CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group

Edited by

Anders G.J. Rhodin, John B. Iverson, Peter Paul van Dijk,
Craig B. Stanford, Eric V. Goode, Kurt A. Buhlmann, and Russell A. Mittermeier

Testudo marginata Schoepff 1793 –
Marginated Tortoise,
Kraspedochelóna, Breshka Malore, Testuggine Marginata

Daniel Escoriza, Elias Tzoras, and Henrik Bringsøe

Chelonian Research Monographs
Number 5 (Installment 17) 2023: Account 122

Published by
Chelonian Research Foundation and Turtle Conservancy

in association with
IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, Re:wild,
Turtle Conservation Fund, and International Union for Conservation of Nature / Species Survival Commission

CHELONIAN RESEARCH MONOGRAPHS
Contributions in Turtle and Tortoise Research

CHELONIAN RESEARCH MONOGRAPHS (CRM) (ISSN 1088-7105) is an international peer-reviewed scientific publication series for monograph-length manuscripts, collected proceedings of symposia, edited compilations, and other longer research documents focused on turtles and tortoises. The series accepts contributions dealing with any aspects of chelonian research, with a preference for conservation or biology of freshwater and terrestrial turtles and tortoises. Bibliographic and other reference materials are also of potential interest. Submit manuscripts directly to Anders Rhodin at the e-mail address above. The series is published on an occasional basis, from 1996–2016 by Chelonian Research Foundation, and from 2017 and on by Chelonian Research Foundation and Turtle Conservancy.

Published CRM Issues

CRM 1. The Galápagos Tortoises: Nomenclatural and Survival Status. 1996. By PETER C.H. PRITCHARD. 85 pp. Open access pdf download available at www.chelonian.org/wp-content/uploads/file/CRM%201/CRM_1_1996_Pritchard_Galapagos_Tortoises.pdf.

CRM 2. Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia. 2000. Edited by PETER PAUL VAN DIJK, BRYAN L. STUART, AND ANDERS G.J. RHODIN. 164 pp. Open access pdf download available at www.chelonian.org/wp-content/uploads/file/CRM%202/CRM_2_Asian_Turtle_Trade_2000.pdf.

CRM 3. Biology and Conservation of Florida Turtles. 2006. Edited by PETER A. MEYLAN. 376 pp. Open access pdf download available at www.chelonian.org/wp-content/uploads/file/CRM%203/CRM_3_2006_Meylan_Florida_Turtles2.pdf.

CRM 4. Defining Turtle Diversity: Proceedings of a Workshop on Genetics, Ethics, and Taxonomy of Freshwater Turtles and Tortoises. 2007. Edited by H. BRADLEY SHAFFER, NANCY N. FITZSIMMONS, ARTHUR GEORGES, AND ANDERS G.J. RHODIN. 200 pp. Open access pdf download available at www.chelonian.org/wp-content/uploads/file/CRM%204/CRM_4_Defining_Turtle_Diversity_2007.pdf.

CRM 5 (Installments 1–17, 122 accounts to date). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. 2008–2023. Edited variously by ANDERS G.J. RHODIN, JOHN B. IVERSON, PETER PAUL VAN DIJK, KURT A. BUHLMANN, PETER C.H. PRITCHARD, CRAIG B. STANFORD, ERIC V. GOODE, RAYMOND A. SAUMURE, AND RUSSELL A. MITTERMEIER. 2574 pp. to date. All accounts available as open access pdf downloads at www.iucn-tftsg.org/cbftt/.

CRM 6. Turtles on the Brink in Madagascar: Proceedings of Two Workshops on the Status, Conservation, and Biology of Malagasy Tortoises and Freshwater Turtles. 2013. Edited by CHRISTINA M. CASTELLANO, ANDERS G.J. RHODIN, MICHAEL OGLE, RUSSELL A. MITTERMEIER, HERILALA RANDRIAMAHAZO, RICK HUDSON, AND RICHARD E. LEWIS. 184 pp. Open access pdf download available at www.chelonian.org/wp-content/uploads/file/CRM%206/CRM_6_Castellano_etal_2013.pdf.

CRM 5 (Installment 8). Turtles and Tortoises of the World During the Rise and Global Spread of Humanity: First Checklist and Review of Extinct Pleistocene and Holocene Chelonians. 2015. TEWG [TURTLE EXTINCTIONS WORKING GROUP: ANDERS G.J. RHODIN, SCOTT THOMSON, GEORGIOS L. GEORGALIS, HANS-VOLKER KARL, IGOR G. DANILOV, AKIO TAKAHASHI, MARCELO S. DE LA FUENTE, JASON R. BOURQUE, MASSIMO DELFINO, ROGER BOUR, JOHN B. IVERSON, H. BRADLEY SHAFFER, AND PETER PAUL VAN DIJK]. 66 pp. Open access pdf download available at www.iucn-tftsg.org/wp-content/uploads/file/Accounts/crm_5_000e_fossil_checklist_v1_2015.pdf.

CRM 7. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (8th Ed.). 2017. TTWG [TURTLE TAXONOMY WORKING GROUP: ANDERS G.J. RHODIN, JOHN B. IVERSON, ROGER BOUR, UWE FRITZ, ARTHUR GEORGES, H. BRADLEY SHAFFER, AND PETER PAUL VAN DIJK]. 292 pp. Open access pdf download available at www.iucn-tftsg.org/wp-content/uploads/file/Accounts2/TTWG_checklist_v8_2017.pdf.

CRM 8. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (9th Ed.). 2021. TTWG [TURTLE TAXONOMY WORKING GROUP: ANDERS G.J. RHODIN, JOHN B. IVERSON, ROGER BOUR, UWE FRITZ, ARTHUR GEORGES, H. BRADLEY SHAFFER, AND PETER PAUL VAN DIJK]. 472 pp. Open access pdf download available at www.iucn-tftsg.org/wp-content/uploads/crm.8.checklist.atlas_.v9.2021.e3.pdf.

CHELONIAN RESEARCH MONOGRAPHS (CRM) issues are variously available for purchase from Chelonian Research Foundation and Turtle Conservancy. Contact either Turtle Conservancy (www.turtleconservancy.org) or Chelonian Research Foundation (www.chelonian.org/crm; 564 Chittenden Dr., Arlington, VT 05250 USA; 978-807-2902; RhodinCRF@aol.com) for prices, titles, and to place orders for available print copies. Chelonian Research Foundation (founded in 1992) and Turtle Conservancy (founded in 2005 as Chelonian Conservation Center, renamed in 2010) are nonprofit tax-exempt organizations under section 501(c)(3) of the Internal Revenue Code.

Conservation Biology of Freshwater Turtles and Tortoises:
A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group
Rhodin, Iverson, van Dijk, Stanford, Goode, Buhlmann, and Mittermeier (Eds.)
Chelonian Research Monographs (ISSN 1088-7105) No. 5 (Installment 17), doi:10.3854/crm.5.122.marginata.v1.2023

Testudo marginata Schoepff 1793 – Marginated Tortoise, Kraspedochelóna, Breshka Malore, Testuggine Marginata

Daniel Escoriza[1], Elias Tzoras[2], and Henrik Bringsøe[3]

[1]*Grup de Recerca en Ecologia Aquàtica Continental (GRECO), University of Girona, Campus Montilivi, 17071 Girona, Spain [drdanielescoriza@gmail.com];*
[2]*Patras, 26442 Achaia, Greece [eliastzoras@outlook.com];*
[3]*Irisvej 8, 4600 Køge, Denmark [bringsoe@email.dk]*

Summary. — The Marginated Tortoise, *Testudo marginata* (family Testudinidae), is a medium-sized tortoise and largest member of its genus (straightline carapace lengths [SCL] usually up to 40 cm, exceptionally to 47.5 cm), native to Greece and southern Albania, and introduced historically to northeastern Sardinia. The species is entirely restricted to regions with a warm, scorched-dry to sub-humid Mediterranean climate, at low to moderate altitudes (up to 1600 m in southern Greece and 600 m in Sardinia). Morphologically, *T. marginata* differs from other Mediterranean *Testudo* species by the combination of chevron markings arranged symmetrically along the longitudinal axis of the plastron, overall dark carapace coloration, and laterally elongated and pronounced flaring of the posterior marginals (less marked in populations from the Peloponnese Mani peninsula and Sardinia). The size of males is roughly similar to that of females, although sometimes slightly larger (male mean SCL = 30.2 cm, female mean SCL = 28.0 cm; for the smaller southern Peloponnese (*weissingeri*) ecotype, male mean SCL = 21.3 cm, female mean SCL = 20.9 cm). Mating occurs primarily in September–October and to a lesser extent in April–May. Females nest in May–June and produce up to 3 clutches of 4–9 (rarely up to 15) eggs. Hatchlings have an SCL of 30–40 mm. The main threat to *T. marginata* within its natural range is habitat alteration and loss from intensive agriculture and expanding development, including construction of tourist facilities, but many populations are still relatively robust.

Distribution. — Greece and Albania. The species is widespread in central mainland Greece and the Peloponnese peninsula, as well as extreme southern Albania. Native populations also occur on several islands in the Ionian and Aegean seas: Alonissos, Dokos, Elafonisos, Evvia, Kastos, Kyra Panagia, Kythera, Petalas, Poros, Psili, Romvi, Salamina, Sapientza, Sfaktiria, Skiathos, Skyros, Spetses, Spetsopoula, Trizonia, and Valaxa. Viable introduced populations occur on the Aegean islands of Chios and Lesvos. The species previously occurred on Crete, Kos, and Tilos during the Pleistocene and earlier Holocene, but was extirpated from these islands long ago. It was introduced in historical times to northern Sardinia (Italy) and some of its satellite islands. Apparently translocated or introduced specimens and/or populations also occur elsewhere on Sardinia and in continental Italy, as well as on various Ionian and Aegean islands.

Synonymy. — *Testudo marginata* Schoepff 1793, *Testudo graja* Hermann *in* Schoepff 1793, *Testudo graja* Hermann 1804, *Testudo campanulata* Walbaum *in* Strauch 1862, *Peltastes marginatus melas* Gray 1870, *Testudo nemoralis* Schreiber 1875, *Testudo marginata cretensis* † Bachmayer, Brinkerink and Symeonidis 1975, *Testudo marginata sarda* Mayer 1992, *Testudo marginata weissingeri* Trutnau 1994, *Testudo weissingeri* Bour 1996.

Subspecies. — No subspecies are currently recognized.

Status. — IUCN 2022 Red List: Least Concern (LC, assessed 2004); CITES: Appendix II; EU: Annex A (regulation of trade of fauna and flora); EU Habitats Directive: Annexes II and IV (conservation of natural habitats and of wild fauna and flora); Bern Convention: Annex II; Greece: Least Concern (LC); Albania: Least Concern (LC); Italy: Red List, Near Threatened (NT, assessed 2013).

Taxonomy. — The Marginated Tortoise was first described by Walbaum (1782) as *Testudo tabulata campanulata,* but in a nonbinomial work, rendering that name nomenclaturally unavailable. It was subsequently formally described by Schoepff (1793) as *Testudo marginata*, a designation that has remained in effect since then. Several supposed subspecies or closely related species have also been described over the years, but none are currently recognized as distinct: *Peltastes marginatus melas* Gray 1870, *Testudo nemoralis* Schreiber 1875,

Figure 1. Adult *Testudo marginata* from the coastal dunes at Strofylia National Park, northwestern Peloponnese peninsula, Greece. Photo by Henrik Bringsøe.

Testudo marginata cretensis† Bachmayer, Brinkerink and Symeonidis 1975, *Testudo marginata sarda* Mayer 1992, *Testudo marginata weissingeri* Trutnau 1994, and *Testudo weissingeri* Bour 1996. The authority for the name *Testudo marginata* (Schoepff 1793), has often previously been incorrectly cited as Schoepff (1792). However, Schoepff ("1792") was actually published in several separate fascicles between 1792 and 1801 (Sherborn 1902; Mittleman 1944), and *T. marginata* was described in fascicles III–IV in 1793, as noted by TTWG (2007). The common name for *T. marginata* in Greece is *Kraspedochelóna* (Κρασπεδοχελώνα), in Albania, *Breshka Malore* (Highland Tortoise), and on Sardinia, *Testuggine Marginata*.

Molecular analyses have revealed that the Marginated Tortoise is a monotypic species (Fritz et al. 2005), although three subspecies have been described and have previously been considered to be distinct. *Testudo marginata cretensis* was described as an extinct Pleistocene form, native to the island of Crete and differentiated from the mainland subspecies by small differences of shell morphology (Bachmayer et al. 1975). However, these differences are within the range of variability of mainland populations of *T. marginata*, so this subspecies is probably not distinct, and has been synonymized, although molecular data are lacking (Vlachos 2022).

Testudo m. sarda and *T. m. weissingeri* do not show sufficient divergence in their mitochondrial DNA compared

Figure 2. Adult male *Testudo marginata* from Strofylia National Park, northwestern Peloponnese peninsula, Greece. Photo by Elias Tzoras.

Figure 3. Adult female *Testudo marginata* from Strofylia National Park, northwestern Peloponnese peninsula, Greece. Photo by Elias Tzoras.

Figure 4. Subadult female *Testudo marginata* from Pylos, southwestern Peloponnese peninsula, Greece. Photo by Elias Tzoras.

with the nominotypical form (Fritz et al. 2005). The Sardinian phenotype (*T. m. sarda*) has been characterized by small differences in the posterior marginal serrations and the arrangement of the last vertebral plate (Mayer 1992). Based on 11 polymorphic microsatellites for the evolutionary significance of the morphotypes of *T. marginata*, Perez et al. (2012) detected reduced gene flow between the dwarf form from the Peloponnese (*T. m. weissingeri*), which was suggested to have been caused by landscape features and geographical barriers, but not sufficient to warrant recognition as a distinct taxon.

The taxon *Testudo weissingeri* was formally described in detail by Bour (1996); however, that publication had been delayed by two years and the name was briefly and inadvertantly published earlier by Trutnau (1994) in a hobbyist book, as *Testudo marginata weissingeri*. A short diagnosis in that work was provided: "kleiner bleibende" (meaning "remain smaller"), and these smaller tortoises were noted to be from "Peleponnes" (= Peloponnese), but no type specimens were designated. In the absence of evidence to the contrary, this short description may technically be accepted as being diagnostic, which implies that the name *weissingeri* would be attributed to Trutnau (1994). However, petition has been made to the International Commission for Zoological Nomenclature to have this earlier name suppressed (Escoriza et al., submitted).

The phylogenetic sister species of *T. marginata* is the southeastern Mediterranean species *T. kleinmanni*. Based on DNA data from 15 nuclear loci, the separation between the two species occurred ca. 11 mya ago (Thomson et al. 2021). *Testudo graeca* is the closest species to this subclade, with an estimated divergence between the two groups of 14 mya (Thomson et al. 2021).

Description. — In comparison with other Western Palaearctic tortoises, *T. marginata* is a large species, generally attaining a straightline carapace length (SCL) of 32–34 cm (Bour 2004a). But much larger individuals exceeding 40 cm SCL are also known. An extremely large male *T. marginata* with SCL 47.5 cm was reported by Philippen (2008) in captivity in Italy. Allegedly it had been collected in the nature reserve Parco Naturale della Maremma in Tuscany (Italy) where other individuals were observed; however, most probably it had escaped or was released from captivity. A very young female collected near Athens in 1943 and subsequently kept in captivity in Austria, attained an SCL of 40.3 cm decades later (Ducotterd 1997, 1998; Ruttenstorfer and Artner 1997). Huge individuals also exist in the wild: a very large female *T. marginata* of 42 cm SCL was reported by Kordges (1984) south of Amfilochia at Limni Amvrakia in Aetolokarnania (F.B. Ludescher, pers. comm.), and a large male measuring 41.3 cm SCL was found in the Feneos Basin, northern Peloponnese by Koppitz et al. (2018) (see Table 1).

In Albania, the maximum SCL recorded was 31 cm (Haxhiu 1995; Bour 1996). The dwarf *weissingeri* ecotype from Peloponnese is smaller, normally reaching an SCL of up to 25 cm, seldom to 26.5–27.2 cm (Bour 2004b). The size at maturity is greater in females than in males (Willemsen and Hailey 2003). On Crete, the Pleistocene fossil remains show sizes similar to those reported on the mainland, with an SCL between 29–31 cm (Vlachos 2022).

On Sardinia, the maximum sizes also do not exceed those reported for the Greek mainland populations. According to Mayer (1992) some individuals are more compact in build and proportionally heavier, and have a maximum SCL of

Figure 5. *Testudo marginata* (dwarf form, *weissingeri* ecotype) from Mani peninsula, southern Peloponnese, Greece. *Left*: Adult male from Exochori. *Right*: Adult female from Kambos. Photos by Henrik Bringsøe.

Figure 6. Young male *Testudo marginata*, Gallura, Sardinia, Italy. Photos by Daniel Escoriza.

Figure 7. Adult female *Testudo marginata*, Gallura, Sardinia, Italy. Photos by Daniel Escoriza.

Figure 8. Large adult male *Testudo marginata*, Gallura, Sardinia, Italy. Note the overall darker coloration than the male in Fig. 6 above, and the roundness of the posterior marginals, characteristic of some Sardinian individuals. Photos by Daniel Escoriza.

Figure 9. Carapacial lateral profiles of *Testudo marginata*, adult female (*back*), young male (*front*), both individuals belonging to the same population, Gallura, Sardinia, Italy. Photo by Daniel Escoriza.

29 cm. However, Wegehaupt (2004) reported a maximum SCL for Sardinian individuals of 32 to possibly 35 cm, with a body mass of 4000–5000 g.

Male and female *T. marginata* are of similar size, or males are slightly larger (Bour 2004a,b; Wegehaupt 2004). Willemsen and Hailey (2003) found that males and females were similar in SCL, with females (average SCL 24.7 cm) being insignificantly larger than males (average SCL 24.2 cm). The appearance of the carapace is similar in both sexes, but males are more bell-shaped due to the greater flaring of the posterior marginals. Males also show proportionally larger heads, a longer and thicker tail, deeper abdomino-femoral plastral concavity, and anal plates arranged at a more open angle (Bour 2004a,b), creating a wider anal notch.

Bour (1996; 2004b) provided maximum SCLs of *T. marginata* for most of its Greek range as well as from Sardinia (see Table 1). In the Feneos Basin of northern Peloponnese, average SCL of males was 30.3 cm and body mass 3207 g (n = 90), while average SCL of females was 28.9 cm and body mass 3453 g (n = 63) (Koppitz et al. 2017). On the northeastern Peloponnese peninsula, two adult specimens were recorded by Buttle (1987) having SCLs of 25 cm and 28 cm. Additionally, Buttle (1988) cited a male individual of 31 cm SCL from the Gythio region, southern Peloponnese.

But in southern Messinia on the southwestern "finger" of the peninsula and near Gythio, Madsen (unpubl. data) observed fully adult individuals of the dwarf *weissingeri* ecotype form, with all individuals in the populations being smaller than 25 cm SCL. Keymar and Weissinger (1987) also mentioned the occurrence of the dwarf form on the southwestern Peloponnese peninsula. These populations were in the same latitudinal range as those of the Mani peninsula populations. On Skyros Island, two individuals were measured with carapace lengths of 21.1 cm and 22.7 cm, respectively (Kock and Storch 1979). On Skiathos Island,

Figure 10. Juvenile *Testudo marginata*, 48 mm SCL, from Vravrona, Spata-Artemida, Attica, Greece. Photos by Henrik Bringsøe.

Figure 11. Detail of the head of an adult male *Testudo marginata*, Gallura, Sardinia, Italy. Photo by Daniel Escoriza.

Cattaneo (1997) reported a male with an SCL of 26 cm. On Alonissos Island, a male individual was recorded with an SCL of 35 cm, and a female with an SCL of 20 cm (Broggi 2010). On Elafonisos Island (southwestern Aegean), the maximum SCL was 29 cm (Broggi 2016a). On Paros and Milos islands (Cyclades archipelago, Aegean Sea), two translocated males had SCLs of 18.7 cm and 30 cm, respectively (Clark 1970; Cattaneo 1984).

Table 1. Maximum SCL of *Testudo marginata* from different regions, following Bour (1996, 2004b). Only the western Mani region on the southern Peloponnese peninsula pertains to the dwarf ecotype *weissingeri*. Larger sizes of single individuals were recorded by *Kordges (1984), **Wegehaupt (2004), and ***Koppitz et al. (2018); these individuals were not included in the sample size, *n*.

Region and area of origin	Maximum SCL	*n*
Albania and northern mainland Greece:		
South Albania	31.0 cm	8
Thesprotia	30.5 cm	11
Imathia	33.0 cm	6
Ioannina	29.0 cm	8
Trikala	30.0 cm	10
Larisa	31.0 cm	25
Southern and southwestern mainland Greece:		
Preveza	27.0 cm	10
Aetolokarnania	26.0 cm	30
	42.0 cm*	
Fokida	27.0 cm	50
Fthiotida	27.5 cm	25
Southeastern mainland Greece:		
Evvia	30.0 cm	50
Viotia	34.0 cm	20
Attica	34.0 cm	70
Peloponnese peninsula, southern Greece:		
Corinthia	31.5 cm	20
	41.3 cm***	
Argolida	28.5 cm	200
Arcadia	31.0 cm	50
Messinia	30.5 cm	>400
Laconia	31.0 cm	>100
Mani (weissingeri)	27.2 cm	910
Sardinia, Italy:		
Gallura	32.0 cm	30
	35.0 cm**	

Typically, the carapace of *T. marginata* is narrow in the middle, rectangular and high-domed with a trapezoidal (bell-shaped) appearance in dorsal view, due to the extensive serration and flaring of the posterior marginals. In adults, the elongated carapace is highest just behind the center, with abruptly descending sides. The carapace is more elongated than in *T. graeca* and *T. hermanni* (Bringsøe et al. 2001), though *T. graeca* may exhibit an elongated, low-profile carapace in southern Turkey (Weissinger 1987). Similarly, for these three *Testudo* species, the slope of the SCL – body mass relationship is lowest (= lightest) for *T. marginata* and highest (= heaviest) for *T. graeca*, which applies for males, females, and subadults (Willemsen and Hailey 2002). Thus, among these three species, *T. marginata* is the lightest at a given SCL, due to the elongated and posteriorly flared shell.

As in *T. graeca*, the carapace of *T. marginata* is typically covered with 5 vertebral, 8 costal, and 22 marginal scutes (11 on each side), with one nuchal and one undivided supracaudal scute. However, in *T. marginata* the supracaudal plate is always disposed more horizontally, forming part of

Figure 12. Large female *Testudo marginata* with SCL 42 cm, held by Fritz Ludescher and found at Limni Amvrakia (Aetolokarnania, western mainland Greece) in 1982. Photo by Egbert Golz.

the posterior carapacial flaring with the marginal scutes. The flaring of the posterior marginals is usually more evident in males, but is also present in females. The species shows a wide variability in the shape of the carapace (more robust or slender) and serration of the marginals (slightly marked in individuals of the *weissingeri* ecotype; Bour 2004a).

According to Mayer (1992), adult Sardinian individuals can be differentiated from those from Greece by a less obvious serration of the posterior marginals. Individuals from Greece typically exhibit longer, more leaf-shaped, deeply serrated posterior marginals, whereas in those from Sardinia the posterior marginals are less protruding and more rounded, about one cm shorter than in Greek specimens of equivalent mass (Mayer 1992). We also found some large Sardinian individuals with smoothly rounded posterior marginals, lacking plate serration (Escoriza, unpubl. data), but it is not clear to what extent such variations also appear in Greek individuals. Mayer (1992) also noted some variation in the transition between the last vertebral and the supracaudal scute, which would be arranged perpendicularly in lateral view in Greek individuals and without forming a pronounced angle in lateral view in Sardinian individuals. However, we have observed some Sardinian individuals with almost perpendicular angulation between the fifth vertebral and the supracaudal scute. The carapace of hatchlings is more rounded or circular, without flaring on the marginals, which does not develop until an SCL of at least 12–14 cm is reached (Bour 2004a).

The plastron has six pairs of scutes, in which the abdominals are particularly large and the plastral formula (based on mid-seam contact lengths) is: abdominal > anal > humeral >< pectoral >< femoral > gular (Ernst and Barbour 1989). A central concavity of the plastron is present in males. The forelobe is upturned, tapered, and bulging anteriorly as in *T. graeca* (Ernst and Barbour 1989; Bringsøe et al. 2001). In old individuals, the posterior plastral lobe is feebly movable with a hinge between the hypoplastra and xiphiplastra, which corresponds to the abdominal-femoral seam (Bringsøe et al. 2001; Vlachos 2022). A single axillary and one or two moderately sized inguinals, which may touch the femoral plate, occur on the broad bridge (Ernst and Barbour 1989). The anal notch is V-shaped, with a wider opening in males.

In adults, the coloration is identical in both sexes. The ground color of the carapace is generally dark, black, or dark brown, although the center of the costals, vertebrals, and the posterior halves of the central marginal scutes (M4-M7/M8) can be lighter (yellow-white or orange). The coloration is very similar in the Sardinian populations, although Mayer (1992) reported that they could be less intensely black. However, almost completely black individuals of both sexes are common on Sardinia (Wegehaupt 2004; Escoriza 2008).

In hatchlings and juveniles, the ground coloration is lighter, brownish-yellow to cafe-au-lait brown, with contrasting black or brown elements. The dark elements on the costals and vertebrals are mainly located on the anterior and lateral edges, extending a bit to the center of these scutes and normally comprising more than half of the surface of each scute. In this way they form a vague, dark, horseshoe-like outline. The marginal scutes are particularly light-colored, with a faint dark pattern (limited to a band or triangle) in the front of the marginals which may even reach the costal-marginal and vertebral-marginal seams, but this dark coloration is usually indistinct or absent on marginals M5-M7. The juvenile pattern progressively darkens with growth. An albinistic juvenile from the vicinity of Olbia has been recorded (Bringsøe et al. 2001) as well as some cases of complete albinism on Sardinia (Forestas 2005).

The plastron has a yellowish background with darker, chevron-shaped markings (black with a slight garnet gradient on the edges) or sometimes otherwise irregular polygonal shapes on the pectoral, abdominal, femoral, and anal scutes (subtriangular on the abdominal, femoral, and anal scutes), more rarely also on the humeral and gular scutes. The diagnostic plastral chevrons are arranged symmetrically along the longitudinal axis. Seldom, the blotches can connect, particularly those on the humeral and abdominal scutes. The same pattern is present in juveniles, but the background color is usually lighter and the markings may be rather blurred. This

symmetrical plastral pattern easily differentiates this species from *T. hermanni* and *T. graeca*. The only other species in the genus that features this symmetric subtriangular pattern is *T. kleinmanni*, the phylogenetic sister species (van der Kuyl et al. 2002; Fritz et al. 2005; Thomson et al. 2021). On the other hand, the two species *T. marginata* and *T. kleinmanni* differ notably in their size and osteological structure of the shell, only sharing a similar shape of the pectoral-abdominal scute contact (Delfino et al. 2009).

The head is black, with black eyes and indistinct pupils. The cephalic scales are dark and defined with clear margins. The prefrontal and frontal scales are single and very large, while the frontoparietal and temporal scales are asymmetrical and irregularly shaped. Juveniles exhibit a yellowish head and limbs, with small diffuse dark spots. Like the carapace, this coloration darkens with increasing growth.

In *T. marginata* two small spurs may occur on the posterior thighs, as in *T. graeca* (Perälä 2002; Escoriza et al. 2022), although they are usually smaller or absent (de Broin et al. 2006). The limbs have large imbricate triangular scales in 5–6 longitudinal series; there are 5 claws on the forelimbs and 4 on the hindlimbs. The leg scales are black, but those on the inner part of the limbs are a lighter color, orange or vanilla yellow. The tail is relatively shorter than in other species of the genus, particularly when compared to *T. hermanni*. The tail lacks a well-defined terminal horny scale or claw. The tail is thicker and larger in males, and the cloaca of the male is more distal. The tip of the tail is dark, but the tail becomes lighter at its base.

The karyotype is 2n = 52 (Belcheva et al. 1990), consisting of 14 pairs of macrochromosomes which are divided into two groups (group A: 9 pairs; group B: 5 pairs), and 12 pairs of microchromosomes (group C). In group A, the first and second pairs are comprised of large submetacentric chromosomes. The fifth, seventh and eighth pairs are also submetacentric, but are considerably smaller. The third, fourth, sixth and ninth pairs are metacentric. In group B, the first and second chromosome pairs are subtelocentric, whereas the other pairs are acrocentric. No sex chromosomes have been recorded. The karyotype of *T. marginata* is very similar to those of *T. graeca* and *T. hermanni* (Belcheva et al. 1990).

Distribution. — *Testudo marginata* is native to Greece and the southern tip of Albania. It has been introduced to northern Sardinia in historical times. During the Pleistocene and early Holocene, it was also present on Crete and the Aegean islands of Kos and Tilos (Charkadio Cave, 4–7 kya; Bachmayer and Symeonidis 1975; Vlachos 2015, 2022).

In Greece, *T. marginata* is widely represented from the eastern slopes of Mount Vermio on the northern mainland (but absent from the northeastern part), throughout most of the west and southern edges of the country, including the Peloponnese peninsula (Loumbourdis and Kattoulas 1983; Reynolds 1984; Keymar and Weissinger 1987; Bour 1996; Bringsøe et al. 2001; TTWG 2021). The oldest fossil records of *T. marginata* are from the Early Pleistocene of Lakonia, southern Peloponnese (Schleich 1982a). The species also naturally occurs on several Aegean and Ionian islands: Alonissos, Dokos, Elafonisos, Evvia, Kastos, Kyra Panagia, Kythera, Petalas, Poros, Psili, Romvi, Salamina, Sapientza, Sfaktiria, Skiathos, Skyros, Spetses, Spetsopoula, Trizonia, and Valaxa (Watson 1962; Gruber and Fuchs 1977; Kock and Storch 1979; Bringsøe 1986; Clark 1989; Cattaneo 1997; Chondropoulos and Chiras 1997; Bringsøe et al. 2001; Broggi 2010, 2016a,b; Tzoras et al. 2019, 2023).

Incidental cases of translocations in Greece have been recorded outside of its native range, where it has been cited both in continental (e.g., from the peri-urban forest Seich Sou, Thessaloniki city [Strachinis 2023]), and insular Greece (e.g., Amorgos, Andros, Chios, Corfu, Kefalonia, Lefkada, Lesvos, Milos, Naxos, Paros, Samos, and Syros [Clark 1970; Cattaneo 1984; Dimitropoulos 1987; Keymar and Weissinger 1987; Tsunis and Dimitropoulos 1994; Bringsøe et al. 2001; Hofstra 2003, 2008; Broggi 2007; Sindaco and Rossi 2020; Tzoras et al. 2021]). Established introduced populations exist on Chios and Lesvos islands, where the species has been detected in great numbers (Dimitropoulos 1987; Tsunis and Dimitropoulos 1994; Hofstra 2003). On Corfu, there are several recent and old records from the 1970s of isolated individuals in the northeastern and central parts of the island, but they were introduced by humans and populations have never become established (Stille and Stille 2017).

In Albania, the species occurs in the southwestern part of the country across the border from Greece, having a very restricted distribution in certain regions, i.e., Çuke Ksamil, Butrinti, Saranda, Mali i Stillos, and Konispoli (Haxhiu 1995, 1998; Mizsei et al. 2017). Currently, it is known from the highlands of Gjirokastra and the mountainous zones of Saranda and Delvina (Oruçi 2010).

On Crete, fossil remains of *T. marginata* have been found in various archaeological sites in northwestern Crete (Late Pleistocene): Bate, Gerani, Simonelli and Zourida (Bachmayer et al. 1975; Kotsakis 1977; Brinkerink 1996; Vlachos 2022). Gerani cave (Rethymno) is the Pleistocene type locality of the form *T. m. cretensis* (Bachmayer et al. 1975), which was present on Crete throughout the Pleistocene, becoming extirpated from there at the end of this period for unknown reasons (Vlachos 2022). However, an anthropogenic cause cannot be ruled out due to the abundance of remains (including tortoise limbs) suggesting prehistoric human consumption of tortoises (Georgalis and Kear 2013; see also TEWG 2015). More recently, a decaying carapace was found on the northern coast of Crete (at Stalida); it was assumed to have come from a released or escaped pet (Hofstra 2000).

On northern Sardinia, the presence of this species has been reported since the end of the 19th century (Giglioli 1879; Angelini 1899, 1907; Siebenrock 1906). The first records came from the region of Sassari (Terranova), where the species is still present. At that time, the population was

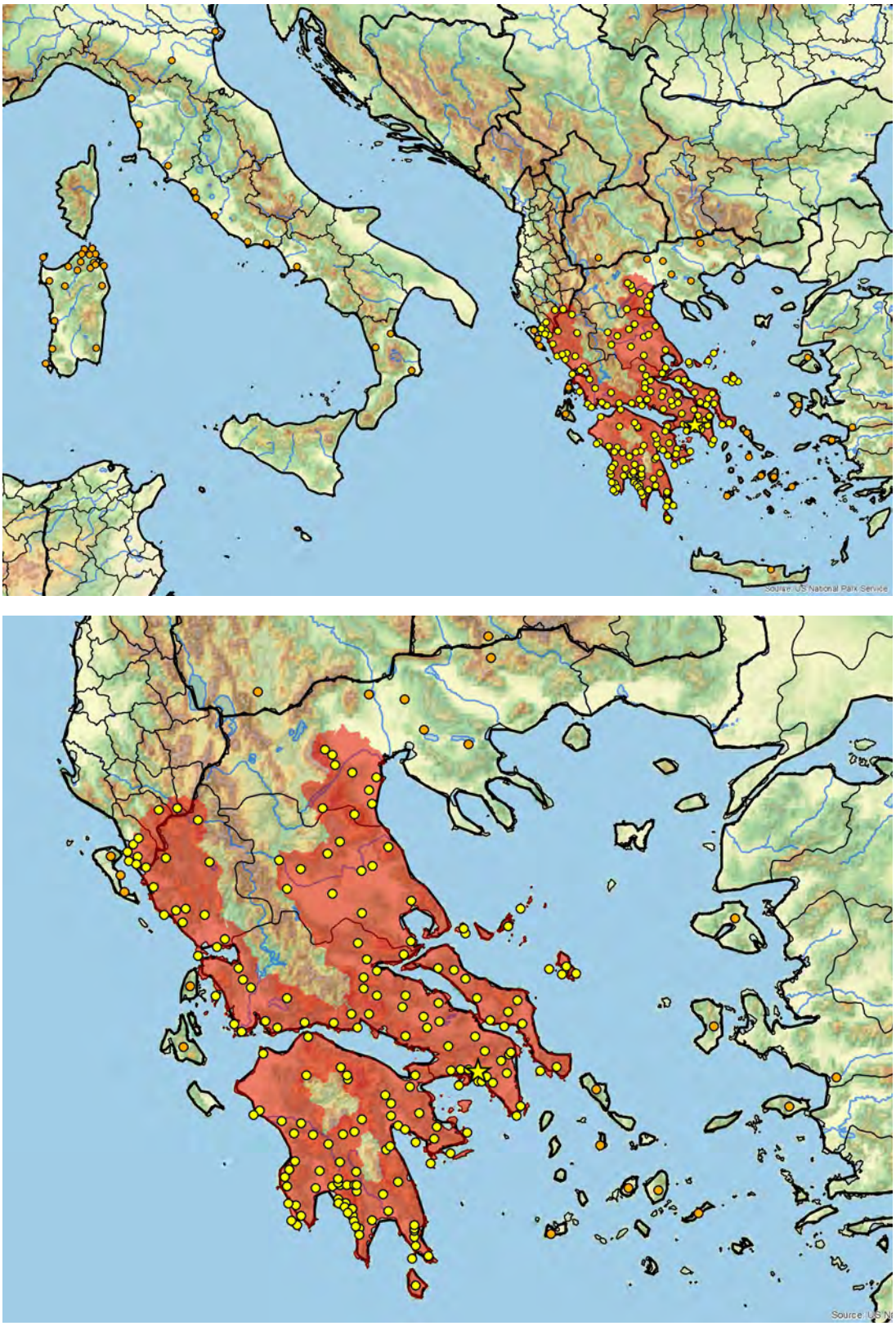

Figure 13. Distribution of *Testudo marginata* in the wider Mediterranean region (*top*) and in Albania and Greece (*bottom*). Yellow dots = museum and literature occurrence records of native populations based on Iverson (1992), other more recent literature records (see TTWG 2021), and authors' additional data; orange dots = introduced or possibly historically relict populations or individual trade or translocated specimens; yellow star = restricted estimated type locality. Distribution based on fine-scaled GIS-defined level 12 HUCs (hydrologic unit compartments) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs based on Buhlmann et al. (2009), TTWG (2017, 2021), and data from authors and other sources.

reported to be abundant, with several age groups (juveniles to adults of 5–6 kg), suggesting that they were already naturalized (Angelini 1907). Bruno (1986) proposed that the origin of these populations could be dated from the end of the 18th century and that they were introduced by Franciscan monks, who would use the tortoises as food during liturgical fasting. Now and then it has been postulated that *T. marginata* was originally introduced to Sardinia during World War II; however, the records from the literature of the late 19th century rule out that explanation (Mayer 1992). It is also feasible that there may have been repeated introductory events onto Sardinia (Tiedemann 1978; Bruno 1986; Perez et al. 2012). No fossil remains of *T. marginata* have been found on the island, which supports the hypothesis of an allochthonous origin of this species (Zoboli et al. 2022).

Currently *T. marginata* is found throughout northeastern Sardinia, between Castelsardo to the west and Olbia to the east, reaching the Mount Albo massif (Siniscola), and with some isolated records in the province of Oristano: Sinis Peninsula and Bosa (Corti 2016; Mulargia et al. 2018; Leonetti et al. 2020). It also appears on some satellite islands and in La Maddalena archipelago (Budelli, Caprera, Cala Santa Maria, La Maddalena, and Santo Stefano), Tavolara, Molara, San Pietro and Piana di Asinara (Cesaraccio and Lanza 1984; Poggesi et al. 1996; Bassu et al. 2008).

On the Italian mainland there are occasional and isolated records of the occurrence of *T. marginata* in the Tyrrhenian and Adriatic coastal regions of the central and southern peninsula (Bruno 1986; Carpaneto 2006): Calabria, Campania (surroundings of Napoli), Emilia-Romagna (Riserva Naturale del Boscone della Mesola), Lazio , Marches, Molise and Tuscany (Cecina, Parco Naturale della Maremma, San Rossore, and Tombolo), although naturalization has not been confirmed in any of these localities (Carpaneto 2006; Philippen 2008; Sperone et al. 2010; Corti 2016; Ferri et al. 2020; Leonetti et al. 2020). In Calabria, it has been found at several localities: Roccabernarda, Rose, San Vicenzo La Costa and Tarsia, in a range of elevations between 160–800 m (Sperone et al. 2010; Leonetti et al. 2020). In Tuscany, it has been found between 20–800 m, in Viterbo (Carpaneto 2006). In Lazio, the first record was from the Parco Nazionale del Circeo (Latina) (Carpaneto 1986), but it has subsequently been found in other reserves: Parco Regionale Riviera di Ulisse (Latina), Oasi WWF Macchia Grande (Fiumicino), Monumento Naturale La Frasca (Civitavecchia), and Riserva Naturale Saline di Tarquinia (Tarquinia) (Ferri et al. 2020).

Figure 14. Dorsal (left) and ventral (right) views of the shell of the holotype of *Testudo marginata cretensis* † (AMPG 3/1974) from the Pleistocene of Gerani Cave (Rethymnon, northwestern Crete). Photos by Evangelos Vlachos.

Overall, the records from the Italian peninsula are more common in disturbed habitats near settlements (e.g., edges of cultivated areas), which suggests recent translocations (Carpaneto 2006; Sperone et al. 2010). However, the presence of carapace remains of *T. marginata* in some archaeological sites of Etruria (Tuscany and Latium) suggests much older introductions, perhaps mediated by Phoenicians, Greeks, or Romans, dated approximately from 2.5 kya (Ballasina 1995). Archaeological remains of this species (and *T. graeca*) have also been reported in southern Italy (Puglia, Basilicata, Calabria) and it is possible that the shells were used to build musical instruments (Delfino 2020).

Boscà (1880) reported the presence of *T. marginata* in southern Spain around Almonte and Rosio (El Rocio, Huelva), but these citations should be attributed to *T. graeca whitei*, still present in eastern Huelva (Escoriza et al. 2022). In Spain, *T. marginata* became popular as a pet after the trade of native tortoises was banned during the 1980s, and it is often bred in private gardens. Accidentally escaped individuals have been recorded in the coastal regions around the city of Barcelona (El Garraf, Alella, and Teia) and in the Serra de l'Albera, Girona (Soler et al. 2010; Pfau and Budó 2019; Pfau et al. 2020; Martínez-Silvestre, Soler, and Franch, unpubl. data). These records correspond to isolated adult and juvenile individuals (Pfau and Budó 2019). There are apparently no naturalized populations in Spain (Martínez-Silvestre, Soler, and Budó, pers. comm.).

It is unlikely that any native or introduced populations of *T. marginata* occur in Turkey. A single individual found in the vicinity of the ancient city of Ephesus was recorded by Brinckmeier et al. (1989); however, careful and repeated searches by Türkozan et al. (2001) proved unsuccessful, and it was concluded that *T. marginata* is unlikely to occur in the Ephesus region or elsewhere in Turkey. This conclusion was later echoed by Franzen et al. (2008), who added that the earlier record might have been due to misidentification of a *T. graeca*.

On Cyprus, single records of released or escaped individuals have been cited in the past, e.g. around Paphos on southwestern Cyprus (Demetropoulos and Lambert 1986; Hadjisterkotis and Reese 1994), but stable populations of *T. marginata* are not present on the island (Baier et al. 2013).

The species has also been listed as occurring in the Maghreb, Libya (Peters 1880; Luiselli et al. 2012), possibly due to confusion with *T. kleinmanni* (Bauer et al. 2017). In

Figure 15. Habitats of *Testudo marginata*. **A.** Low phrygana formations on Skyros Island, Aegean Sea, Greece. **B.** Phrygana vegetation with sparse Aleppo Pines on Trizonia Island, Gorinthian Gulf, Greece. **C.** Rocky terrain in dense forest of wild olive trees close to Neochori, southwestern mainland, Greece. **D.** Coastal sand dunes at Strofylia National Park, northwestern Peloponnese peninsula, Greece. **E.** Dense macchia vegetation with sporadic wild olive trees on Kastos islet, Ionian Sea, Greece. **F.** Dry valley next to sparse forest of wild olive trees and oaks on Petalas islet, Ionian Sea, Greece. Photos by Elias Tzoras.

Algeria, *T. marginata* (as "*la tortue bordée*") was reported to be common around Pélissier (currently Sayada, Mostaganem) by the herpetologist Lallemant (Doumergue 1901). However, its presence in Algeria was ruled out by Doumergue who used the absence of spurs on the thighs to distinguish *T. marginata* from *T. graeca*.

Habitat and Ecology. — *Testudo marginata* occurs exclusively in warm, scorched-dry (xeric) to sub-humid Mediterranean climates (*Csa*, with hot summer), following the climate classes of the Köppen classification (Beck et al. 2018). Based on GIS-supported climate models (Fick and Hijmans 2017), populations in the extreme southern Balkans (Greece and Albania) occupy a region with average annual temperatures of 16°C with average annual rainfall of 664 mm. The populations on Sardinia occupy a climatically similar region, although slightly drier, with mean annual temperatures of ca. 16°C and with average annual rainfall of 499 mm. In contrast, the sister species *T. kleinmanni* occupies a much warmer and more arid climatic environment (20°C; 176 mm/y), indicating low phylogenetic niche inertia

Figure 16. Habitats of *Testudo marginata* (dwarf form, *weissingeri* ecotype). *Left*. Hilly macchia habitat, at Eleochori, Mani peninsula, southern Peloponnese, Greece. *Right*. Olive groves with minor areas of other crops at Exochori, Mani peninsula, southern Peloponnese, Greece. Photos by Henrik Bringsøe.

Figure 17. Habitats of *Testudo marginata* in Sardinia. *Left*. Low montane subhumid macchia of *Pistacia lentiscus* and *Rhamnus alaternus* interspersed with open forest pastures. *Right*. Rocky coastal habitat with scattered shrubby formations of *Juniperus phoenicia turbinata* and *Cistus monspeliensis*. Photos by Daniel Escoriza.

during the evolutionary divergence of this clade (Escoriza and Ben Hassine 2022).

Statistical models have suggested a potentially more extensive distribution of *T. marginata* in the Mediterranean based upon current climatic conditions (Escoriza and Ben Hassine 2022). These models also suggested that the glacial refugia of *T. marginata* would have been confined to the coastal regions of the Peloponnese and on the island of Crete. Therefore, the extirpation of *T. marginata* from Crete can probably not be attributed to climatic causes, given that this island has maintained stable conditions for this species throughout the Pleistocene (Escoriza and Ben Hassine 2022). The limited geographic range of the glacial refugia could also explain the current distribution of *T. marginata*, which may have slowed or stopped its post-glacial expansion by secondary contact with *T. graeca* in northeastern Greece (Thrace), while the northwestern parts of the Balkans are mostly unsuitable for *T. marginata* (Escoriza and Ben Hassine 2022). The persistence of this species during the last glacial maximum on the southern Peloponnese (Mani peninsula) is also supported by fossil remains found in Kalamakia cave, where *T. marginata* appears together with *T. hermanni* and a wide array of squamate reptiles, including thermophilic snake species like *Eryx jaculus* and *Zamenis situla* (Harvati et al. 2013).

In Greece, *T. marginata* occurs up to 1600 m asl, but is more frequently observed at lower elevations, where it shares habitat with the coexisting *T. hermanni,* although it has proved less abundant and prefers somewhat more elevated habitats (Buttler et al. 1982; Kordges 1984; Kordges and Hemmer 1987; Bringsøe et al. 2001; Bour 2004a). In this elevational range it occupies a wide range of habitats, but it is more common in rocky and open habitats, with abundant shrubby vegetation (Bour 2004a). The typical Greek habitat of *T. marginata* consists of macchia habitat with scrub vegetation which may be impenetrable, generally 1.5–3.5 m tall and largely composed of evergreen sclerophyllous plants. To a lesser extent, similar phrygana habitat is also occupied, namely an open dwarf scrub dominated by low, often cushion-shaped, aromatic, spiny or gray-leaved shrubs, rarely exceeding 60 cm in height. Occasionally, *T. marginata* also occurs in garrigue habitats, which are often equated with phrygana, but they differ in being a type of dense, spiny evergreen scrub generally 60–120 cm tall and influenced by cutting and grazing. These definitions of vegetation habitat types follow Strid and Tan (1997). Common shrubs and

smaller plants in these habitats are *Sarcopoterium spinosum*, *Calicotome villosa*, *Genista acanthoclada*, *Euphorbia acanthothamnos*, *Cistus* spp., *Erica manipuliflora*, *Phlomis fructicosa,* and *Salvia pomifera* (Bringsøe et al. 2001). Furthermore, the following oak trees with a shrub-like growth are common in these habitats: *Quercus coccifera*, *Q. ilex,* and *Q. pubescens*. Olive groves with *Olea europaea* and stone terraces form a suitable habitat for *T. marginata* throughout low and moderate altitudes of its natural range. At its upper altitudinal range in the northern Taygetos mountains on the Mani peninsula on the southern Peloponnese, it occurs at the margins of dense coniferous forests, dominated by Greek Firs, *Abies cephalonica* (Escoriza, unpubl. data).

On the southwestern mainland and the northwestern Peloponnese peninsula, the species inhabits deltas and coastal sand dunes composed of sparse shrubs of Oleander (*Nerium oleander*) and Junipers (*Juniperus* spp.), and Aleppo Pine (*Pinus halepensis*) (Buttler et al 1982; Kordges 1984; Kordges and Hemmer 1987; Artner 1998; Bringsøe et al. 2001; Mamasis and Tzoras 2021). The *weissingeri* ecotype was initially considered to be confined to an elevational range between 0–600 m on the western flank of the Taygetos mountains on the Mani peninsula on the southern Peloponnese (between Kalamata and Areopolis; Bour 2004b). In this region it occupies both sparsely vegetated habitats (near Kardamili) dominated by thorny bushes, to dense shrubby areas and olive groves in rocky terrain with steep slopes (Artner 2000; Bour 2004b).

On Kyra Panagia islet (Sporades archipelago, Aegean Sea), *T. marginata* inhabits stone fields in macchia vegetation (Kock and Storch 1979). On the island of Salamina, it occupies macchia vegetation on hillsides (Bringsøe 1986). On Skiathos island, the species has been found in macchia vegetation bordering fields of Olive trees (*Olea europaea*) (Cattaneo 1997). On Sfaktiria islet (Ionian Sea) macchia habitats with *Arbutus* spp., *Phillyrea latifolia*, *Q. coccifera*, and *Pistacia lentiscus* are occupied, while on the adjoining islet of Sapietza (Ionian Sea), the species is present among Kermes Oaks (*Q. coccifera*) and Lentisk (*P. lentiscus*) (Chondropoulos and Chiras 1997). On Trizonia island in the Corinthian Gulf, *T. marginata* prefers dense shrubby formations of *P. lentiscus* and phrygana formed by *Sarcopoterium spinosum*, where these plants frequently are mixed with olive trees and Aleppo Pines (Tzoras, unpubl. data). On Kastos and Petalas islets, it occupies openings in dense macchia vegetation usually composed of Lentisk bushes (*P. lentiscus*) and sparse forests of olive trees and oaks (Tzoras et al., in press).

A habitat occupied by *T. marginata* and *T. hermanni* in the Feneos Basin of the Peloponnese was dominated by oak forest (44%), mixed forest (12%), burned forest (11%), and to smaller extents, open pasture, meadow, fir forest, and macchia (Koppitz et al. 2016, 2017); *T. marginata* selected roughly the same percentages of vegetation types, but with a slightly higher proportion of mixed forest and open pasture than *T. hermanni,* whereas *T. hermanni* was more prevalently associated with oak forest and dense shrubby vegetation (macchia).

It has been hypothesized that the elongated shape of *T. marginata* is an adaptation to life in its typical densely vegetated habitat, because this species has not been observed trapped in thick vegetation, whereas *T. graeca* and *T. hermanni* have both been (Willemsen and Hailey 2003).

In Albania, the species appears in rocky and densely vegetated valleys (Haxhiu 1998). It is mostly observed at low altitudes, as high as 500 m above sea level, and more rarely at higher elevations, between 1100 and 1300 m (Oruçi 2010; Mizsei et al. 2017). In southern Albania, it can also be found coexisting with *T. hermanni* (Bruno 1989).

On Sardinia, *T. marginata* occurs from sea level to 600 m, but more frequently between 0–440 m (Sperone et al. 2010; Di Nicola and Mezzadri 2018). It is sympatric with *T. hermanni* in a few localities in the Gallura region; *T. hermanni* is more frequent in the northwestern region of Sardinia where *T. marginata* is occasionally recorded, but probably not established (Corti et al. 2013). The two species also coexist on some small islands northeast of Sardinia: Santa Maria, La Maddalena, Caprera, Tavolara, and Molara (Sindaco et al. 2007). The third species of tortoise also present on Sardinia, *T. graeca nabeulensis*, is mostly confined to the southwest and southeast of the island (Escoriza 2008). In this way, the three species of *Testudo* present on Sardinia are distributed nearly allopatrically, with very limited sympatry (Bassu et al. 2008; Corti et al. 2013).

In northeastern Sardinia, *T. marginata* occupies open habitats, including dunes and retro-dunal habitats, dense shrubby formations (macchia), meadow forests, and occasionally traditional agriculture fields (olive groves) (Cimatti 2007; Di Nicola and Mezzadri 2018; Escoriza, unpubl. data). For example, a coastal habitat occupied by this species in Gallura (elevation = 72 m) was composed of 80% bushes (maximum height 145 cm), 15% stones, and 5% herbs (Escoriza, unpubl. data). This community was dominated by perennial bushes, *Pistacia lentiscus* (33%), *Euphorbia pithyusa* (20%), *Juniperus phoenicea turbinata* (20%), *Crithmum maritimum* (15%), and *Phillyrea angustifolia* (12%); i.e., thermophilic and salt-tolerant littoral species (Jeanmonod and Gamisans 2007). In a macchia habitat occupied by this species at low- to mid-elevation (302 m), the vegetation was composed of 65% bushes, 15% herbs, 10% rock and stones, 5% trees (maximum height 310 cm), and 5% bare ground (Escoriza, unpubl. data). The plant community was more diverse than in the coastal habitat: *Calicotome villosa* (25%), *Erica arborea* (12%), *Cistus monspeliensis* (10%), *Rubus ulmifolius* (10%), *Phillyrea angustifolia* (9%), *Lavandula stoechas* (8%), *Cistus salviifolius* (8%), *Arbutus unedo* (7%), *Cistus halimifolium* (4%), *Daphne gnidium* (3%), *Genista corsica* (2%), and *Myrtus communis* (1%), i.e., macchia habitat evolutionarily transitional to forest (Jeanmonod and Gamisans 2007).

Figure 18. Adult *Testudo marginata* in its overnight retreat, partly hidden under a rock. West of Delfi, central Greece. Photo by Henrik Bringsøe.

Juveniles of *T. marginata* are more secretive than adults and are often found hidden under rocks and other objects (see Bringsøe 1986). The microclimate of such places is relatively humid, which may be favorable to juveniles. Adema and In den Bosch (1980) even found a muddy juvenile in a swampy habitat near Levadia in central Greece.

Daily Activity. — *Testudo marginata* is exclusively diurnal throughout its distribution (Bringsøe et al. 2001; Cimatti 2020). It thermoregulates by basking and is typically active with average body temperature ranging between 26.8 and 31.6°C, beginning its activity with an air temperature of 18°C and body temperature of 20°C, as observed in captivity (Andrews 1989).

In a population near Gythio, southern Peloponnese, Willemsen (1991) studied activities and thermoregulation during the active season. The activity pattern was unimodal in spring, but already in May it had become bimodal, which continued during the summer with very limited activity in August. In autumn it was again unimodal, shifting towards the middle of the day, with high activity in October. The frequency of feeding in *T. marginata* was 47% in May, 40% in June and 46% in October. During May a maximum body temperature of 36°C was found in basking individuals and a maximum of 37°C in feeding tortoises, which is higher than in the syntopic *T. hermanni* (i.e., *T. marginata* has a higher body temperature tolerance). In all the samples of Willemsen's (1991) study, the body temperature of *T. marginata* was significantly higher than in *T. hermanni*, and specifically in feeding individuals the body temperature of *T. marginata* was 3°C higher than in *T. hermanni*. However, Panagiota and Valakos (1992) found no difference in body temperature between *T. marginata* and *T. hermanni,* though *T. marginata* tolerated lower temperatures.

Clark (1963) observed that *T. marginata* (misidentified as *T. graeca* [Clark 1997]) exhibited pronounced autumn activity on the Greek island of Spetses at the onset of rains at the end of September. According to Bour (2004b), the *weissingeri* ecotype on the western Mani peninsula exhibits a bimodal activity pattern in spring and autumn, whereas no tortoises were found from mid-June through September, which was interpreted as estivation.

On Sardinia, activity is intermittent shortly after hibernation, with basking in the middle of the day (1200–1500 hrs) as tortoises move little and usually remain in the vicinity of the winter shelter. Activity gradually increases at the end of March, and is only interrupted on rainy or cloudy days. Activity progressively becomes bimodal in April, with feeding early in the morning and late in the afternoon and reducing activity in the middle of the day (1100–1600 hrs) (Escoriza, unpubl. data). Cimatti (2007, 2020) also described a bimodal pattern of activity, but starting in May, and avoiding the middle of the day. During this period, the tortoises, except for some adult males, reduced their activity considerably and remained close to the summer refuge. According to this author, the activity becomes unimodal in August as it only appears in the late afternoon. In October the activity is also unimodal, but during the central hours of the day (Cimatti 2007, 2020).

Annual Activity. — Panagiota and Valakos (1992) measured body temperatures throughout the year for *T. marginata* in an outdoor enclosure of 150 m^2 in Attica, Greece. The authors provided the following average daily temperature values for the individual seasons: spring (March to May) 26.9°C, summer (June to August) 30.0°C, autumn (October) 18.8°C, and winter (November, February) 13.6°C. The entire temperature range was 8.0–34.7°C. At lower temperatures the tortoises were inactive, whereas they retreated into shade at higher temperatures. For the entire year an average body temperature of 25°C was calculated. Overall, *T. marginata* is considered a thermoconformer due to the concordance between the body temperatures and the corresponding monthly air temperatures (Panagiota and Valakos 1992).

On the Mani peninsula on the southern Peloponnese, Bour (1996) mentioned a brief hibernation from mid-December to late January, but later concluded that the tortoises do not really hibernate, instead they just reduce their activity during the coldest winter periods and enter a state of dormancy during the coldest days (Bour 2004b). These tortoises may take refuge in burrows several meters long when available, in which up to 6–8 individuals can be found (Bour 2004b). After emerging in early spring, tortoises

remain active until mid-June, when they begin an estivation period that lasts until September.

Seasonal variation in body mass condition at various sites in Greece was recorded by Willemsen and Hailey (2002), who noted that the condition index was highest in summer with a peak in July.

Generally, in its overall distribution, *T. marginata* will hibernate at low temperatures, but some individuals bask in sunny weather at ca. 8°C. Contrary to *T. hermanni*, *T. marginata* does not hibernate buried in the soil (Panagiota and Valakos 1992). Under such circumstances, hibernating *T. marginata* may become exposed to severe frost, especially in montane environments. Under naturalized captive conditions (a fenced area) at Platamona (100 m asl) at the foot of Mts. Ossa and Olympos in northern Greece, hibernating *T. marginata* were exposed to freezing ground temperatures down to –12°C; they appeared frozen and even frozen to the ground (Bringsøe 2002). However, all tortoises survived and two weeks later three individuals were observed basking at 8°C. In a *T. marginata* habitat on Mt. Ossa (850 m asl) a lower temperature of –22°C was recorded during the same time period; it is likely that the tortoises were exposed to these low temperatures and also survived. On Mt. Olympos, a few *T. marginata* were even observed basking at –3°C (Pitzer 2016), and it was noted that several individuals became active under favorable and sunny conditions during the winter. Pitzer (2016) speculated that *T. marginata* probably contains cryoprotectants, thus tolerating the freezing of extracellular body fluids while overwintering. But freeze avoidance through supercooling may be more likely than direct freeze tolerance, as per studies of North American turtles (Costanzo and Lee 2013).

In the northern coastal regions of Sardinia, adults can be found outside of winter shelters in mid-February and remain active to late October or early November. Cimatti (2020) reported that surface activity restarted with air temperatures of 8–10°C, and feeding resumed at 18°C. On Sardinia, most individuals do not apparently estivate, but strongly reduce their activity, mostly constrained to the early hours of the morning and late afternoon, between the end of June and the beginning of September (Escoriza, unpubl. data). Cimatti (2007) reported a period of maximum activity in spring and autumn, with a period of winter dormancy, in which, however, some adult males exhibited basking activity on the warmest days.

Home Range. — Some authors have described *T. marginata* as an animal that exhibits site fidelity (e.g., Koppitz et al. 2017). Out of 183 *T. marginata* recorded in their study in the Feneos Basin from 2005 to 2015, 51 were recaptured in different years. Of these 51 tortoises, 23 were observed in the study area up to 10 years after the first observation, confirming their long-term stationary or sedentary behavior (Koppitz et al. 2017). Additionally, 91 individuals (sex ratio close to 1:1) were found at three or more places and 20 of these were recorded more than three times in different years. Nine of these 20 (four males and five females) were highly stationary, with one male occupying a small range of <1 ha. Other individuals moved more; e.g., one female was constantly found at different sites throughout the years and in three days in May had moved a total of 860 m. Pairs often stay close together (Hine 1982; Bringsøe, unpubl. data).

Reproduction. — Sexual maturity is achieved at 6–8 yrs in males and 10–12 yrs in females, with a minimum body mass of 2300 g in captive females (Heimann 2016; Cimatti 2020). During courtship the male approaches the female and positions himself in front of her, with horizontal, and to a lesser degree vertical, oscillating movements of the head, interspersed with biting her forelegs and neck, sometimes ramming her carapace with his (Bringsøe et al. 2001; Willemsen and Hailey 2003; Bour 2004a). Biting may cause serious wounds on the female's forelegs as some scutes can be torn off; the breaking of the leg scutes can be heard over distances of more than 10 m. It has been observed in captivity that females can suffer carapace lesions, even losing some costal scutes during this aggressive courtship (Coutard 2006). The female displays her disposition by remaining still and retracting her head and forelimbs. Males emit loud vocalizations during copulation, which lasts between 5 and 30 min and can be repeated several times during the day (Trutnau 1994, captive individuals). Male mounting success is positively associated with a larger size of the male relative to the female, with the number of bites and rams, and with the duration of vocalizations emitted during mating (Sacchi et al. 2003, captive individuals). In addition, the frequency of vocalizations is associated with male body mass, which could indicate to other nearby females or males the body fitness of that male (Sacchi et al. 2003). Courtship behavior is similar in Sardinian populations, and includes aggressive interactions of the male towards the female, including biting and carapace ramming (Cimatti 2007).

Clark (1963) was first to note increased sexual activity in *T. marginata* in the autumn. At Gythio, Willemsen (1991) recorded mating activity mainly in October ($n = 9$) and to a small extent in May ($n = 1$). Similarly, for the *weissingeri* ecotype in the western parts of the Mani peninsula, Bour (1996) only observed mating activity (and male-male combat behavior) in October. But in some cases, mating may occur occasionally on warm winter days, especially in late February (Tzoras, unpubl. data). It has been hypothesized that large size in male *T. marginata* is more related to success in courtship than aggressive behavior (Willemsen and Hailey 2003).

Females nest from late April to August, and lay up to 3 clutches of hard-shelled eggs in a season. On the lower slopes of Mt. Olympos in northern Greece, Hailey and Loumbourdis (1988) recorded an average of 2.6 ± 0.7 clutches per year, with a clutch size of 4–7 eggs (average 5.6). Considerably larger clutch sizes in the wild are well known, for instance 9 eggs per clutch on Sardinia, 10 eggs on Romvi Island (previously called Tolo Island) off the northeastern Peloponnese, and even up to 15 eggs at Skroponeria Bay in central Greece

(Hine 1982; Bringsøe et al. 2001). Under captive conditions, the number of eggs per clutch is positively related to the size of the female, with a ratio of body mass of 0.20–0.28 kg/egg (Collins 1980). According to some authors, the dwarf ecotype *weissingeri* lays fewer eggs per clutch (mean 5.8 eggs vs. 6.6 eggs in the larger ecotype) and also fewer clutches per year (1–2 vs. 2–3; Coutard 2006, captive individuals). The literature has provided additional data from individuals kept in captivity: average clutch sizes range between 5.8 and 13.0 eggs, with egg sizes 31.9–34.2 mm x 28.6–32.0 mm, and egg masses between 14.4 and 18.4 g. Clutch mass ranges between 83.5 and 184.4 g, which constitutes 4.3–4.8% of the of female's gravid body mass (Stemmler-Gyger 1964; Rohr 1970; Collins 1980; Heimann 1987; Artner 1998; Lesueur 2002; Coutard 2006).

Under captive conditions, the female actively selects loose soil exposed to the sun to build the nest and normally requires between 20 min and 2 hrs to dig the nest cavity. During the process it urinates frequently which makes the digging process easier (Collins 1980). A typical nest is about 15 cm deep, bell-shaped, with the widest part at the bottom chamber (Collins 1980; Trutnau 1994). Eggs are laid at 2–3 min intervals each and have a protective fluid that envelops them and are rarely broken during this process (2.3%, in a period of 4 years; Collins 1980, in captivity).

Generally, the egg length is 33–34 mm and the width 29–30 mm (Hailey and Loumbourdis 1988), but these dimensions are variable and the length may range from 29 to 37 mm and the width from 27 to 36 mm (Bringsøe et al. 2001). Usually the eggs are almost spherical (usually more spherical than in other species of the genus; Coutard 2006), but some eggs are noticeably oval (Hailey and Loumbourdis 1988). Eggs incubated at 30–35°C hatch after 60–70 days, and hatchlings measure 34–36 mm SCL with a body mass of about 12 g (Hailey and Loumbourdis 1990; Bringsøe et al. 2001; Coutard 2006). On the southern Peloponnese, the clutches of the small *weissingeri* ecotype consist of 2–4 eggs, measuring on average 34.6 x 30.5 mm (range, 31–36 x 28–32 mm) and the SCL of hatchlings is 35–42 mm, with a body mass of about 10.7 g (Bour 1996; Coutard 2006).

On Sardinia, data on reproduction are scarce. According to Cimatti (2007), mating occurs in the spring. Egg deposition takes place at the beginning of summer and clutches consist of 6–8 eggs (exceptionally 10–11), which hatch after 2–3 months, at the end of summer or beginning of autumn (Cimatti 2007).

Hailey and Loumbourdis (1990) recorded average hatchling wet mass/egg wet mass as 60.5%, which was less than in *T. graeca* (61.7%) and *T. hermanni* (63.2%). The corresponding hatchling dry mass/egg wet mass was 17.6% in *T. marginata,* being slightly less than in *T. graeca* (18.0%), but much higher than that of *T. hermanni* (12.9%).

Testudo marginata has temperature-dependent sex determination, TSD type Ia, where low temperatures (26–28°C) produce a predominance of males, while higher temperatures produce females (Heimann 2016; Krueger 2021; in captivity); however, observations to date have not been made under controlled laboratory conditions. In a few cases twins have developed from a single egg, once in a clutch detected in the wild (Dimitropoulos 1985) and in three cases in captivity (Heimann 1993).

Diet. — *Testudo marginata* is a generalist herbivore subsisting on many different native plant species and some recently introduced ones, such as cacti of the introduced genus *Opuntia* (Di Nicola and Mezzadri 2018). The diet consists of a wide variety of plant matter, especially monocotyledonous and dicotyledonous species. Strongly aromatic plants like *Thymus capitatus* are usually avoided (Bringsøe et al. 2001). Common food plants (summarized by Bringsøe et al. 2001) are *Dianthus multipunctatus*, *Anemone coronaria*, *Medicago orbicularis*, *Trifolium stellatum*, *Anagallis arvensis*, *Cyclamen persicum*, *Plantago lagopus*, *Anthemis* spp., *Calendula arvensis*, *Leontodon tuberosus*, *Sonchus* spp., *Taraxacum officinale*, *Muscari parviflorum*, *Ornithogalum tenuifolium*, *Asphodelus* spp., and *Drimia* (= *Urginea*) *maritima*. Particularly *D. maritima* is frequently eaten; fresh and withered leaves are consumed and the bulb is gnawed if exposed at the surface, although the plant is toxic to mammals, including humans (Bringsøe et al. 2001). Bite marks on its leaves are a good indicator of the presence of *T. marginata*. During hot and dry summer periods, the bulbs of *Asphodelus* spp. are eaten. Various succulents and grasses also form part of its diet.

Where occupied habitats border agricultural land and gardens with vegetables, tortoises eat tomatoes, whose red color attracts them. They may occasionally consume carrion, and can be found scavenging dead animals, usually domestic species (Artner 1998). Coprophagy has also been observed, as *T. marginata* may eat feces of domestic animals such as sheep, goats, and dogs (Bringsøe et al. 2001). From observations in captivity, it is known that this species, like its congenerics, is attracted to food items based on their odors and colors.

Predation. — Observations of predation on *T. marginata* in the wild are scarce. In Laconia (southeast Peloponnese) an adult Eastern Montpellier Snake (*Malpolon insignitus*) had consumed a juvenile *T. marginata* of SCL 45 mm (Schleich 1982b). Glutz et al. (1979) described that the Bearded Vulture (*Gypaetus barbatus*) may treat *T. marginata* and its congeners in the same way as big bones, being dropped on rocky ground from heights of 50–80 m. Various larger mammals and birds which are known to prey on tortoises in the Mediterranean are also hypothesized to eat *T. marginata,* though this may generally be rare in Greece (Bringsøe et al. 2001). On Sardinia, the Italian Hedgehog (*Erinaceus europaeus italicus*), Red Fox (*Vulpes vulpes*), and Wild Boar (*Sus scrofa*) have been cited as opportunist predators of nests and eggs (Cimatti 2007).

Parasites and Ectobionts. — *Testudo marginata* is often heavily infested with ticks of the species *Hyalomma*

aegyptium during its entire active season (Bringsøe et al. 2001, Široký et al. 2006, 2011). In the periphery of the Kardamyli area, southern Peloponnese, the Brown Dog Tick, *Rhipicephalus sanguineus,* was also collected on four adult individuals (2 males, 2 females; Široký et al. 2006). Hemogregarine protozoans belonging to *Hemolivia* cf. *mauritanica* have been found in the erythrocytes of *T. marginata* (Široký et al. 2004, 2005).

In a study of nematodes in the three *Testudo* species in Italy, high levels of infestation were found in *T. marginata* (Traversa et al. 2005). The nematode species were *Alaeuris numidica*, *Mehdiella microstoma*, *M. uncinata*, *Tachygonetria longicollis*, *T. conica,* and *T. palearcticus,* which all belong to Pharyngodonidae, as well as *Atractis dactyluris* (Atractidae) and *Angusticaecum holopterum* (Ascarididae). These nematodes were also found in *T. graeca* and *T. hermanni*. All tortoises less than 1 yr of age were parasite-free. Schneller and Pantchev (2008) reported pinworms (oxyurid nematodes) as parasites of *T. marginata*.

Sardinian wild individuals of *T. marginata* can be infected by the bacterium *Mycoplasma agassizii*, which causes chronic inflammatory rhinitis in the form of upper respiratory tract disease (URTD) and is transmissible to other species of Mediterranean tortoises (Lecis et al. 2011). In Olbia, Sardinia, a single individual infected by *Salmonella* serotype Abony was detected (Lecis et al. 2011).

Population Status. — *Testudo marginata* often occurs in sparse populations with low population densities throughout its natural range (Willemsen and Hailey 1989; Bringsøe et al. 2001). Although few data regarding population parameters are presented in the literature, a few authors have provided information on population size and density, mostly concentrated in four geographically separate regions of southern Greece: southern central mainland, and northwestern, northern, and southern Peloponnese peninsula (Willemsen and Hailey 1989; Herz 1994; Ioannidis et al. 2006; Koppitz et al. 2017; Mamasis and Tzoras 2021).

Herz (1994) observed 63 individuals (26 males and 37 females) of *T. marginata* in a habitat covering 1.2 km^2 near Athens during ten days in May 1992. They represented all size groups except small juveniles, with the largest measuring 34 cm SCL.

On the northwestern Peloponnese, in the robust population in Strofylia National Park, Ioannidis et al. (2006) estimated a density of 12 turtles/ha in a study area of 5.3 ha in 2004, while in 2006 the population density was estimated at 15.2 turtles/ha. In this region, the species is common in low-lying habitats of macchia or coastal sand dunes.

In the Feneos Basin of northern Peloponnese, the estimated population size of *T. marginata* was 95 individuals in a study area of 33 ha in 2015, with a population density of ca. 3 turtles/ha (Koppitz et al. 2017). The populations of the two native tortoise species were investigated from 2005 to 2015. During these years 183 *T. marginata* and 738 *T. hermanni* were recorded in the area of 33 ha (Koppitz et al. 2016, 2017). In 2015, using a POPAN model, population sizes of ca. 95 *T. marginata* (confidence interval, 50–140 individuals) and ca. 210 *T. hermanni* (c.i., 160–260 individuals) were calculated for the entire area. Although this is an average for *T. marginata* of ca. 3 turtles/ha, the occurrences were comparatively unevenly distributed with a number of high density centers, though the centers were fewer and more pronounced in *T. hermanni*.

Further north, in the Messolonghi Lagoon National Park (southwest central Greece), Mamasis and Tzoras (2021) studied population size of *T. marginata* at five different sites. Two populations were estimated at 4.1 turtles/ha in two study areas of 30 and 61.8 ha, respectively. In the remaining sites the population densities were estimated at 16.2 turtles/ha (7 ha study area), 14.5 turtles/ha (9 ha study area) and 20.7 turtles/ha (13 ha study area) (Mamasis and Tzoras 2021).

The dry habitats in the Peloponnese region occupied by the dwarf *weissingeri* ecotype have been revisited various times through the years, where its high abundance has been extensively documented (Willemsen and Hailey 1989; Bour 1996; Bour et al. 2002). In the 1980s and 1990s there was evidence of high population densities on the western Mani peninsula. In a comprehensive study, more than 950 individuals were measured and marked during 15 trips of one to three weeks duration over ten years (Bour et al. 2002). Results by Artner (1996) in the same area were in agreement; in two days, he measured and marked 80 individuals, 30 of which were found in four hours. However, illegal over-collection has since resulted in major population declines (Trapp 2007; Herz 2016).

On northwestern Sardinia, a density of 19 turtles/ha has been estimated, of which 72% were males (Biaggini et al. 2018). However, the duration of this study was very limited (four consecutive days, with an average of 6.5 sightings per day) and therefore its conclusions must be taken with caution.

Willemsen and Hailey (1989) reported low population densities of *T. marginata* throughout most of the studied populations in Greece (n = 22), but also emphasized the higher population density in the area of Gythio on the southern Peloponnese peninsula. This dense tortoise population was further threatened by a widespread wildfire in the early 1990s, which was considered a major disaster for the species and may have caused a population decline (Hailey and Willemsen 2003).

On the Attica peninsula (southeastern mainland of Greece), urban areas such as archaeological sites like the Acropolis or restricted and marginal sites throughout greater Athens are often inhabited by the species, where frequent observations have also been reported in the past (Dimitropoulos and Gaethlich 1986, Kandolf 1995, Annousis et al. 2021). Though none of the aforementioned works commented on population status, Dimitropoulos and Gaethlich (1986) listed *T. marginata* as the most common

Figure 19. Adult *Testudo marginata* from Evvia, central Greece, previously either damaged by agricultural machinery, otherwise traumatized, or stepped upon by a goat or sheep, but survived. Photo by Henrik Bringsøe.

Figure 20. Former olive grove habitat of *Testudo marginata* turned into large-scale industry of vineyards and therefore highly degraded. South of Souli, Nemea region, northeastern Peloponnese, Greece. Photo by Henrik Bringsøe.

reptile species in the area, exhibiting high abundance in the montane ranges of greater Athens: Lykavitos, Tourkovounia, Ymittós, Parnitha, Pedeli, and Aegaleo. Additionally, Annousis et al. (2021) mentioned that *T. marginata* was the most common chelonian in Attica, representing 72% of known records.

Threats to Survival. — Illegal capture and sale of *T. marginata* is currently much less prevalent than in the 20th century. Previously, the species was regularly collected and sold in some European countries and, on one occasion a single collector brought 500 individuals to Switzerland from Greece (Lambert 1984).

Tortoises living in agricultural areas and with livestock grazing are exposed to potential physical damage, which can often cause mortality. In the olive groves around Kardamili, many individuals have serious carapacial injuries, accidentally caused by agricultural equipment (Artner 2000). Large domestic grazers such as sheep, goats, cattle, and horses can accidentally step on tortoises or they can be struck by agricultural machinery such as ploughs (Willemsen and Hailey 1989; Staerk et al. 2018). Tortoises may also be killed deliberately by local people (Bringsøe 1986), and individuals crossing roads can be killed by vehicles.

Herz (1994) stressed that natural tortoise habitats in greater Athens were being destroyed for the construction of hotels and other tourist facilities. In Varkiza, south of Athens, large-scale establishment of tourist accommodation has caused destruction of *T. marginata* habitats (Bringsøe 1986; Bringsøe et al. 2001). However, the species thrives well in several urban parks inside the city of Athens (Lycabettus, Filopappou, and Athens National Garden). After having surveyed tortoise localities in Greece for decades, Herz (2016) noted that the natural habitats had continued to shrink.

Wirth (2010) described major habitat destruction due to construction projects aiming at tourism as well as further development of agriculture. Forest fires were also emphasized as a severe threat, which was earlier echoed by Bour (1996) for the population on the western Mani peninsula, where 12–15% of the tortoises had been injured by burning.

The region of Nemea on the northeastern Peloponnese is known for its wine production and vineyards, and this has turned previous tortoise habitats of macchia and olive groves with stone terraces into large scale vineyards. During field work in April 2008, it was observed that major areas north of Nemea up to near the village of Souli had undergone these negative changes (Bringsøe and Madsen, unpubl. data).

Near Olympia on the Peloponnese, Willemsen and Hailey (2001) observed significantly increased mortality in a population of *T. hermanni* due to spraying with the herbicides 2,4-dichlorophenoxyacetic acid (2,4-D) and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) which selectively act on dicotyledons and are used to control broad-leafed weeds and woody perennials. There was additional mortality of 34% per year as compared to annual survival rates of 85–90% in unaffected areas. It is highly likely that *T. marginata* would suffer from poisoning to the same degree if exposed to these herbicides.

Wildfires kill many *T. marginata*, whereas those tortoises surviving fires bear shell damage. Buttler et al. (1982) and Kordges (1984) considered this species severely threatened by fires in the deltas, especially in western Greece.

Since the description of the dwarf ecotype variant of the Mani peninsula as a distinct species, *T. weissingeri*, by Bour (1996), these populations have been exposed to major illegal over-collection for the herpetoculturist trade (Trapp 2007; Herz 2016). Perez et al. (2012) described the increased impact of human activities changing from traditional agriculture to mechanization and extensive use of chemicals, notably on the Mani peninsula.

In Albania, a wide variety of threats to *T. marginata* were listed by Oruçi (2010): habitat destruction caused by conversion to pastures with grazing, other kinds of agriculture, and construction projects associated with urbanization. Additionally, collection of tortoises for consumption, for pets locally, and for commercial sale was also mentioned.

On Sardinia, anthropogenic habitat degradation could affect some populations, since the coast of Gallura is undergoing increasing urban development (Carpaneto 2006; Corti 2016; Sechi et al. 2020). Occasionally, individuals can be found killed on roads, particularly at the end of summer and beginning of autumn, after the first torrential rains that trigger massive juvenile dispersal (Escoriza, unpubl. data). Sporadic smuggling by tourists is reported in the local press, since its large size makes the tortoise a preferred species for illegal collection and trade (Corti et al. 2022). This species is also affected by summer bush fires and mechanical clearing of vegetation along roads, and occasionally it is deliberately destroyed because it is considered harmful to agriculture (Corti 2016; Cimatti 2020).

Actions involving destruction of habitats and intentional killing are probably violations of the EU Habitats Directive, where *T. marginata* is listed in Annex IV, forming a particularly strict protection. The global trade in *T. marginata* on the basis of compiled import data from the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) showed that 5,596 individuals were traded across borders during 1975–2005, i.e., an average of 187 per year; however, only ca. 1.5% were wild-caught whereas the vast majority were captive-bred (Türkozan et al. 2008). On the other hand, the exact extent of illegal collection from the wild remains unknown, particularly of dwarf tortoises from the habitats on the southern Peloponnese.

Conservation Measures Taken. — *Testudo marginata* is assessed as Least Concern (LC) on the IUCN Red List (van Dijk et al. 2004), and has been included on CITES Appendix II as part of all *Testudo* spp. since 1975. In Greece, the species is listed as Least Concern in the Red Book of threatened animals of Greece (Legakis and Maragou 2009). Furthermore, it is present in numerous protected areas in Greece under the natura 2000 network, i.e., Oros Olympos, Aisthitiko Dasos Koiladas Tempon, Limnohalassa Kalogrias- Dasos Strofylias Kai Elos Lamias – Araxos, Limni Stymfalia, Oros Parnitha, Amvrakikos Kolpos – Delta Lourou Kai Arachthou, Thines Kyparissias, Ethnikos Drymos Oitis, Akrokorinthos, Oros Erymanthos, Thines Kai Paraliako Dasos Zacharos-Limni Kaiafa-Strofylia-Kakovatos, Limni Ozeros, Kentriko Tmima Zagoriou , Ethnikos Drymos Vikou, Aoou , Kato Olympos, Kallipefki – Stena Kalamakiou, Oros Taygetos, Oros Geraneia, Koilada Kai Ekvoles Spercheiou Maliakos Kolpos Mesochori Spercheiou, Delta Acheloou, Limnothalassa Mesolongiou-Aitolikou – Ekvoles Evinou -Nisoi Echinades – Nisos Petalas, Oros Parnona, Antichasia Ori Kai Meteora – Spilaio Melissotrypa, Agrafa , Ymittos – Aisthitiko Dasos Kaisarianis – Limni Vouliagmenis, Ethniko Thallassio Parko Alonnisou – Voreion Sporadon – Anatoliki Skopelos, Periochi Neapolis Kai Nisos Elafonisos, and Limnothalassa Pylou (Divari) Kai Nisos Sfaktiria – Agios Dimitrios.

In Albania, the species is categorized as Lower Risk/conservation dependent (LR/cd) in the National Red List of Flora and Fauna of Albania and occurs in at least three protected areas: Rrepet e Këllezit, Kanioni i Leshnicës and Kanali i Vivarit.

On Sardinia, this species has been included in the Legge della Regione Sardegna (no. 23) since 1988 as "fauna selvatica particolarmente protetta" (especially protected wildlife). Protected populations of this species on Sardinia appear in several nature reserves included in the natura 2000 network: Isola Rossa-Costa Paradiso, Monte Russu, Monte Limbara, Capo Testa, Capo Figaro, Foci del Coghinas, Isola Tavolara, Isola Molara, and Parco Nazionale dell'Arcipelago di La Maddalena. There is a captive reproductive group in the Riserva Naturale Gran Bosco della Mesola (Parco Veneto Delta del Po), which has a stock of juveniles to be reintroduced into protected areas on Sardinia (Cimatti 2020).

The trade of this species is strictly regulated in Europe. To prevent fraudulent sale of individuals from wild populations, microchip-based methods for individual identification have been implemented (Brugnola et al. 2013; Brown 2020).

Conservation Measures Proposed. — Effective habitat protection will be necessary to prevent further population declines of *T. marginata*. Due to the Annex IV listing of the species under the EU Habitats Directive, the member states are obliged to enforce strict protection, namely both species protection (e.g., against killing and collection) and habitat protection.

It is recommended that the EU member countries inhabited by *T. marginata*, notably Greece, implement stricter habitat protection, so that any deterioration or destruction of habitats will no longer be possible, in accordance with EU rules. In very exceptional cases, mitigation by release into areas not currently inhabited by any of the affected Annex IV species should be created before the habitats in question can be destroyed, preferably with active involvement of local NGOs.

Captive Husbandry. — *Testudo marginata* reproduces easily in captivity and is tolerant of a wide range of temperatures. It has previously been legally offered in large numbers in the international pet market (USA and Europe mainly; Türkozan et al. 2008). However, it can be susceptible to respiratory infections (chronic rhinitis) if the housing conditions are inadequate (excessive air humidity and/or too low temperatures; Sanz-Villar and Valverde 2000; Lesueur 2002; Martínez-Silvestre 2005; Coutard 2006; Avanzi 2017). Some authors have reported that *T. marginata* is more sensitive than *T. hermanni* or *T. graeca ibera* to respiratory infections (Coutard 2006).

Testudo marginata requires more space than other species of Mediterranean tortoises due to its larger size and more intense exploratory activities (Sanz-Villar and Valverde 2000; Cimatti 2020). Among the abundant reports on captive husbandry and breeding, very different recommendations for minimum enclosure or vivarium size are provided, ranging from 1–2 m^2 for a small group to 5–8

m^2 per adult (Lesueur 2002; Coutard 2006; Datzberger 2006; Cimatti 2020).

Outdoor housing is highly recommended, even in countries much farther north than its natural distribution, for instance, in central Europe (e.g., The Netherlands, northern France, or England; Collins 1980; Hine 1982; Eendebak 2002; Coutard 2006; Prest 2012), northern Europe (e.g., Denmark; Madsen 2003b, 2004a,b) and in many parts of North America (USA; Leone and Hermes 2016). Likewise, it can also adapt to being outdoors all year round in subtropical desert zones (e.g. Tucson, Arizona), if it is provided with suitable shelter and water (Crawford 1992). With weather sometimes being unfavorable for captive tortoises, the use of cold frames or mini greenhouses is recommended to enable them to escape rain and prolonged periods of cold weather (Collins 1980; Eendebak 2002; Madsen 2003b; Coutard 2006; Leone and Hermes 2016).

Based on captive observations, *T. marginata* is an adept climber and is able to climb various fences to heights of 2 m, and a female was observed basking in a thin-branched shrub at a height of 1 m (Artner 1998; Vinke and Vinke 2006). Thus, sufficiently high vertical and preferably smooth sides of the enclosure must be provided to prevent escapes.

In indoor installations, air temperatures during the day should range between a minimum of 20–24°C to a basking spot reaching 28° to 34°C (Hine 1982; Trutnau 1994; Coutard 2006), whereas the heat may be turned off at night. Juveniles can be kept indoors in a similar temperature range as adults with 25–30°C day temperatures and 18–20°C at night (Hine 1982; Cimatti 2020). A brief hibernation of 30–45 days at 4–8°C is recommended for juveniles to facilitate proper shell development (Coutard 2006; Cimatti 2020).

For hibernation (brumation), 4–6°C (or 0–10°C) is recommended for 2 to 5 months (Trutnau 1994; Prest 2012; Brown 2020). Exposure to temperatures as low as –4.5°C overnight due to thermostat failure did not harm the tortoises (Jönsson 2005). During the hibernation of several months the weight loss will usually only comprise ca. 2% of the body mass (Madsen 2003a). Higher weight loss will often be due to dehydration and if it exceeds 10% one should consider interrupting the hibernation for rehydration. Outdoors, supplemental heat may be required to maintain temperatures above 4–6°C. In indoor installations, a UVB light bulb is recommended, following the circadian periodicity (Trutnau 1994).

The diet must be high in fiber, with low protein, fat and sugars, rich in calcium (Ca), and low in phosphorus (P; ideal ratio of Ca/P = ca. 1.5–2) to avoid metabolic bone disease and accelerated growth (Brown 2020). In the diet of wild individuals of the genus *Testudo*, the ratio of Ca/P has been estimated to be ca. 4:1 (Highfield 1994). This diet should be composed of a wide range of wild plants (weeds, including flowers) and cultivated plants such as dandelions, clover, sow thistles, thistles, chicory, ground elder, white and red dead-nettle, shepherd's purse, mallow, *Hibiscus*, plantains, grass, roses, hollyhocks, parsley, clematis, chamomile, thyme, and bedding hay (Hine 1982; Trutnau 1994; Madsen 2003b; Prest 2012; Fife 2019; Cimatti 2020). Commercially produced vegetables should only be offered occasionally when wild plants (weeds) are not available because the calcium content in them is usually low. Various fruits are best avoided or should be offered in very low quantities. Particularly for juveniles and reproducing females, the diet should be enriched with calcium, which can be added with cuttlefish bone, bone fragments, or chicken egg shells (Collins 1980; Hine 1982; Trutnau 1994).

Incubation of eggs should be carried out at temperatures between 28–32°C, with a relative humidity of 65–90%, with hatching 65–80 days later (Avanzi 2017). The sex of the embryos depends on the incubation temperature, as females are produced at higher temperatures (above 32°C). Incubation temperatures above 35°C or below 25°C in a sustained manner may yield deformities (e.g. supernumerary scutes) or even embryonic death (Avanzi 2017; Cimatti 2020), but other possible explanations for supernumerary scutes, such as low genetic diversity and inbreeding have also been proposed (Farke and Distler 2015). Usually, hatchlings will start feeding after 2–4 days, but may eat their first meal earlier or even as late as after more than a week. Juveniles should be offered sufficiently humid refuges to prevent pyramiding (lumpy growth of the carapacial scutes), also maintaining a relative air humidity of 40–50% to 70–80% to reduce the risk of dehydration, to which juvenile are particularly sensitive (Prest 2012; Avanzi 2017; Fife 2019; Cimatti 2020).

It has been observed in captivity that *Testudo marginata* is less aggressive and more peaceful towards other tortoises than *T. graeca,* and males may ignore the females of *T. graeca* and *T. hermanni* (Jenvey 1982). However, it has regularly been reported that *T. marginata* may hybridize with *T. graeca ibera* in captivity (Stemmler-Gyger 1963; Heimann 1986; Bruekers 1994; Hofstra 2003).

Current Research. — Current work is being conducted on increasing knowledge about the demographic status of the species in Italy and other Mediterranean regions, focusing on the presence of populations established outside the historical distribution range (Leonetti et al. 2020; Corti et al. 2022). In Greece, current research is focused on assessing the occurrence and status (native or introduced) of this species on the islands.

Acknowledgments. — We are grateful to Francisco Welter-Schultes (Georg-August-Universität Göttingen, Germany) for valuable advice on nomenclatural rules in relation to the *weissingeri* taxon. Jan Grathwohl (Næstved, Denmark), Christian Koppitz (Anhalt University of Applied Sciences, Bernburg, Germany), Mario Schweiger (Obertrum, Austria), and John B. Iverson (Richmond, IN, USA) provided literature. Otto Høj Madsen (Næstved, Denmark) generously shared his observations on dwarf populations from the

southern Peloponnese. Thomas Kordges (Ökoplan Kordges, Hattingen, Germany) and Fritz B. Ludescher (University of Essen, Germany) provided information on and a photo of a large *T. marginata* from Central Greece, and Evangelos Vlachos (Aristotle University of Thessaloniki, Greece) gave us photos of the extinct form *cretensis*. Daniel Jablonski (Comenius University in Bratislava, Slovakia) and Edvárd Mizsei (Conservation Ecology Research Group, Centre for Ecological Research, Hungary) provided information regarding Albania. Joan Budó (CRT), Albert Martínez-Silvestre (CRARC), Quim Soler (CRARC) and Marc Franch (UdG) provided information about the species occurrence in Catalonia (NE Spain). We thank John Iverson and Anders Rhodin for their editorial review.

We dedicate this paper to the memory of Roger Henri Bour (9 July 1947 – 7 March 2020) on the occasion of remembering his lifelong contributions to chelonian research, with a focus on his impressive work with the Marginated Tortoise, notably the *weissingeri* ecotype from the southern Peloponnese. His research in the field in Greece and at the Muséum national d'Histoire naturelle de Paris, France, has been a great inspiration to our past and ongoing work.

Literature Cited

Adema, J.P.H.M. and In den Bosch, H.A.J. 1980. Enige faunistische resultaten van de excursie Griekenland. Leiden: Rijksmuseum van Natuurlijke Historie, unpublished report, 37 pp.

Andrews, H. 1989. Behaviour and thermoregulation of the Marginated tortoise (*Testudo marginata*). Hamadryad 14(2):22–26.

Angelini, G. 1899. Notizie ed osservazioni intorno alla naturalizzazione della *Testudo nemoralis*, Aldrov., in Sardegna. Bollettino della Societá Romana per gli Studi Zoologici 8:50–52.

Angelini, G. 1907. Sulla naturalizzazione della *Testudo nemoralis* (Aldrov.) in Sardegna. Bollettino della Società Zoologica Italiana (2)8:53–54.

Annousis, I., Kapsalas, G., and Pafilis, P. 2021. Review of the herpetofauna of Attica, mainland Greece. Herpetozoa 34:1–8.

Artner, H. 1996. Beobachtungen an der Zwerg-Breitrandschildkröte *Testudo marginata* in Messinien / Griechenland und Diskussion über die Validität ihres Artstatus. Emys 3(3):5–12.

Artner, H. 1998. Haltung und Nachzucht der Breitrandschildkröte *Testudo marginata* Schoepff 1792 nebst Beobachtungen im natürlichen Lebensraum. Emys 5(4):5–24.

Artner, H. 2000. Beobachtungen an der Zwerg-Breitrandschildkröte *Testudo weissingeri* Bour, 1996 in Messenien (Griechenland) und Diskussion über die Validität ihres Artstatus. In: Artner. H. and Meier, E. (Eds). Schildkröten Symposiumsband. Münster: Natur und Tier Verlag, pp. 34–38.

Avanzi, M. 2017. Tartarughe terrestri. Milano: De Vecchi, 132 pp.

Bachmayer, F. and Symeonidis, N. 1975. Schildkrötenreste (*Testudo marginata* Schoepff) aus der Höhle "Charkadio" auf der Insel Tilos (Dodekanes, Griechenland). Annales Géologiques des Pays Helléniques 26:324–327.

Bachmayer, F., Brinkerink, J.P., and Symeonidis, N. 1975. Pleistozäne Schildkröten aus Höhlen der Insel Kreta. Annales Geologiques des Pays Helleniques 27:110–122.

Baier, F., Sparrow, D.J., and Wiedl, H.J. 2013. The Amphibians and Reptiles of Cyprus. Frankfurt am Main: Chimaira, 364 pp.

Ballasina, D. 1995. Red Data Book on Mediterranean Chelonians. Bologna: Edagricole, 190 pp.

Bassu, L., Nulchis, V., Satta, M.G., Fresi, C., and Corti, C. 2008. Atlas of amphibians and reptiles of Sardinia – state of the art and general considerations. In: Corti, C. (Ed.). Herpetologia Sardiniae. Latina: Belvedere, pp. 52–58.

Bauer, A.M., DeBoer, J.C., and Taylor, D.J. 2017. Atlas of the Reptiles of Libya. Proceedings of the California Academy of Sciences 64:155–318.

Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., and Wood, E.F. 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. Scientific Data 5(1):1–12.

Belcheva, R.G., Sofianidou, T.S., and Psallidas, V.K. 1990. A karyological study of the tortoise *Testudo marginata*. Amphibia-Reptilia 11:185–204.

Biaggini, M., Romano, A., Di Tizio, L., and Corti, C. 2018. Density and sex-ratio of wild populations of three *Testudo* species in Italy. Herpetozoa 30:203–208.

Boscà, E. 1880. Catalogue des reptiles et amphibiens de la Péninsule Ibérique et des iles Baléares. Bulletin de la Société Zoologique de France 5:24–287.

Bour, R. 1996. Une nouvelle espèce de tortue terrestre dans le Péloponnèse (Grèce). Dumerilia 2:23–54.

Bour, R. 2004a. *Testudo marginata* Schoepff, 1793. In: Guyot-Jackson, G. (Ed.). Numéro special Testudo. Manouria 7(22):27–29.

Bour, R. 2004b. *Testudo weissingeri* Bour, 1995. In: Guyot-Jackson, G. (Ed.). Numéro special Testudo. Manouria 7(22):42–43.

Bour, R., Bringsøe, H., and Vanderhaege, M. 2002. *Triturus vulgaris* (Linnaeus, 1758) at its southern limit: distribution on the Peloponnese, Greece, with range extensions from the Central and South Peloponnese. Alytes 20:67–76.

Brinckmeier, C., Bode, F., and Hampe, A. 1989. First record of the Marginated Tortoise, *Testudo marginata*, in Turkey. Zoology of the Middle East 3:47–48.

Bringsøe, H. 1986. A check-list of Peloponnesian amphibians and reptiles, including new records from Greece. Annales Musei Goulandris 7(1985):271–318.

Bringsøe, H. 2002. Bredrandede landskildpadder, *Testudo marginata*, direkte udsat for streng frost i Grækenland. Nordisk Herpetologisk Forening 45:83–91.

Bringsøe, H., Buskirk, J.R., and Willemsen, R.E. 2001. *Testudo marginata* Schoepff, 1792. Breitrandschildkröte. In: Fritz, U. (Ed.). Handbuch der Reptilien und Amphibien Europas. Band 3/IIIA, Schildkröten (Testudines) I. Wiebelsheim: Aula-Verlag, pp. 291–334.

Brinkerink, H.P., 1996. Tortoises and turtles from the Pleistocene of Crete. In: Reese, D.S. (Ed.), Pleistocene and Holocene Fauna of Crete and it's First Settlers. Madison: Monographs in World Archaeology, Prehistory Press 28, pp. 207–210.

Broggi, M.F. 2007. Herpetological notes on the island of Amorgos (Cyclades, Greece). Herpetozoa 20:94–96.

Broggi, M.F. 2010. The herpetofauna of Alonissos (Northern Sporades, Greece). Herpetozoa 23:71–78.

Broggi, M.F. 2016a. The reptile fauna of the Island of Elafonisos (Peloponnese, Lakonia, Greece). Herpetozoa 28:198–203.

Broggi, M.F. 2016b. The herpetofauna of the Island of Kythera (Attica, Greece). Herpetozoa 29:37–46.

Brown, S. 2020. Mediterranean tortoises. In: Kubiak, M. (Ed.). Handbook of Exotic Pet Medicine. Hoboken: John Wiley & Sons, pp. 327–359.

Bruekers, J. 1994. Bastaard-vorming tussen *Testudo marginata* en *Testudo graeca ibera*. De Schildpad 20(2):15–24.

Brugnola, L., Biancardi, C., Di Francesco, N., Di Tizio, L., and Gheorghiu, A. 2013. DataDotDNA: an alternative marking system for tortoises of genus *Testudo*. Acta Herpetologica 8:163–166.

Bruno, S. 1986. Guida a Tartarughe e Sauri d'Italia. Florence: Giunti Martello, 255 pp.

Bruno, S. 1989. Introduction to a study of the herpetofauna of Albania. British Herpetological Society Bulletin 29:15–41.

Buhlmann, K.A., Akre, T.S.B., Iverson, J.B., Karapatakis, D., Mittermeier, R.A., Georges, A., Rhodin, A.G.J., van Dijk, P.P., and Gibbons, J.W. 2009. A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. Chelonian Conservation and Biology 8:116–149.

Buttle, D. 1987. Observations on some of the herpetofauna of the Peloponnese. British Herpetological Society Bulletin 20:22–28.

Buttle, D. 1988. Further notes on reptiles and amphibians of the Peloponnese. British Herpetological Society Bulletin 26:14–20.

Buttler, M., Chawallek, J., and Kordges, T. 1982. Reptiles and Amphibians. In: Szijj, J. (Ed.). Ecological Assessment of the Delta Area of the Rivers Louros and Arachtos at the Gulf of Amvrakia. Essen: University of Essen, unpublished report, pp. 208–244.

Carpaneto, G.M. 1986. Osservazioni preliminari sugli Anfibi e sui Rettili del Parco nazionale del Circeo (Amphibia et Reptilia). In: Aspetti faunistici e problematiche zoologiche del Parco Nazionale del Circeo. Sabaudia: Parco Nazionale del Circeo, pp. 145–155.

Carpaneto, G.M. 2006. *Testudo marginata* Schoepff, 1792. In: Sindaco, R., Doria, G., Razzetti, E., and Bernini, F. (Eds.). Atlante degli Anfibi e dei Rettili d'Italia. Firenze: Societas Herpetologica Italica/Polistampa, pp. 396–399.

Cattaneo, A. 1984. Reperti erpetologici nelle Cicladi occidentali: *Testudo marginata* a Milos, *Hemidactylus turcicus* ed *Elaphe situla* a Sifnos (Reptilia). Natura (Milano) 75:75–78.

Cattaneo, A. 1997. L'erpetofauna del'isola greca di Skiathos (Sporadi settentrionali). Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 136/1995 (II):145–156.

Cesaraccio, G. and Lanza, B. 1984. Nuovi dati sull' erpetofauna dell'Arcipelago della Maddalena (Sardegna NE). Bollettino della Società Sarda di Scienze Naturali 23:137–143.

Chondropoulos, B. and Chiras, G. 1997. Geographic distribution. *Testudo marginata* (Marginated Tortoise). Herpetological Review 28:209.

Cimatti, E. 2007. *Testudo marginata*. Ritratto Sardo. Reptilia 15:60–69.

Cimatti, E. 2020. La Testuggine Marginata. Torrazza Piemonte: Amazon Italia, 77 pp.

Clark, R.J. 1963. On the possibility of an autumnal mating in the tortoise (*Testudo graeca ibera*). British Journal of Herpetology 3:85–86.

Clark, R.J. 1970. A definite record of *Testudo marginata* Schöpff, 1972 from the Cyclades, Greece. British Journal of Herpetology 4:188–189.

Clark, R.J. 1989. A check list of the herpetofauna of the Argo-Saronic Gulf district, Greece. British Herpetological Society Bulletin 28:8–24.

Clark, R.J. 1997. The herpetofauna of the uninhabited islands of the Spetsai/Hydra Island complex, Greece. British Herpetological Society Bulletin 58:36–43.

Collins, P.W.P. 1980. The captive breeding of Mediterranean tortoises in Britain. In: Townson, S., Millichamp, N.J., Lucas, D.G.D., and Millwood, A.J. (Eds.) The Care and Breeding of Captive Reptiles. London: The British Herpetological Society, pp. 21–36.

Corti, C. 2016. *Testudo graeca* L., 1758, *T. marginata* Schoepff, 1792. In: Stoch, F., and Genovesi, P. (Eds). Manuali per il monitoraggio di specie e habitat di interesse comunitario (Direttiva 92/43/CEE) in Italia: specie animali. ISPRA, Serie Manuali l inee guida, 141/2016:253–255.

Corti, C., Bassu, L., Biaggini, M., Bressi, N., Capula, M., Di Cerbo, A.R., Di Francesco, N., Di Tizio, L., Fiacchini, D., Lo Cascio, P., Mastropasqua, F., Nulchis, V., Oneto, F., Ottonello, D., Richard, J., Romano, A., Satta, M.G., Scillitani, G., Spilinga, C., and Vanni, S. 2013. Aggiornamento sulla distribuzione italiana delle testuggini terrestri appartenenti al genere *Testudo*. Atti II Congresso Societas Herpetologica Italica Sezione Abruzzo-Molise Testuggini e Tartarughe. Pescara: Ianieri Edizioni, pp. 153–170.

Corti, C., Biaggini, M., Nulchis, V., Cogoni, R., Cossu, I.M., Frau, S., Mulargia, M., Lunghi, E., and Bassu, L. 2022. Species diversity and distribution of amphibians and reptiles in Sardinia, Italy. Acta Herpetologica 17:125–133.

Costanzo, J.P. and Lee, R.E., Jr. 2013. Avoidance and tolerance of freezing in ectothermic vertebrates. Journal of Experimental Biology 216:1961–1967.

Coutard, C. 2006. Note sur la maintenance et la reproduction en captivité de *Testudo marginata* Schoepff, 1795 et *Testudo weissingeri* Bour, 1995. Manouria 9(31):18–26.

Crawford, T. 1992. Husbandry of the Marginated Tortoise. In: Hardy, D. (Ed.). Collected Papers of the Tucson Herpetological Society. Tucson: Tucson Herpetological Society, pp. 223–224.

Datzberger, A. 2006. Gestaltung eines naturnahen Geheges für Breitrandschildkröten (*Testudo marginata*). Sacalia 13:39–41.

de Broin, F., Bour, R., and Perälä, J. 2006. *Eurotestudo* (Chelonii, Testudinidae): définition, approche morphologique. Deuxième partie. Annales de Paléontologie 92:325–327.

Delfino, M. 2020. Testuggini e tartarughe italiane in una prospettiva temporale. In: Ottonello, D., Oneto, F., Piccardo, P., and Salvidio, S. (Eds). Associazione Emys Liguria. Atti II Congresso Nazionale Testuggini e Tartarughe, pp. 16–24.

Delfino, M., Chesi, F., and Fritz, U. 2009. Shell morphology of the Egyptian Tortoise, *Testudo kleinmanni* Lortet, 1883, the osteologically least-known *Testudo* species. Zoological Studies 48:850–860.

Demetropoulos, A. and Lambert, M. 1986. Herpetology in Cyprus. British Herpetological Society Bulletin 17:22–23.

Di Nicola, M.R. and Mezzadri, S. 2018. Anfibi e rettili di Sardegna, guida fotografica. Milano: Libreria della Natura, 175 pp.

Dimitropoulos, A. 1985. A case of living twins in a single egg of Marginated Tortoise (*Testudo marginata*, Schoepff, 1792) in a clutch taken from the wild. The Herptile 10:79–80.

Dimitropoulos, A. 1987. First record of Marginated Tortoise, *Testudo marginata* Schoepff, 1792 – from the eastern Aegean. The Herptile 12:137–139.

Dimitropoulos, A. and Gaethlich, M. 1986. The reptiles of Athens. The Herptile 11:62–65.

Doumergue, F. 1901. Essai sur la faune erpétologique de l'Oranie: avec des tableaux analytiques et des notions pour la détermination de tous les reptiles et batraciens du Maroc, de l'Algérie et de la Tunisie. Oran: L. Fouque, 397 pp.

Ducotterd, J.M. 1997. Notes sur la taille record d'une *Testudo marginata*. CITS Bulletin 9:41–42.

Ducotterd, J.M. 1998. Record de taille pour *Testudo marginata*. Manouria 1(1):5.

Eendebak, B. 2002. *Testudo hermanni boettgeri* and *Testudo marginata*. A sustainable breeding program. Vienna: International Turtle and Tortoise Symposium 2002, pp. 17–20.

Ernst, C.H. and Barbour, R.W. 1989. Turtles of the World. Washington DC: Smithsonian Institution Press, 313 pp.

Escoriza, D. 2008. Els Rèptils de Còrsega i Sardenya. Part I: Tortugues i Gecònids. Barcelona: Treballs de la Societat Catalana d'Herpetologia, 43 pp.

Escoriza, D. and Ben Hassine, J. 2022. Niche diversification of Mediterranean and southwestern Asian tortoises. PeerJ 10:e13702.

Escoriza, D., Díaz-Paniagua, C., Andreu, A., and Ben Hassine, J. 2022. *Testudo graeca* Linnaeus 1758 (Western Subspecies Clade: *Testudo g. graeca, T. graeca cyrenaica, T. graeca marokkensis, T. graeca nabeulensis, T. graeca whitei*) – Mediterranean Spur-thighed Tortoise, Moorish Tortoise, Libyan Tortoise, Moroccan Tortoise, Tunisian Tortoise, Souss Valley Tortoise. In: Rhodin, A.G.J., Iverson, J.B., van Dijk, P.P., Stanford, C.B., Goode, E.V., Buhlmann, K.A., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 5(16):117.1–18.

Farke, C.M. and Distler, C. 2015. Ontogeny and abnormalities of the tortoise carapace: a computer tomography and dissection study. Salamandra 51:231–244.

Ferri, V., Grano, M., Marini, D., Soccini, C., Filippi, E., Cervoni, F., and Masulli, A. 2020. La biodiversità aliena dei Cheloni nel Lazio: monitoraggio dei nuclei di testuggini esotiche terrestri e palustri introdotti negli ambienti naturali della regione. In: Ottonello, D., Oneto, F., Piccardo, P., and Salvidio, S. (Eds). Associazione Emys Liguria. Atti II Congresso Nazionale Testuggini e Tartarughe, pp. 107–113.

Fick, S.E. and Hijmans, R.J. 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.

Fife, R. 2019. Care Sheet: Hermann's and Marginated Tortoises. The Batagur 9:64–66.

Forestas (Agenzia Forestale Regionale per lo Sviluppo del Territorio e del'Ambiente della Sardegna). 2005. SardegnaForeste. Ritrovato un esemplare albino di *Testudo marginata*. https://www.sardegnaforeste.it/notizia/ritrovato-un-esemplare-albino-di-testudo-marginata.

Franzen, M., Bussmann, M., Kordges, T., and Thiesmeier, B. 2008. Die Amphibien und Reptilien der Südwest-Türkei. Bielefeld: Laurenti-Verlag, 328 pp.

Fritz, U., Široký, P., Kami, H., and Wink, M. 2005. Environmentally caused dwarfism or a valid species—is *Testudo weissingeri* Bour, 1996 a distinct evolutionary lineage? New evidence from mitochondrial and nuclear genomic markers. Molecular Phylogenetics and Evolution 37(2):389–401.

Georgalis, G.L. and Kear, B.P. 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios 46:299–311.

Giglioli, H.H. 1879. Beiträge zur Kenntniss der Wirbelthiere Italiens. Archiv für Naturgeschichte, Berlin 45:93–99.

Glutz von Blotzheim, U.U., Bauer, K.M., and Bezzel, E. 1971. Handbuch der Vögel Mitteleuropas. Band 4. Falconiformes. Frankfurt am Main: Akademische Verlagsgesellschaft, 943 pp.

Gray, J.E. 1870. Supplement to the Catalogue of Shield Reptiles in the Collection of the British Museum. Part I. Testudinata (Tortoises). London: British Museum, 120 pp.

Gruber, U. and Fuchs, D. 1977. Die Herpetofauna des Paras-Archipels (Zentral-Agäis). Salamandra 13:60–77.

Hadjisterkotis, E. and Reese, D.S. 1994. Palaeontological and archaeological evidence for turtles on Cyprus, with new information on living tortoises. British Herpetological Society Bulletin 49:16–18.

Hailey, A. and Loumbourdis, N.S. 1988. Egg size and shape, clutch dynamics, and reproductive effort in European tortoises. Canadian Journal of Zoology 66:1527–1536.

Hailey, A. and Loumbourdis, N.S. 1990. Population ecology and conservation of tortoises: demographic aspects of reproduction in *Testudo hermanni*. Herpetological Journal 1:425–434.

Hailey, A. and Willemsen, R.E. 2003. Changes in the status of tortoise populations in Greece 1984-2001. Biodiversity and Conservation 12:991–1011.

Harvati, K., Darlas, A., Bailey, S.E., Rein, T.R., El Zaatari, S., Fiorenza, L., Kullmer, O., and Psathi, E. 2013. New Neanderthal remains from Mani peninsula, southern Greece: the Kalamakia Middle Paleolithic cave site. Journal of Human Evolution 64:486–499.

Haxhiu, I. 1995. Results of studies on the chelonians of Albania. Chelonian Conservation and Biology 1:324–326.

Haxhiu, I. 1998. The Reptilia of Albania: species composition, distribution, habitats. Bonner Zoologische Beitrage 48:35–57.

Heimann, E. 1986. Bastardierung zwischen *Testudo graeca ibera* und *Testudo marginata*. Elaphe (Kulturbund der DDR) 86/3:48–50.

Heimann, E. 1987. Pflege und Zucht der Breitrandschildkröte, *Testudo marginata*. Aquarien-Terrarien 34(1):29–31.

Heimann, E. 1993. Drei Zwillingspaare bei *Testudo marginata*. Salamandra 29:167–172.

Heimann, E. 2016. AF3-generation of Marginated Tortoises (*Testudo marginata* Schoepff, 1792) in captive care. Radiata 25(2):45–50.

Hermann, J. 1804. Observationes Zoologicae. Opus posthumum edidit Fridericus Ludovicus Hammer. Argentorati [Strasbourg]: A. Koenig, 332 pp.

Herz, M. 1994. Beobachtungen an Breitrandschildkröten *Testudo marginata* Schoepff, 1792 in freier Natur. Sauria 16(1):27–30.

Herz, M. 2016. Further observations on Marginated Tortoises in Greece. Radiata 25(2):4–15.

Highfield, A.C. 1994. Tortoise Trust Guide to Tortoises and Turtles. London: Carapace Press, 209 pp.

Hine, M.L. 1982. Notes on the Marginated Tortoise (*Testudo marginata*) in Greece and in captivity. British Herpetological Society Bulletin 5:35–38.

Hofstra, J. 2000. Some herpetological observations on Crete. Podarcis 1:8–15.

Hofstra, J. 2003. Herpetological observations on the Greek island of Lesbos. Podarcis 4:101–111.

Hofstra, J. 2008. An addition to the herpetofauna of the Greek island Lesbos. Podarcis 9(1):2–10.

Ioannidis, Y., Kardakari, N., and Chiras, G. 2006. Action Plan for the herpetofauna of the protected area of Kotychi-Strofylia Wetlands (in Greek). LIFE2002NAT/GR/8491.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately Printed, 363 pp.

Jeanmonod, D. and Gamisans, J. 2007. Flora Corsica. Aix-en-Provence: Édisud, 921 pp.

Jenvey, J. 1982. Observations on *Testudo marginata* in captivity. British Herpetological Society Bulletin 5:39–43.

Jönsson, K. 2005. Kort notits om *Testudo marginata* og lave temperaturer. Nordisk Herpetologisk Forening 48:121–123.

Kandolf, F. 1995. Herpetologische Eindrücke aus dem südlichen Griechenland. Die Aquarien- und Terrarien Zeitschrift 48:448–449.

Keymar, P.F. and Weissinger, H. 1987. Distribution, morphological

variation and status of *Testudo marginata* in Greece. In: Van Gelder, J.J., Strijbosch, H., and Bergers, P.J.M. (Eds.). Proceedings of the 4th Ordinary General Meeting of the Societas Europaea Herpetologica (Faculty of Sciences/SEH). Nijmegen: Societas Europaea Herpetologica, pp. 219–222.

Kock, D. and Storch, G. 1979. *Testudo marginata* Schoepff, 1792 auf den Nördlichen Sporaden, Ägäis (Reptilia: Testudines: Testudinidae). Salamandra 15:101–105.

Koppitz, C., Kolleck, J., Kurtz, M., Hildebrandt, P., and Richter, K. 2016. Populationsökologische Langzeituntersuchung an *Testudo marginata* Schoepf, 1792 und *Testudo hermanni* Gmelin, 1789 im Becken von Feneos (Peloponnes, Griechenland). Oldenburg: 52 Jahrestagung der Deutschen Gesellschaft für Herpetologie und Terrarienkunde (DGHT), 17 pp.

Koppitz, C., Kolleck, J., Kurtz, M., Hildebrandt, P., and Richter, K. 2017. Die Leier des Hermes – Einblicke in das Leben zweier Landschildkrötenarten auf der Peloponnes. Elaphe 4/2017:34–43.

Koppitz, C., Holm, P., Kurtz, M., Kolleck, J., and Richter, K. 2018. Body size of two *Testudo*-species in the northern Peloponnese highlands. Magdeburg: 54th DGHT Annual Meeting, 1 p.

Kordges, T. 1984. Beitrag zur Herpetofauna griechischer Delten. Essen: Universität-GHS, unpublished report, 220 pp.

Kordges, T. and Hemmer, G. 1987. Studies on reptiles in Greek delta areas. Biologia Gallo-Hellenica 13:83–88.

Kotsakis, T. 1977. I resti di anfibi e rettili pleistocenici della grotta "Bate" (Rethymnon, Creta). Atti della Accademia Nazionale dei Lincei 63:571–582.

Krueger, C.J. 2021. The evolution of sex-ratio reaction norms in turtles according to 50 years of research. Masters Thesis, Iowa State University, Ames.

Lambert, M.R.K. 1984. Threats to Mediterranean (West Palaearctic) tortoises and their effects on wild populations: an overview. Amphibia-Reptilia 5:5–15.

Lecis, R., Paglietti, B., Rubino, S., Are, B.M., Muzzeddu, M., Berlinguer, F., Chessa, B., Pittau, M., and Alberti, A. 2011. Detection and characterization of *Mycoplasma* spp. and *Salmonella* spp. in free-living European tortoises (*Testudo hermanni, Testudo graeca,* and *Testudo marginata*). Journal of Wildlife Diseases 47:717–724.

Legakis, A. and Maragou, P. 2009. The Red Book of Threatened Animals of Greece. Athens: Hellenic Zoological Society, 525 pp.

Leone, C. and Hermes, A. 2016. *Testudo marginata*: care statistics in regions of the United States with notes on the recognition of possible subspecies. Radiata 25(2):16–43.

Leonetti, F.L., Giglio, G., Tripepi, S., and Sperone, E. 2020. New distributional records of *Testudo marginata* Schoepff, 1793 in southern Italy. Herpetology Notes 13:977–979.

Lesueur, L. 2002. Maintenance et reproduction en captivité de *Testudo marginata*. Manouria 5(16):8–15.

Loumbourdis, N.S. and Kattoulas. M.E. 1983. A northernmost locality for *Testudo marginata* Schoepff 1792 in Greece (short note). British Journal of Herpetology 6:348–349.

Luiselli, L., Civetta, F., Masciola, S., Milana, G., and Amori, G. 2012. Spatial turnover and knowledge gaps for African chelonians mirror those of African small mammals: conservation implications. Tropical Conservation Science 5:365–380.

Madsen, O.H. 2003a. Europæiske landskildpadder i vinterhi. Nordisk Herpetologisk Forening 46:53–64.

Madsen, O.H. 2003b. Bredrandet landskildpadde (*Testudo marginata*) – og lidt om andre europæiske landskildpadder, 1. del. Nordisk Herpetologisk Forening 46:129–142.

Madsen, O.H. 2004a. Bredrandet landskildpadde (*Testudo marginata*) – og lidt om andre europæiske landskildpadder, 2. del. Nordisk Herpetologisk Forening 47:8–25.

Madsen, O.H. 2004b. Frilandsanlæg til europæiske landskildpadder. Nordisk Herpetologisk Forening 47:129–146.

Mamasis, D. and Tzoras, E. 2021. Estimation of the population condition of *Testudo marginata* with the capture-recapture method in the responsibility area of the Management Body of Messolonghi lagoon – Akarnanian Mountains. Lousika Achaias: Technical Report, 90 pp.

Martínez-Silvestre, A. 2005. Enfermedades de los Reptiles. Barcelona: Reptilia, 210 pp.

Mayer, R. 1992. Europäische Landschildkröten. Leben – Haltung – Zucht. Kempten: Agrar Verlag Allgäu, 127 pp.

Mittleman, M.B. 1944. The status of *Testudo terrapin* Schoepf. Copeia 1944:245–250.

Mizsei, E., Jablonski, D., Végvári, Z., Lengyel, S., and Szabolcs, M. 2017. Distribution and diversity of reptiles in Albania: a novel database from a Mediterranean hotspot. Amphibia-Reptilia 38:157–173.

Mulargia, M., Corti, C., and Lunghi, E. 2018. The herpetofauna of the Monte Albo, Sardinia (Italy). Russian Journal of Herpetology 25(3):172–176.

Oruçi, S. 2010. Data on geographical distribution and habitats of the Marginated Tortoise (*Testudo marginata* Schoepff, 1792) in Albania. Natura Montenegrina 9(3):495–498.

Panagiota, M. and Valakos, E.D. 1992. Contribution to the thermal ecology of *Testudo marginata* and *T. hermanni* (Chelonia: Testudinidae) in semi-captivity. Herpetological Journal 2:48–50.

Perälä, J. 2002. Occurrence and taxonomic significance of thigh-spurs in *Testudo marginata* Schoepff, 1792 and *Testudo weissingeri* Bour, 1995 (Testudines: Testudinidae). Herpetozoa 14:123–126.

Perez, M., Leblois, R., Livoreil, B., Bour, R., Lambourdiere, J., Samadi, S., and Boisselier, M.C. 2012. Effects of landscape features and demographic history on the genetic structure of *Testudo marginata* populations in the southern Peloponnese and Sardinia. Biological Journal of the Linnean Society 105:591–606.

Peters, W.C.H. 1880. Über die von Hm. Gerhard Rohlfs und Dr. A. Stecker auf der Reise nach der Oase Kufra gesammelten Amphibien. Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin 1880:305–309.

Pfau, B. and Budó, J. 2019. Autochthone und allochthone Landschildkröten in Katalonien. Radiata 28(3):18–34.

Pfau, B., Budó, J., and Martínez-Silvestre, A. 2020. Autochthone und allochthone Landschildkröten in Katalonien – Update 2020. Testudo 29(3):4–20.

Philippen, H.-D. 2008. "Il Gigante" – die größte lebende Breitrandschildkröte (*Testudo marginata*). Marginata 5(4):57–59.

Pitzer, B. 2016. Antifreeze in the blood – about the hibernation of *Testudo marginata* in central Greece. Radiata 25(3):16–21.

Poggesi, M., Agnelli, P., Borri, M., Corti, C., Finotello, P.L., Lanza, B., and Tosini, G. 1996. Erpetologia delle isole circumsarde. Biogeographia 18:583–618.

Prest, D. 2012. Keeping and breeding the Marginated Tortoise, *Testudo marginata*, in the United Kingdom. The Batagur 2:32–38.

Reynolds, P.L. 1984. An enquiry regarding the distribution of *Testudo marginata* on mainland Greece. British Herpetological Society Bulletin 10:37–38.

Rohr, W. 1970. Die Bedeutung des Wärmefaktors für Fortpflanzungsperiodik und Eiablageverhalten südeuropäischer Landschildkröten im Terrarium. Salamandra 6:99–103.

Ruttenstorfer, W. and Artner, H. 1997. Rekordgröße bei der Breitrandschildkröte *Testudo marginata*. Emys 4(5):34–36.

Sacchi, R., Galeotti, P., Fasola, M., and Ballasina, D. 2003.

Vocalizations and courtship intensity correlate with mounting success in Marginated Tortoises *Testudo marginata*. Behavioral Ecology and Sociobiology 55:95–102.

Sanz-Villar, A. and Valverde, F.J. 2000. *Testudo marginata*, mantenimiento y cría. Reptilia 24:56–61.

Schleich, H.-H. 1982a. *Testudo marginata* Schoepff aus Plio/Pleistozänen Ablagerungen SE-Lakoniens (Peloponnes, Griechenland). Paläontologische Zeitschrift 56:259–264.

Schleich, H.-H. 1982b. Ein Fall von Cheloniophagie bei der Griechischen Eidechsennatter, *Malpolon monspessulanus insignitus* (Geoffroy). Salamandra 18:354–355.

Schneller, P. and Pantchev, N. 2008. Parasitology in Snakes, Lizards and Chelonians. Frankfurt am Main: Chimaira, 203 pp.

Schoepff, J.D. 1792. Historia Testudinum Iconibus Illustrata. Erlangae: Ioannis Iacobi Palm, 136 pp.

Schoepff, J.D. 1793. Historia Testudinum Iconibus Illustrata. Fasciculus III et IV. Erlangae: Joannis Jacobi Palm, pp. 33–80.

Schreiber, E. 1875. Herpetologia Europaea: eine systematische Bearbeitung der Amphibien und Reptilien welche bisher in Europa aufgefunden sind. Braunschweig: F. Vieweg und Sohn, 639 pp.

Sechi, L., Moscarelli, R., and Pileri, P. 2020. Planning tourist infrastructures to regenerate marginalised territories: the study case of North Sardinia, Italy. City, Territory and Architecture 7(1):1–12.

Sherborn, C.D. 1902. Index Animalium. London: C.J. Clay and Sons, 1195 pp.

Siebenrock, F. 1906. Zur Kenntnis der mediterranen *Testudo*-Arten und über ihre Verbreitung in Europa. Zoologischer Anzeiger 30:847–854.

Sindaco, R. and Rossi, R. 2020. Annotated checklist of the herpetofauna (Amphibia, Reptilia) of Lefkada Island (Ionian Islands, Greece). Natural History Sciences. Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano 7(2):57– 68.

Sindaco, R., Doria, G., Razzetti, E., and Bernini, F. 2007. Atlante degli Anfibi e dei Rettili d'Italia. Firenze: Societas Herpetologica Italica/Polistampa, 800 pp.

Široký, P., Kamler, M., and Modrý, D. 2004. Long-term occurrence of *Hemolivia* cf. *mauritanica* (Apicomplexa: Adeleina: Haemogregarinidae) in captive *Testudo marginata* (Reptilia: Testudinidae): evidence for cyclic merogony? Journal of Parasitology 90:1391–1393.

Široký, P., Kamler, M., and Modrý, D. 2005. Prevalence of *Hemolivia mauritanica* (Apicomplexa: Adeleina: Haemogregarinidae) in natural populations of tortoises of the genus *Testudo* in the east Mediterranean region. Folia Parasitologica 52:359–361.

Široký, P., Petrželková, K.J., Kamler, M., Mihalca, A.D., and Modrý, D. 2006. *Hyalomma aegyptium* as dominant tick in tortoises of the genus *Testudo* in Balkan countries, with notes on its host preferences. Experimental and Applied Acarology 40:279–290.

Široký, P., Erhart, J., Petrželková, K.J., and Kamler, M. 2011. Life cycle of tortoise tick *Hyalomma aegyptium* under laboratory conditions. Experimental and Applied Acarology 54:277–284.

Soler, J., Martínez-Silvestre, A., Budó, J., Capalleras, X., and Juárez, J.L. 2010. Análisis de la presencia de tortugas terrestres alóctonas y autóctonas asilvestradas en Cataluña (NE España). Boletín de la Asociación Herpetológica Española 21:63–68.

Sperone, E., Crescente, A., Brunelli, E., Paolillo, G., and Tripepi, S. 2010. Sightings and successful reproduction of allochthonous reptiles in Calabria. Acta Herpetologica 5:265–273.

Staerk, J., da Silva, A.R., Jouvet, L., van Dijk, P.P., Pfau, B., Alexiadou, I., and Conde, D.A. 2018. Manual for the differentiation of captive-produced and wild-caught turtles and tortoises (Testudines). Prepared by Species360 under contract for the CITES Secretariat, 28 pp.

Stemmler-Gyger, O. 1963. Ein Beitrag zur Brutbiologie der mediterranen Landschildkröten. Die Aquarien- und Terrarien-Zeitschift (Stuttgart) 16:181–183.

Stemmler-Gyger, O. 1964. Zur Brutbiologie der mediterranen Landschildkröten (II). Aqua Terra (Biberist) 1(9):65–68.

Stille, B. and Stille, M. 2017. The Herpetofauna of Corfu and Adjacent Islands. Frankfurt am Main: Chimaira, 354 pp.

Strachinis, I. 2023. The herpetofauna of the peri-urban forest Seich Sou (Kedrinos Lofos), Thessaloniki, Greece. Ecologia Balkanica 15:1–7.

Strauch, A. 1862. Chelonologische studien, mit besonderer Beziehung auf die Schildkrötensammlung der kaiserlichen Akademie der Wissenschaften zu St. Petersburg. Mémoires de l'Académie Impériale des Sciences de St.-Pétersbourg (7)5(7):1–196.

Strid, A. and Tan, K. 1997. Flora Hellenica, Vol. 1. Koenigstein: Koeltz, 547 pp.

TEWG [Turtle Extinctions Working Group: Rhodin, A.G.J., Thomson, S., Georgalis, G., Karl, H.-V., Danilov, I.G., Takahashi, A., De La Fuente, M.S., Bourque, J.R., Delfino, M., Bour, R., Iverson, J.B., Shaffer, H.B., and van Dijk, P.P.]. 2015. Turtles and tortoises of the world during the rise and global spread of humanity: first checklist and review of extinct Pleistocene and Holocene chelonians. In: Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Iverson, J.B., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 5(8):000e.1–66.

Thomson, R.C., Spinks, P.Q., and Shaffer, H.B. 2021. A global phylogeny of turtles reveals a burst of climate-associated diversification on continental margins. Proceedings of the National Academy of Sciences 118(7):e2012215118.

Tiedemann, F. 1978. Herpetologische Aufsammlungen in Nordsardinien. Annalen des Naturhistorischen Museums in Wien 81:447–463.

Trapp, B. 2007. Amphibien und Reptilien des griechischen Festlandes. Münster: Natur und Tier-Verlag, 279 pp.

Traversa, D., Capelli, G., Iorio, R., Bouamer, S., Cameli, A., and Giangaspero, A. 2005. Epidemiology and biology of nematodofauna affecting *Testudo hermanni*, *Testudo graeca* and *Testudo marginata* in Italy. Parasitology Research 98:14–20.

Trutnau, L. 1994. Terraristik. Stuttgart: Eugen Ulmer Verlag, 248 pp.

Tsunis, G. and Dimitropoulos, A. 1994. The amphibians and reptiles of Lesvos and Chios (Aegean islands, Greece). Biologia Gallo-Hellenica 22:37–48.

TTWG [Turtle Taxonomy Working Group: Bickham, J.W., Iverson, J.B., Parham, J.F., Philippen, H.D., Rhodin, A.G.J., Shaffer, H.B., Spinks, P.Q., and van Dijk, P.P.]. 2007. An annotated list of modern turtle terminal taxa with comments on areas of taxonomic instability and recent change. Chelonian Research Monographs 4:173–199.

TTWG [Turtle Taxonomy Working Group: Rhodin, A.G.J., Iverson, J.B., Bour, R., Fritz, U., Georges, A., Shaffer, H.B., and van Dijk, P.P.]. 2017. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (8th Ed.). Chelonian Research Monographs 7:1–292.

TTWG [Turtle Taxonomy Working Group: Rhodin, A.G.J., Iverson, J.B., Bour, R., Fritz, U., Georges, A., Shaffer, H.B., and

van Dijk, P.P.]. 2021. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (9th Ed.). Chelonian Research Monographs 8:1–472.

Türkozan, O., Kumlutaş, Y., and Ilgaz, Ç. 2001. On the possible occurrence of the Marginated Tortoise, *Testudo marginata*, in Turkey. Chelonian Conservation and Biology 4:208–210.

Türkozan, O., Özdemir, A., and Kiremit, F. 2008. International *Testudo* Trade. Chelonian Conservation and Biology 7:269–274.

Tzoras, E., Panagiotopoulos, A., Bourdalas, A., and Drakopoulos, P. 2019. Herpetological notes of Trizonia island in Corinthian Gulf, Greece. Butlletí de la Societat Catalana d'Herpetologia 27:72–78.

Tzoras, E., Panagiotopoulos, A., and Papaioannou, S. 2021. First record of *Testudo marginata* (Chelonia: Testudinidae) from the island of Samos, Greece (Eastern Aegean). Parnassiana Archives 9:11–14.

Tzoras, E., Hoese, G., and Mamasis, D. 2023. *Testudo marginata* (Marginated Tortoise). Geographic Distribution. Herpetological Review, in press.

van der Kuyl, A.C., Ballasina, D.L.P., Dekker, J.T., Maas, J., Willemsen, R.E., and Goudsmit, J. 2002. Phylogenetic relationships among the species of the genus *Testudo* (Testudines: Testudinidae) inferred from mitochondrial 12S rRNA gene sequences. Molecular Phylogenetics and Evolution 22(2):174–183.

van Dijk, P.P., Lymberakis, P., and Böhme, W. 2004. *Testudo marginata*. The IUCN Red List of Threatened Species 2004: e.T21653A9307262.

Vinke, T. and Vinke, S. 2006. Bemerkenswertes über die Lebensweise der Breitrandschildkröte *Testudo marginata*. In: Daubner, M. and Vinke, T. (Eds.). *Testudo* – häufig gehaltene Arten. Bergheim: Schildkröten im Fokus Sonderband, Dauvi-Verlag, pp. 145–157.

Vlachos, E. 2015. The fossil chelonians of Greece. Systematics – evolution – stratigraphy – palaeoecology. Ph.D. Thesis, Aristotle University of Thessaloniki.

Vlachos, E. 2022. The fossil record of turtles from the Pleistocene of Crete (Greece). Comptes Rendus Palevol 21(35):771–799.

Walbaum, J.J. 1782. Chelonographia oder Beschreibung einiger Schildkröten. Lubeck: J.F. Gleditsch, 132 pp.

Watson, G.E. 1962. Notes on copulation and distribution of Aegean land tortoises. Copeia 1962:317–321.

Wegehaupt, W. 2004. Sardinien, die Insel der europäischen Schildkröten. Kressbronn: Wegehaupt Verlag, 192 pp.

Weissinger, H. 1987. *Testudo graeca anamurensis* ssp. nov. aus Kleinasien. ÖGH-Nachrichten 10/11:14–18.

Willemsen, R.E. 1991. Differences in thermoregulation between *Testudo hermanni* and *Testudo marginata* and their ecological significance. Herpetological Journal 1:559–567.

Willemsen, R.E. and Hailey, A. 1989. Status and conservation of tortoises in Greece. Herpetological Journal 1:315–330.

Willemsen, R.E. and Hailey, A. 2001. Effects of spraying the herbicides 2,4-D and 2,4,5-T on a population of the tortoise *Testudo hermanni* in southern Greece. Environmental Pollution 113:71–78.

Willemsen, R.E. and Hailey, A. 2002. Body mass condition in Greek tortoises: regional and interspecific variation. Herpetological Journal 12:105–114.

Willemsen, R.E. and Hailey, A. 2003. Sexual dimorphism of body size and shell shape in European tortoises. Journal of Zoology 260:353–365.

Wirth, M. 2010. Die Breitrandschildkröte, *Testudo marginata* – schwarze Riesen aus der griechischen Phrygana. Terraria 5(2), Heft 22:32–43.

Zoboli, D., Georgalis, G.L., Arca, M., Tuveri, C., Carboni, S., Lecca, L., Pillola, G.L., Rook, L., Villani, M., Chesi, F., and Delfino, M. 2022. An overview of the fossil turtles from Sardinia (Italy). Historical Biology 35(8):1484–1513.

Citation Format for this Account:

Escoriza, D., Tzoras, E., and Bringsøe, H. 2023. *Testudo marginata* Schoepff 1793 – Marginated Tortoise, Kraspedochelóna, Breshka Malore, Testuggine Marginata. In: Rhodin, A.G.J., Iverson, J.B., van Dijk, P.P., Stanford, C.B., Goode, E.V., Buhlmann, K.A., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 5(17):122.1–25. doi: 10.3854/crm.5.122.marginata.v1.2023; www.iucn-tftsg.org/cbftt/.