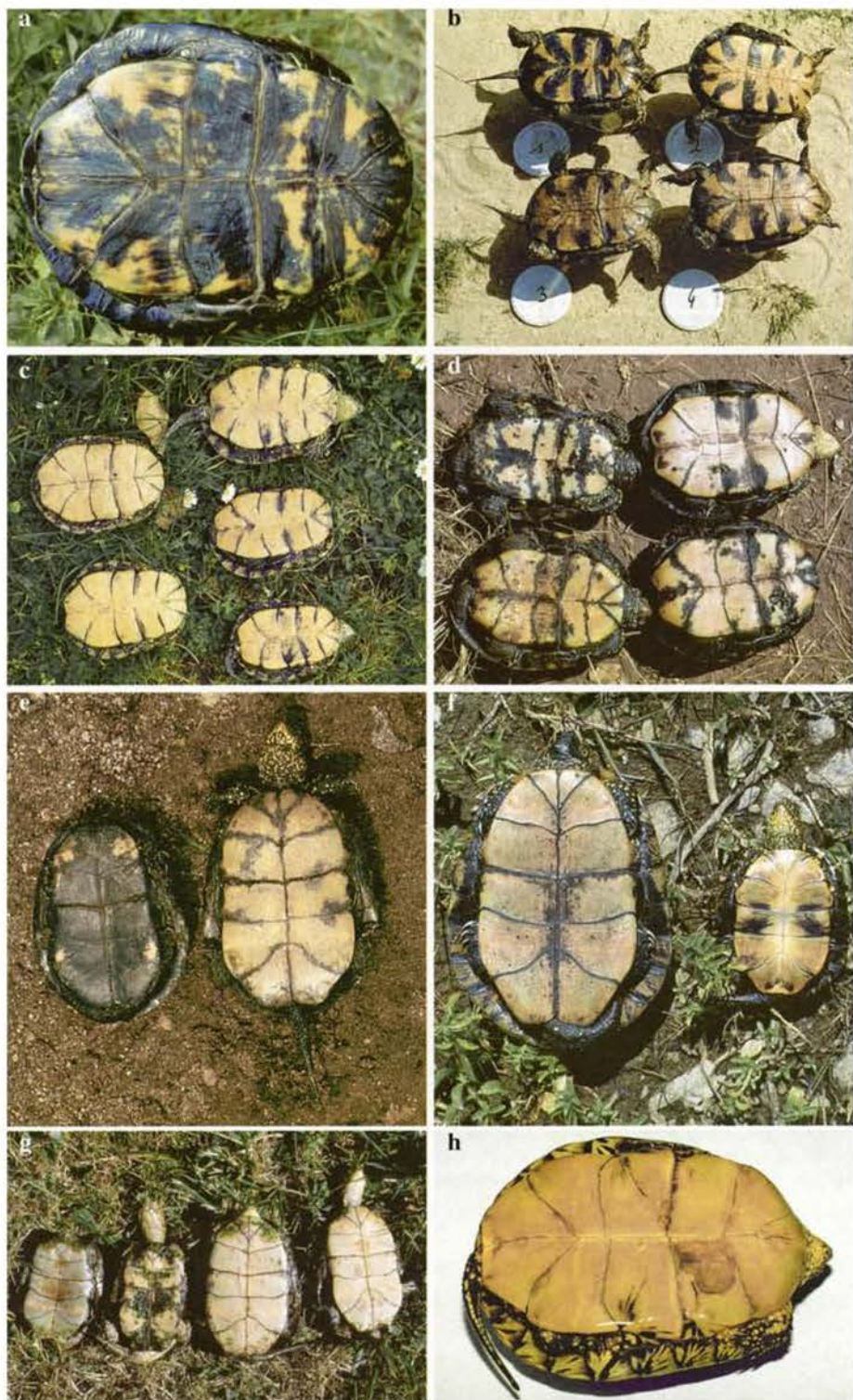
Author: UWE FRITZ, Staatliches Museum für Tierkunde, Forschungsstelle, Augustusstraße 2, D-01067 Dresden.





Plate/Tafel 1.

- (a) *Emys orbicularis occidentalis*, female/Weibchen, surroundings of/Umgebung von Sefrou, Morocco/Marokko (photo by H. BILLING);
- (b) *E. o. fritzjuergenobsti*, male/Männchen, Ebro Delta/Ebro-Delta, Spain/Spanien (photo by S. ROMER);
- (c) *E. o. fritzjuergenobsti*, male/Männchen, Valencia, Spain/Spanien;
- (d) *E. o. (g.) galloitalica*, female/Weibchen, Massif des Maures, France/Frankreich;
- (e) *E. o. (g.) lanzai*, female/Weibchen, Gulf of Sagone/Golf von Sagone, Corsica/Korsika;
- (f) *E. o. (g.) capolongoi*, female/Weibchen, Riu Toltu, Sardinia/Sardinien;
- (g) *E. o. hellenica*, male/Männchen, Kephallenia, Greece/Griechenland;
- (h) Males of/Männchen von *E. o. hellenica* (left/links, Kephallenia, Greece/Griechenland) and/und *E. o. orbicularis* (right/rechts, Balaton, Hungary/Ungarn);
- (i) *E. o. iberica*, young female/junges Weibchen, Aserbaijan/Aserbaidshan (photo by U. SATTLER);
- (j) *E. o. iberica*, aged female/altes Weibchen (holotype of/Holotypus von *E. o. kurae*), Kura Mouth/Kura-Mündung, Aserbaijan/Aserbaidshan;
- (k) *E. o. persica*, male/Männchen, Sharlouk River/Fluß Scharlouk, Turkmenia/Turkmenien (photo by N. ORLOV);
- (l) *E. o. orbicularis*, male/Männchen, Balaton, Hungary/Ungarn;
- (m) *E. o. luteofusca*, female/Weibchen (holotype/Holotypus), Ereğli, Turkey/Türkei;
- (n) South Italian taxon/ Süditalienisches Taxon, male/Männchen, Neto Mouth/Neto-Mündung (Calabria/Kalabrien), Italy/Italien.





Plate/Tafel 2. Ventral views of/Ventralansichten von

- (a) *Emys orbicularis occidentalis*, young female/junges Weibchen, surroundings of/Umgebung von Sefrou, Morocco/Marokko;
- (b) *E. o. hispanica*, females/Weibchen, Doñana, Spain/Spanien (photo by M. BUDDE);
- (c) *E. o. fritzjuergenobsti*, left/links: females/Weibchen, right/rechts: males/Männchen, Valencia, Spain/Spanien;
- (d) *E. o. (g.) galloitalica*, left/links: males/Männchen, right/rechts: females/Weibchen, Massif des Maures, France/Frankreich;
- (e) *E. o. (g.) lanzai*, left/links: male/Männchen, right/rechts: female/Weibchen, L'Oso River near Porto Vecchio/Fluß L'Oso bei Porto Vecchio, Corsica/Korsika (photo by U. KOEPERNICK);
- (f) *E. o. (g.) capolongoi*, left/links: male/Männchen, right/rechts: juvenile/Jungtier, Budoni River/Fluß Budoni, Sardinia/Sardinien;
- (g) *E. o. hellenica*, left/links: males/Männchen, right/rechts: females/Weibchen, Kephallenia, Greece/Griechenland;
- (h) *E. o. iberica*, young female/junges Weibchen, Aserbaijan/Aserbaidshan (photo by U. SATTLER);
- (i) *E. o. persica*, male/Männchen, Sharlouk River/Fluß Scharlouk, Turkmenia/Turkmenien (photo by N. ORLOV);
- (j) *E. o. orbicularis*, females/Weibchen, Kuculishkes, Lithuania/Litauen (photo by E. SNIESHKUS);
- (k) Males of/Männchen von *E. o. luteofusca* (left/links, Central Turkey/Zentraltürkei) and/und *E. o. orbicularis* (right/rechts, Ukraine, photo courtesy of H. ARTNER);
- (l) South Italian taxon/Südtalienisches Taxon, females/Weibchen, Neto Mouth/Neto-Mündung (Calabria/Kalabrien), Italy/Italien.