MORPHOLOGICAL VARIATION AMONG MIDDLE EASTERN *TESTUDO GRAECA* L., 1758 (SENSU LATO), WITH A FOCUS ON TAXONOMY

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Abstract

Morphological variation is analysed among populations attributed to *Testudo graeca terrestris* Forsskål, 1775 sensu Wermuth but excluding Libyan populations. The problematic nomenclature of Middle Eastern tortoises is discussed. *T. g. terrestris* is found to be a composite of no less than five tortoise species: *T. terrestris* Forsskål, *T. floweri* Bodenheimer, *T. antakyensis* Perälä, one new species of eastern affinities described herein, and another from the Levant which is yet undescribed. These taxa are compared with each other, and briefly with *T. ibera* Pallas, the type of *T. buxtoni* Boulenger, and *T. zarudnyi* Nikolski. *T. zarudnyi* lacks a holotype, and a lectotype is designated.

Key words: Testudinidae; *Testudo*; *Testudo graeca terrestris*; Middle East; morphology, taxonomic review; new species

Prologue

Peter Forsskål, a Finnish-born multitalented scientist and former student of Linnaeus, was head of a natural history excursion to Arabia Felix or Lucky Arabia, i.e. Yemen, between 1761-1763, sponsored by the Danish king (Forsskål, 1950; Niebuhr, 1973; Hansen, 1962). The journey did not have a very lucky ending however, as he and all other crew members died of malaria one after the other, except for Carsten Niebuhr (Hansen, 1962). Niebuhr continued his way to India, and he returned to Copenhagen via Mesopotamia, Cyprus, and Palestine in 1767 only (Niebuhr, 1973). He also posthumously edited and published Forsskål's field notes (Forsskål, 1775). Forsskål was primarily an outstanding botanist (systematist), but he is also fondly remembered as the founding father of Red Sea ichthyology (Nielsen, 1993), and for his less advertised activities in social sciences and politics (Steinby, 1971). Forsskål could not have guessed that over two centuries after his death his name would be drawn into one of the most problematic cases in the history of chelonian taxonomy.

Introduction

Currently, all Mediterranean to West-Central Asian tortoises from North Africa and southern Europe to Asia Minor, Near East, Caucasus and eastern Iran featuring thigh-spurs are generally accepted to represent a single species *Testudo graeca* Linnaeus, 1758 with numerous subspecies, by most contemporary reviewers (e.g., Iverson, 1992; Gasperetti et al., 1993; Schleich et al., 1996). *Testudo graeca terrestris* Forsskål, 1775 sensu Wermuth (1958) occurs as the single representative of *T. graeca* from N Syria as far west as Libya (e.g., Wermuth, 1958; Wermuth & Mertens, 1961; Pritchard, 1979; Ernst & Barbour, 1989), or, as above but including southern Turkey (Hatay province) (Herrn, 1966; Eiselt & Spitzenberger, 1967; Schleich, 1987, 1989; among others). According to Gasperetti et al., (1993) and Disi (1998), *terrestris* is confined to S Turkey, Syria, possibly Iraq, Lebanon, Israel, and western Jordan. This taxon is characterized almost solely by a small size and a pale-yellow coloration according to Wermuth (1958), although tortoises from within the above mentioned range were known to vary considerably by both their dimensions and coloration, as suggested by classic texts (e.g., Siebenrock, 1913; Flower, 1933).

Testudo ibera Pallas, 1814, *Testudo zarudnyi* Nikolski, 1896 and *Testudo floweri* Bodenheimer 1935, the latter originally described with a single sentence, "The tiny variety found in the Negeb may be called *T. floweri*, in honor of the well-known zoologist" (Bodenheimer, 1935), were classified as subspecies of *T. graeca* in a revision by Mertens (1946), following earlier writings by Stanley Flower (1924, 1926, 1933), and in the wake of the theoretical concept of polytypic species and "Rassenkreise" gaining popularity among zoologists. Two years before the publication of Bodenheimer's (1935) "Animal Life...", Flower (1933) wrote about a "South Palestine form", "the smallest geographical race of *T. graeca*, which has superficial resemblance to *T. leithii* in its small size and yellow colour" and that it "can be found between Hebron and Beersheba" (= Be'er Sheva), in what is currently the Judean hill country in Israel ("*T. leithii*" = *Testudo leithii* Günther, 1869 i.e. *T. kleinmanni* Lortet, 1883; but see Perälä, 2001 in press). Flower's text is a rebuttal of writings by Tristram (1884) – who apparently follows Lortet (1883) – about the occurrence of *T. kleinmanni* in southern Levant. Flower, a productive semi-professional zoologist whose father was once Director of the British Museum (Natural History), received four living specimens of the "South Palestine form" from Major Portal, which animals the latter had collected between Gaza and Bir Salem near Jaffa (Yafo) (Flower, 1933). One of these specimens is preserved in the London Natural History Museum. The dry shell in question (BMNH 1933.9.3.4) led Loveridge & Williams (1957) to conclude that its existence seemed to support the view of a "dwarf race" living in southern Palestine (Fig. 1).

Testudo graeca floweri, a taxon Mertens (1946) admits to never having seen a single specimen of, was attributed to *T. g. ibera* by Mertens & Wermuth (1955) based on Mertens' correspondence with J. Hoofien of Tel Aviv, who doubted the validity of *floweri* (Wermuth, 1958). Hoofien recognized no differences between tortoises from Gaza and his children's pet collected in Tel Aviv (copy of original letter examined by the author courtesy of J. Buskirk, who received it from Hoofien). Meanwhile, *T. terrestris* Forsskål was revalidated with a designated type locality "Arabia" in a paper dealing with long forgotten names (Wermuth, 1956). The name was already earlier rejected by Strauch (1862), and Anderson (1896), the last mentioned who states it is useless trying to identify this animal by its description, but that it may possibly be *Testudo leithii* from "the desert country between Ismailia and El Arish" (NE Egypt–Sinai). Wermuth (1956) himself considered to request the suppression of this name by the International Commission on Zoological Nomenclature. However, after having studied specimens from Aleppo (Syria) and Derna (Libya), he came to other thoughts. *T. floweri* Bodenheimer was suddenly placed in junior synonymy with *Testudo terrestris* Forsskål, 1775 (Wermuth, 1958). The resurrection of the name for Middle Eastern tortoises required Wermuth to ask the invalidation of the nominal species *Testudo terrestris* Fermin, 1765 by the ICZN (Wermuth, 1958), a radical change in attitude as noted by Bour (in: David, 1994). *T. terrestris* Forsskål was originally described from "Lohajæ", i.e. Al Luhayyah in modern Yemen, but other geographical localities mentioned are Cairo ("Káhira"), Aleppo, Lebanon Mountains ("...montem Libanon"), Lebanon ("Libanon") and Lattakia (Forsskål, 1775). Wermuth (1958) restricted the type locality of *T. terrestris* (as *T. g. terrestris*) to "Libanon-Gebirge, Israel", which in this case can only mean the southernmost foot of the Lebanon Mountains in Upper Galilee. Forsskål did not visit this region, but his posthumous editor and travel companion Niebuhr voyaged in northern Levant and Palestine (Niebuhr, 1973). Gasperetti et al. (1993) suggested that it may actually be Niebuhr who is responsible for the name. After Forsskål's death, Niebuhr sent all natural history specimens collected by Forsskål by mail from Bombay, via London, to Copenhagen, and it was only thereafter, on his return journey, when he visited Aleppo, Libanon, and Palestine as the sole surviving member of the Danish expedition (Niebuhr, 1973).

In a study of skull characters, Bour (1989) suggested the separation of *T. g. floweri* with a type locality in "Negev, Palestine, probably outskirts of Gaza" and a distribution in SW Israel only. Bour (1989) emended the type locality for *terrestris* to the vicinity of Aleppo in Syria without explanation, as noted by Gasperetti et al. (1993), the distribution of which taxon was said to include southern Turkey, Lebanon, Israel, western Jordan, Syria, and northern Iran. Additionally he suggested that the skulls of subspecies *ibera* and *graeca* may be distinguished by subtle differences, and that it may be that both populations have reached their specific individuality, and that two distinct species exist: *T. graeca* (occidental) and *T. terrestris* (oriental) (Bour, 1989). Based on this inference, and because *terrestris* is an older name and has thus priority over *ibera*, David (1994) classified *Testudo graeca* into two species: (1) *Testudo graeca* and, (2) *Testudo terrestris*, the latter with several subspecies of oriental affinities, and including *T. terrestris floweri*. This classification generated hefty criticism among peers (Fritz et al, 1996; Ernst et al., 2000). *Testudo antakyensis* Perälä, 1996 was described some time ago from Antakya, Hatay province in S Turkey, in a paper the author would rather want to forget (Perälä, 1996). Fritz et al. (1996) acknowledge the problems surrounding the name *terrestris*, but adhere to the generally accepted *T. graeca* taxonomy on conservative grounds until further evidence is provided, and regard *T. floweri* and *T. antakyensis* as junior synonyms of *T. g. terrestris*. The phenotypic variation shown by SW Syrian *T. g. terrestris* is considered an adaptation to local conditions according to Gloger's rule, and a substrate race phenomenon with no taxonomic relevance, by the same authors.

It is noteworthy that, while the vast majority of herpetologists with papers on *T. graeca* systematics have taken Wermuth's (1958) *T. g. terrestris* at face value, Israeli herpetologists have traditionally considered *floweri* a valid taxon, in addition to *T. g. terrestris* (e.g., Arbel, 1984; Werner, 1988; Mendelssohn & Geffen, 1995; Mendelssohn in: Bringsøe & Buskirk, 1998). In his survey of the Israeli herpetofauna, Werner (1988) states that, "In the SW of the range of *T. graeca* in Israel, the delimitation of *T. g. floweri* remains unclear; in the NE of the country, the taxonomic significance of the morphological distinction of *T. graeca* on the Golan awaits clarification". With regard to *T. g. terrestris* from the Golan and Mt. Hermon, Sivan & Werner (1992) stress their conviction of a taxonomic problem lurking there.

It is of taxonomic interest that, both *T. terrestris* Forsskål and *T. floweri* Bodenheimer lack type specimens. The type of *terrestris* (originally not designated) is said to be "apparently lost" (Webb in: Iverson, 1992). Wermuth's (1958) *T. g. terrestris* is not fixed to any specimen either. Bodenheimer (1935) did not designate a type for *T. floweri*, and there is no reference to possible syntypes. Contrary to Crumly's (1988) opinion, the single adjective "tiny" characterizing *T. floweri* (Bodenheimer, 1935: 197) does not constitute a description, according to Ernst et al. (2000). It is possible that Bodenheimer did not intend to describe a species at all. The type of *T. antakyensis* is stored in London (BMNH 1998.70).

Field and museum work has made it very clear that morphological variation among tortoises from the

Middle East is much greater than current taxonomy suggests. In this study, populations from the region given in Bour (1989) for his *T. terrestris* and *T. g. floweri* are examined. The Cyrenaican population, attributed also to *T. g. terrestris* by Wermuth (1958), is taxonomically distinct (Pieh & Perälä, 2002 in press) and will not be discussed here. *T. g. ibera* and *T. g. terrestris* are full species according to Gmira (1993), and Lapparent de Broin (2000a, 2001), and *T. graeca* sensu lato (i.e., with its numerous subspecies) is not a natural group (Perälä, 2002 in this volume). Therefore, *ibera*, *terrestris* and *zarudnyi* are here considered to represent full species by default.

Materials and Methods

Material examined. – Museum specimens from the Middle East were examined in 16 collections: The Natural History Museum, London (BMNH); Field Museum of Natural History, Chicago (FMNH); Museum of Zoology, Hebrew University of Jerusalem (HUJ); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Muséum d'Histoire Naturelle Lyon (MG); Muséum National d'Histoire Naturelle, Paris: (MNHN) Zoology and, (MNHN-P) Palaeontology; Staatliches Museum für Tierkunde, Dresden (MTKD); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Naturhistorisches Museum Wien (NMW); Chelonian Research Institute, Oviedo (PCHP); Staatliches Museum für Naturkunde, Stuttgart (SMNS); Zoological Museum, Tel Aviv University (TAU); Florida Natural History Museum, University of Florida, Gainesville (UF); Zoological Museum, University of Jordan, Amman (UJZM); National Museum of Natural History, Washington D.C. (USNM). Museum acronyms follow suggestions by Leviton et al. (1985) except for MNHN-P, and PCHP (formerly Peter C. H. Pritchard collection). Additional specimens were investigated in the collection of the author at the University of Bristol, UK (JP) and, in the field (JP-F) in Turkey, Syria, Jordan and Israel. Field data are deposited in the Finnish Museum of Natural History, Helsinki. Data were also derived from two living tortoises, collected by Ted Papenfuss (MVZ) in May 2000 near Kerman, Iran, courtesy of T. P., James Parham (MVZ), and Jim Buskirk. Specimens examined, and localities, are listed in the Appendix. Specimens from the UJZM partly lack reference numbers which were dissolved in formaldehyde over the years – thus exact locality data are not always available for these (but the material is from Jordan; Disi pers. comm.). Some populations from the easternmost Levant (Trans-rift chain in Syria and Jordan) await analysis, and are not dealt with here. Because males are morphologically more distinct than females, subsequent analyses deal in principle with males only, with a few exceptions where this was necessary.

Grouping. – The material was divided into five basic populations based on morphological homogeneity, and which categories are considered to represent natural groups: (1) *T. terrestris*, for the group occurring at the emended type locality of *T. terrestris* (Bour, 1989). This group shows a rough distribution from Aleppo north- and eastwards along the Turkish-Syrian border region to Mosul in Iraq. (2) *T. antakyensis* from the Iskenderun Bay - southern Amanos Mountains region in Turkey towards the south, approximately as far as the Golan Heights in Israel, and adjacent regions in SW Syria and NW Jordan. (3) "Iran" from NE Iraq, towards the southeast along the Zagros Mountains in Iran as far as approximately Kerman. (4) "Highland" (Hi). Basically a highland population on the Cis-rift mountain chain (at least) in Israel (and the Lebanon border area?). (5) "Lowland" (Low). A coastal population from near Gaza along the Israeli coast to at least Beirut in Lebanon. [Basically same group as "*floweri*" in Pieh & Perälä (2002 in press), except for a few specimens from northeastern localities.] Additional specimens used in comparisons: (a) Five specimens of true *T. ibera* Pallas, 1814. Four of these come from Tbilisi (Tiflis) in the middle portion of the Kura River valley (in Georgia, Caucasus), the type locality of *ibera* according to Mertens (1946). One *ibera* specimen originates from Baku, Azerbaijan. (b) Four specimens of true *T. zarudnyi* Nikolski, 1896 from Khorāsan province in Iran. (c) The type of *Testudo buxtoni* Boulenger, 1920 from "Manjil, N Persia" (Boulenger, 1920) ("Menjil", according to the original specimen tag), on the southern coast of the Caspian Sea – this taxon being generally considered a junior synonym of *T. ibera* (Wermuth & Mertens, 1961, among others).

Systematics. – On theoretical and empirical grounds (Frost and Hillis, 1990; Collins, 1991, 1992; Frost et al., 1992; Frost & Kluge, 1994; Grismer, 1999; among others), taxonomic inferences are made in accordance with the lineage-based evolutionary species concept (Simpson, 1961) in its revised form (Wiley, 1978, and later).

Measurements. – Quantitative data were recorded from 45 shell characters using calipers straight-line to the nearest 0.1mm, as in Perälä (2001 in press). Recorded characters included maximum (not midline) carapace length (CL), maximum plastron length (PL), midline (minimum) plastron length (PL-m), maximum mid-body width within central bridge area at marginals 5-6 (MI), maximum width of shell at posterior marginals 7-9 (MA), maximum (not midline) gular scute length, maximum (combined, i.e. left plus right) gular scute width (GU-w), gular scute height in a 90 degree angle to horizontal plastron level as the minimum distance between gular scute/humeral midline crossing and dorso-median gular lip surface (GU-h), maximum shell height (HE), maximum inner width of anterior shell opening parallel to horizontal level (ASO-w), maximum inner height of anterior shell opening parallel to median axis (ASO-h), left minimum bridge length (BR), maximum (combined) humeral scute width (and subsequent plastron scute widths) in a 90 degree angle to median axis (HUM-w), maximum (combined) pectoral scute width (PEC-w), maximum (combined) abdominal scute width (ABD-w), maximum (combined) femoral scute width (FEM-w), maximum (combined) anal scute width (AN-w), maximum nuchal scute length (NU-l), maximum nuchal scute width (NU-w), maximum gular midline (intergular) length (GU-m), left humeral midline (interhumeral) seam length (HUM-m), left pectoral midline (interpectoral) seam length (PEC-m), left abdominal midline (interabdominal) seam length (ABD-m), left femoral midline (interfemoral) seam length (FEM-m), maximum anal midline (interanal) seam length (AN-m), maximum width of first vertebral scute (V1-w), maximum width of second vertebral scute (V2-w), maximum width of third vertebral scute (V3-w), maximum width of fourth vertebral scute (V4-w), maximum width of fifth vertebral scute (V5-w), maximum median length of first vertebral scute (V1-l), maximum median length of second vertebral scute (V2-l), maximum median length of third vertebral scute (V3-l), maximum median length of fourth vertebral scute (V4-l), maximum median length of fifth vertebral scute (V5-l), first costal length as the minimum straight-line distance between the anteriormost and posteriormost contact points with adjacent (normally first and fifth) marginal scutes (C1), costal two ventral length along marginals (C2), costal three ventral length along marginals (C3), costal four ventral length along marginals (C4), maximum dorsal width of supracaudal scute (SUP-d), maximum ventral (= max. total) width of supracaudal scute (SUP-v), maximum median length of supracaudal scute (SUP-l), maximum head width (HEAD), minimum distance between right eye and tympanum (EYE-TY) and, minimum distance between right eye and nostril (EYE-NO). Additionally, categorical variables pertaining to shell, scutes, limbs, head, tail, osteology, coloration, markings and potential abnormalities were examined routinely, when present.

Data Analysis. – Statistical analyses were performed using MINITAB, Release 12.1 (Minitab, Inc.). Measurements used in univariate analysis of variance (one-way ANOVA) were standardized for CL. Basic investigations of data, ANOVA, post-ANOVA procedures, and standardization of data follow methodologies described in Perälä (2001 in press), except that no specimens with a maximum carapace length of less than 100 mm were used in morphometric analyses due to allometry. Significance level for ANOVA and related tests was set at $\alpha = 0.05$. Experiments were made to determine which parameters could be used to separate the populations in multivariate space. This was done using Factor Analysis (FA) on unstandardized data with maximum likelihood extraction and varimax rotation. Discriminant Function Analysis (DFA), using linear discriminant function (Mahalanobis distance) and additionally cross-validation to compensate for an optimistic apparent error rate, was used to test how reliably specimens were classified into known groups using FA scores from the first three factors. Only museum specimens were used in multivariate analyses.

Results and Discussion

The "Iran" population was found to be morphologically distinct. Because this population differs significantly from all other populations in the *T. graeca* s.l. species complex, and because no clinal effects with regard to other tortoise populations can be determined – indicating an independent evolutionary history – it is here described as:

Testudo perses sp. nov.
Zagros Mountains tortoise
(Figs. 2–6)

Holotype. – FMNH 130820, adult female in alcohol from "West Central Iran: 3mi W village of Lalabad & 25 mi NW Kermānshāh, in rocks among bushes, above large spring" (in Kermānshāhān province, approximately at 34°27' N 46°50' E), collected by Charles A. Reed, 4 March 1960.

Paratypes. – 18 specimens; locality and collectors' data as catalogued, comments in brackets. Males: FMNH 73484, Iran: Zagheb, between Durud and Khurramabad, coll. Henry Field (no date); FMNH 73488, Iran: Khurramabad, coll. Henry Field (no date); FMNH 74504, Iraq: Erbil Liwa, Valley of Bastura R., W Salahedin-Erbil Rd, ca 1700', coll. Charles A. Reed, 15 October 1954; FMNH 74950, Iraq: Erbil Liwa, Nahiyah of Shaklawah, grassy field near village of Sisawah, ca 2500', coll. Charles A. Reed, 15 October 1954; MCZ 53824, Iran: Luristan, between Durud & Khurramabad, H. Field, (possibly 1950); MCZ 53836, Iran: Luristan, Khurramabad, H. Field, (1950?); MTKD D 31816, Iran: Yazd, ca. 550 km SO von Teheran, 1000-1500 mNN, S. Tschimer don. VII 1991; MVZ 10753, Mt. Kuh-e Segoch, btw Sirac and Mahan - Kerman highway, SE Kerman, Iran, coll. T. Papenfuss, June 1999; NMW 32898:2, Iran: 60-70 Km E Neyriz, Kerman, 3 km W d. Naturschutzgebiet, (no data on collector or date); USNM 158528 (subad.), Iran: Kurdistan, Sanandaj, 32 km WNW, Robert G. Tuck Jr., 20 May 1965. Females: BMNH 76.11.23.2, Mahi (= Māhī), Karman, SE Persia, 6500 ft, coll. W. T. Blanford [no date but certainly between 1870-1872 (Blanford, 1876)]; FMNH 141621, Iran: Isfahan, Galatappeh, hibernating in hole among rocks, D. M. Lang, W. S. & J. K. Street, 23 December 1962; FMNH 141631, Iran: West Azerbaijan, 23 mi SE Rezaiyeh, D. M. Lang, W. S. & J. K. Street, 18 September 1962; MCZ 53817, Iran: Luristan, Khurramabad, H. Field, (1950?); MCZ 53825, Iran: Luristan, between Durud & Khurramabad, H. Field, (1950?); MCZ 53834, Iraq: Havidian village at foot of Jebel Barradort, near Rowanduz, no data on collector & date; NMW 32897, Iran: 20 km NE Dehbid (NNE Schiraz), 2400 m. Gebirge, Polsterpflanzen, leg. Eiselt, 22.6.1968; USNM 154515 (subad.), Iran: Kermanshah, 42 km W, Robert G. Tuck, Jr., 28 June1964.

Type locality. – Vicinity of Lalabad village, some 25 mi NW of Kermānshāh, Kermānshāhān province, W Iran.

Etymology. – The specific name *perses* is a Latin masculine noun for a Persian, pertaining to the main distribution and the masculine or robust overall appearance of the new species.

Distribution. – *Testudo perses* has a huge distribution basically along the NW-SE oriented Zagros Mountains and adjacent chains, and commencing in the north from at least Esendere (Hakkari province) in SE Turkey, and areas W of Lake Urmia in Iran, and extending through NE Iraq, Lorestān and Kermānshāhān provinces in NW and West-Central Iran, as far SE as Yazd, and the vicinity of Kermān (Kermān province). The taxonomic status of spur-thighed tortoises occurring in the

Balūchestān va Sīstān province in SE Iran remains unclear.

Description. – *T. perses* is distinguished from all other taxa in the genus *Testudo* sensu stricto (in the sense of Gmira, 1995; Lapparent de Broin, 2000a, 2000b, 2001; Hervet, 2001; Perälä, 2002 in this volume), by the following combination of characters subject to individual variation and pertaining to adults and both sexes unless stated otherwise: Robustly built tortoise with a xiphiplastral hinge (showing xiphiplastral kinesis), ventrally short diagonal length of first costal, short fifth vertebral, dorsally wide supracaudal, very broad fourth vertebral and, with extremely long and wide anal scutes; anal midline seam (interanal) typically much longer than seam separating femorals; transverse seam separating humerals and femorals typically double-S-shaped, with or without a laterally straight proximal section; broad first vertebral; first vertebral almost always widest and sharp-edged anteriorly and, frequently elongated anteriorly in its proximal parts (modestly infundibular); fifth vertebral ventrally narrow; midbody (at bridge) of medium width relative to length, and rounded in dorsal view; in lateral view, outline of carapace mostly ventrally indented at anterior portion of first vertebral and, posteriormost marginals covering part of supracaudal (lateral outline of semi-adults can resemble that of *T. kleinmanni*); outline of carapace relatively angulate in anterior view, with perpendicular outermost (upper) surfaces of bridge marginals (i.e. lateral surfaces above the marginal crest which is well developed), edged upper arch (at costals) and relatively flat top with a slightly elevated proximal portion (central vertebral area); in posterior view the lower outline has a bell-shaped curvature due to marginal flaring, especially in males; carapace highest at slightly less than 2/3 length; supracaudal slightly flared to the rear, wide and almost box-shaped (rectangular) in females except for a vertically thin to more pronounced, laterally oriented and spiky offshoots towards the marginals in ventral corners, and with a more or less 90-100 degree inner angle between dorsolateral and dorsal sides; supracaudal of males more massive, usually flared to the rear (only rarely inverted) and also with ventrolateral offshoots, the inner angle between dorsolateral and dorsal sides being in the region of 90-120° and, with proximally elongated, smoothly U-shaped ventral extension becoming less apparent and more V-shaped towards the southeast of the range; outermost lateral extensions of bridge marginals (the crest separating dorsal and ventral portions of the scutes) typically in a 12-17 degree angle with respect to horizontal level, the open angle oriented cranially; inguinals relatively large, usually longer than broad, typically not touching femorals, and associated with smaller accessory scales (which may touch femorals); anterior and posterior free marginals flared to strongly flared, and serrated, convexly-rimmed towards the outside, and typically without much reversion; anteriormost (1st) marginals elongated, often protruding infront of second marginals; posteriormost (11th) marginals often extending posteriorly beyond supracaudal; lateral flaring of posterior marginals begins at, and is inclusive of, 8th marginal; 8th marginal featuring an anteriorly skewed, ventrally oriented half-dome to pyramid-shaped bulge with a more or less rounded apex and outer surface; greatest width at 8th or (more often) 9th marginals; anterior and posterior free marginals may extend beyond bridge marginals in dorsolateral (and ventrolateral) view, more so in males than in females; anterior plastron lobe ventrally convex in lateral view; nuchal scute (cervical) long and relatively narrow, and widest posteriorly or at around 3/4 length; gulars clearly set off from anterior lobe, and relatively long both ventrally and dorsally; length of bridge very variable, and not typically relatively shorter in males than in females (as opposed to most *Testudo* s. s.); anterior feet relatively massive and thick, featuring relatively long, almost drop-shaped, triangularish to four-edged scales with longest lateral sides facing claws, closely packed against the surface, and with generally not much overlap between scales; fore-feet with five relatively straight claws, the innermost of which are shorter than the rest, posterior extremities with four claws; tail relatively long, longer in males than in females, and very slender towards the tip; tip of tail features mostly a conspicuously enlarged, medium-sized twin-scale (not claw); upper thigh region typically with (at least) one horny spur on each thigh; thigh-spurs very broad at base; outline of open eyes in life more round than oval; bony carapace rim proximally convex towards the anterior; triturating surfaces of maxilla featuring only one longitudinal, modestly elevated central ridge; parietal bones straight or just very slightly notched in lateral view; supraoccipital crest (parietal-supraoccipital complex) long.

Basic coloration (in alcohol): Ground colour of carapace and plastron from pale greenish-yellow (USNM 154515; subadult), to light or very dark-brown colour with a reddish or orange tinge (typical), or even completely grey or black. Plastron is usually not much darker than carapace.

Markings: Small juveniles (post-hatchlings) with a transverse dark band located centrally on 1st vertebral; 2nd to 5th vertebrals with small, more or less round central blotches with thin lateral offshoots of dark pigment not connected with the blotch. In lateral view, 1st costal features a horizontal dark stripe located at 1/3 height and running parallel to horizontal level; in 2nd and 3rd costals this band is also at 1/3 height, but it runs in a slight angle so that the posterior end is located highest. 4th costal has a central blotch. 2nd to 4th costals feature additionally centrally located vertical stripes at the anteriormost seams. Plastral markings may be completely absent, or there are tiny black blotches on the lower central region of the abdominals. Anterior marginals may feature dark semi-triangular markings. Bridge marginals with dark bands along anterior vertical borders. Posterior marginals with anterior and dorsal bands connected dorsolaterally. Larger juveniles and semi-adults: The central blotch on 1st vertebral divides laterally into two sister flecks. Costals may retain vertical bands near the anteriormost side of areolae, horizontal bands fade away or develope into larger, irregular blotches. Separately from these, extremely thin centrally oriented stripes appear at anterior and lateral, and anterior and ventrolateral borders of vertebrals and costals. These may develope into dark bands. The supracaudal may feature triangular lateral markings. These may later fade away, especially in the dorsal border region. Markings on marginals become darker and more defined. The plastron is irregularly pigmented with dark grey to blackish elements, darkest regions being located posterolaterally. Gulars and anals may be lighter coloured than other scutes. In adults, regions on and adjacent to the areolae seem to feature most pigmentation, dark blue-grey to black blotches with irregular borders. Markings around scute edges diffuse into centrally oriented rays which may or may not be connected to the central flecks. Dark blotches may appear on posterior ventral corners of (especially) the bridge marginals, or around the marginal crest. Many adult specimens are completely dark: grey, intensively dark-brown or black, with hardly any markings visible. Basic coloration of head and leg scutes varies from greenish-grey and grey to (as typical) light or deepish-dark chocolate-brown. The ground colour on most parts of the head is either uniform or it may feature blackish regions especially in the snout area, and darker brown to black, or, occasionally found yellowish scales towards the temple. Completely black heads are a rarity. The jaw region features often a dark grey to blackish triangular pattern, or a "Schnautzendreieck" sensu Eiselt & Spitzenberger (1967). Leg scutes have mostly a dark-brown, dark-violet to blackish tip, also on the hind legs. The base of leg scutes may be pale brown, pale grey or yellowish. Claws are light or dark chocolate-brown to dark violet and dark grey. Skin in soft parts is pale greyish, light brown or reddish-brown coloured. Eyes in life are very dark brown.

Description of holotype. – Large adult female; 1st - 4th vertebrals wide in dorsal view, the 1st being anteriorly elongate at proximal region, and considerable broader anteriorly than posteriorly, with slightly convex lateral and concave anterior sides; 5th vertebral relatively narrow and scallop-shaped; free marginals somewhat flared and serrated, more so posteriorly; 1st marginals relatively long and wide with lateral sides slightly proximally oriented in dorsal view; anal scutes very long; interabdominal seam length > interanal > intergular > interhumeral > interpectoral > interfemoral; transverse seam separating humerals and pectorals double-S-shaped without straight proximal section; seam separating pectorals and abdominals relatively straight transversely, slightly posteriorly bent laterally; gular scute complex more or less heart-shaped; inguinals large; ventral dome present on 8th marginals; supracaudal modestly flared to rear with relatively weakly developed lateral offshoots (ventrally); lateral outline of the carapace with marked anterior notch (depression) at region of 1st vertebral; carapace highest at vertebral 3, at around 2/3 length; vertebrals with minute humps at areolae; anterior outline of shell edged; both thighs with one spur on each; tail with a small tubercle at tip (enlarged twin-scale); basic coloration of shell chocolate-brown with lighter yellowish-brown tinge towards scute edges; vertebrals, costals and plastral shields with irregularly-shaped large, blackish areolar blotches with a deep-blue tinge; especially anterior and lateral scute borders with mottled centrally oriented ray-pattern; marginals with diffuse blotches on areolae, and a mottled ray-pattern: markings most pronounced on 3rd and 8th, and bridge marginals; last three posteriormost marginals with dark dorsal and anterior rays; anteriormost marginals with diffuse lateral rays; nuchal scute with anterior dark pigmentation; supracaudal with faint, laterally and dorsally initiating dark rays oriented towards the center of scute growth; head with few yellowish but mostly light and dark brown scutes, and a dark brown to lightly violet-tinged "Schnautzendreieck"; anterior limbs featuring light brown, and posterior extremities dark brown, scutes, with dark brown tips; claws on front feet lightly brownish; claws on hind feet dark brown-violet; skin greyish-violet.

Dimensions of holotype. – CL: 194.0 mm, PL: 180.8 mm (93.2% of CL), PL-m: 171.0 mm (88.1%), MI: 143.0 mm (73.7%), MA: 149.0 mm (76.8%), GU-l: 29.9 mm (15.4%), GU-w: 35.1 mm (18.1%), GU-h: 19.5 mm (10.1%), HE: 99.4 mm (51.2), ASO-w: 97.7 mm (50.4%), ASO-h: 30.7 mm (15.8%), BR: 92.6 mm (47.7%), HUM-w: 91.1 mm (47.0%), FEM-w: 95.8 mm (49.4%), AN-w: 75.7 mm (39.0%), NU-l: 17.7 mm (9.1%), NU-w: 7.3 mm (3.8%), GU-m: 27.1 mm (14.0%), HUM-m: 20.3 mm (10.5%), PEC-m: 17.4 mm (9.0%), ABD-m: 65.1 mm (33.6%), FEM-m: 8.7 mm (4.5%), AN-m: 39.4 mm (20.3%), PEC-w: 126.6 mm (65.3%), ABD-w: 128.8 mm (66.4%), V1-w: 56.3 mm (29.0), V2-w: 55.0 mm (28.4%), V3-w: 63.9 mm (32.9%), V4-w: 54.6 mm (28.1%), V5-w: 51.6 mm (26.6%), V1-l: 44.5 mm (22.9%), V2-l: 41.0 mm (21.1%), V3-l: 37.0 mm (19.1%), V4-l: 40.2 mm (20.7%), V5-l: 43.0 mm (22.2%), C1: 56.1 mm (28.9%), C2: 44.0 mm (22.7%), C3: 39.5 mm (20.4%), C4: 36.7 mm (18.9%), SUP-d: 33.7 mm (17.4%), SUP-v: 55.1 mm (28.4%), SUP-l: 26.5 mm (13.7%), HEAD: 29.3 (15.1%), EYE-TYMP: 7.8 (4.0%), EYE-NO: 9.5 (4.9%).

Record length. – The largest *T. perses* specimen examined measures 240.0 mm (NMW 32898:2; male).

Remarks. – *Testudo perses* specimens have commonly been attributed to *T. g. ibera*, or mistaken for *T. zarudnyi* both in museum records and in literature (e.g., Pritchard, 1966; Tuck, 1971; Anderson, 1974, 1979; Pieh & Perälä, 2000; all in part). Natural history information for animals representing *T. perses* is given in Pritchard (1966, in part), and Anderson (1979, in part). Contrary to previously published information (Iverson, 1992) or "common knowledge", specimen ZIL 8738 cannot represent a holotype of *Testudo zarudnyi* Nikolski, 1896 – according to Articles 72.1.1., and 73.1.3. of the ICZN Code (ICZN, 1999). Upon describing *Testudo zarudnyi*, Nikolski (1896) did not designate a name-bearing type (holotype or syntypes), nor did he provide a depiction of his new taxon, or references to any existing illustrations. The only reference in the original description to material on which the description was based is provided in the title of the article ("Diagnoses Reptilium et Amphibiorum novorum in Persia orientali a N. Zarudny collectorum"), i.e. specimens which were collected by Zarudny in eastern Persia. This material must be regarded to represent syntypes in the sense of Article 72.1.1. of the ICZN Code (ICZN, 1999). At least two of the syntypes survive. One is BMNH 1947.3.5.17 (formerly BMNH 99.7.25.1) donated to London by the St. Petersburg Museum as the "Type of *Testudo* *zarudnyi*" and catalogued as syntype – not paratype as in Pritchard (1966). The second syntype is ZIL 8738, which is the same animal ("No. 8738") from "Birdschan" (city of Birjand) depicted by Nikolski only a year after the original description (Nikolski, 1897). The type locality of *T. zarudnyi*, of which there is no other reference to in the original description than eastern Persia (Nikolski, 1896), is "Berge in der Provinz Birdschan, Ost-Persien", according to Mertens (1946), with reference to Nikolski (1897): "Habitat in montibus provinciae Birdschan in Persia orientali". However, a Province called Birdschan (Birjand) is non-existent in former Persia, and modern Iran. Thus it is more likely that Nikolski (1897) meant the mountains in the vicinity of the city of Birjand, located in what is both historically and currently the Khorāsan province. To maintain taxonomic stability, and to fix the name *T. zarudnyi* Nikolski, 1896 to a standard of a single name-bearing type, one of the (at least two) existing syntypes, ZIL 8738, a mounted dry specimen (apparently a male) from "Birdschan" is hereby designated lectotype of *Testudo zarudnyi* Nikolski, 1896 [Tab. XVII in Nikolski (1897), and Fig. 7]. The locality of collection of ZIL 8738, namely Birjand in Khorāsan province, NE Iran (32°53' N 59°03' E), becomes automatically the type locality of *Testudo zarudnyi*.

The present author has not had access (as of July 2001) to the St. Petersburg collection to examine ZIL 8738, thus mensural information for BMNH 1947.3.5.17 – the former syntype and current paralectotype from "Zirkuch, eastern Persia", i.e. Zir Kuh (34°52' N 57°25' E) in Khorāsan province NE Iran – is presented here for direct comparisons with the type of *T. perses*. Though BMNH 1947.3.5.17 is superficially similar to the type of *T. perses*, characters standardized for maximum length highlight, not only the vast amount of very prominent differences between the two specimens (and species), but also the limitations of human eyes and perception as accurate and useful instruments in biological systematics.

Dimensions of paralectotype BMNH 1947.3.5.17 (adult female; Fig. 8). – CL: 213.5 mm, PL: 193.0 mm (90.4% of CL), PL-m: 181.0 mm (84.8%), MI: 152.0 mm (71.2%), MA: 159.0 mm (74.5%), GU-l: 30.7 mm (14.4%), GU-w: 36.4 mm (17.0%), GU-h: 23.9 mm (11.2%), HE: 103.0 mm (48.2), ASO-w: 98.9 mm (46.3%), ASO-h: 30.1 mm (14.1%), BR: 101.0 mm (47.3%), HUM-w: 93.1 mm (43.6%), FEM-w: 98.2 mm (46.0%), AN-w: 77.6 mm (36.3%), NU-l: 14.3 mm (6.7%), NU-w: 7.3 mm (3.4%), GU-m: 28.3 mm (13.3%), HUM-m: 25.2 mm (11.8%), PEC-m: 12.2 mm (5.7%), ABD-m: 68.1 mm (31.9%), FEM-m: 14.4 mm (6.7%), AN-m: 37.4 mm (17.5%), PEC-w: 136.5 mm (63.9%), ABD-w: 142.0 mm (66.5%), V1-w: 47.9 mm (22.4), V2-w: 55.1 mm (25.8%), V3-w: 63.5 mm (29.7%), V4-w: 56.8 mm (26.6%), V5-w: 59.8 mm (28.0%), V1-l: 42.3 mm (19.8%), V2-l: 43.7 mm (20.5%), V3-l: 43.1 mm (20.2%), V4-l: 47.5 mm (22.2%), V5-l: 38.4 mm (18.0%), C1: 62.6 mm (29.3%), C2: 50.7 mm (23.7%), C3: 44.2 mm (20.7%), C4: 40.6 mm (19.0%), SUP-d: 34.6 mm (16.2%), SUP-v: 50.9 mm (23.8%), SUP-l: 31.6 mm (14.8%).

Results from multivariate statistics. – In Factor Analysis based on plastral seam lengths, length of bridge, height of anterior carapace opening, fifth vertebral length, V1 and V4 widths, *T. perses* is fully separated from *T. ibera*, *T. zarudnyi* and the type of *T. buxtoni* in an FA score plot on axes Factor 2 (F2) and Factor 3 (F3) (Graph 1). Rotated factor loadings, variances and percentages of information captured are tabulated in Table 1. An FA score plot of F1 + F2 (Graph 2) in which the type of *T. buxtoni* is completely isolated from all other populations on F1 axis suggests that, *T. buxtoni*, currently regarded as a junior synonym of *T. ibera*, is likely to be a valid taxon. This possibility was already hinted at by Chkhikvadze & Bakradze (1991). The taxonomic status of this nominal species will be dealt with at a later stage (Perälä, Pieh & Berglas, in prep.). Additionally, and to give only a few examples, *T. zarudnyi* differs from all other populations (with more than one representative in the sample, i.e. excluding the type of *T. buxtoni*) by its relatively narrow anterior carapace opening (ASO-w/CL ratio) (ANOVA $F_{6,\ 112} = 8.49$, $P < 0.0001$; Fishers's pairwise differences: $P < 0.01$ in all cases). *T. ibera* is likewise distinct by its wide midbody (MI/CL ratio) (ANOVA $F_{6,\ 153} = 3.47$, $P < 0.003$; Fishers's pairwise differences: $P < 0.01$ in all cases). Because the scope of this article is to study variation among populations attributed to *Testudo graeca terrestris* in the sense of most authors, further comparisons inclusive of *T. zarudnyi* and *T. ibera* are omitted until forthcoming publications.

To concentrate on the remaining populations, both *T. perses* and *T. terrestris* (as defined in Materials and Methods) can be discriminated against each other, and with regard to the strictly Levantine populations when the latter are being pooled (combined *T. antakyensis*, Hi and Low populations), by FA scores derived from plastron seam lengths. This is illustrated in an F1 + F2 factor score plot (Graph 3): *terresris* is very well separated on F2 axis with only minor overlap with respect to the Levantine groups, and *perses* is fully separated on F1 axis from any other category. Relevant FA statistics are presented in Table 2. Discriminant Function Analysis classifies 92.1% of individuals correctly into known groups. Correct classification with cross-validation is 90.6% (Table 3): It is noteworthy that *T. terrestris* is the only population in which the representative males have typically (i.e. with only a few exceptions) the interanal seam shorter than the interfemoral, as shown in a bivariate plot (Graph 4).

The Levantine populations, *T. antakyensis*, the "Highland" and "Lowland" groups, which show a very high degree of morphological convergence in their overall appearance, are well separated in multivariate space using FA scores from the following characters: length, plastron length, width of anterior carapace opening, fifth vertebral width, first costal length and, dorsal and ventral supracaudal width. FA statistics for these parameters are found in Table 4. When populations are compared against each other in one-to-one plots using FA scores from analysis of all three populations, the morphological individuality of each group becomes obvious. *Testudo antakyensis* is fully isolated from the "Highland" population in an F1 + F2 plot (Graph 5), and it is also separated from the "Lowland" group on axes F2 + F3, as well as F1 + 3 (Graph 6). The "Highland" and "Lowland" populations are best discriminated against each other in F1 + F2, or F2 + F3 plots featuring no overlap between population clusters (Graph 7). Discriminant Function Analysis with all three purely Levantine groups inclusive classifies 94.7% of specimens correctly into known groups. The percentage of correct classifications in DFA with cross-validation is 93.0 (Table 5). Interestingly, two of the misclassified *antakyensis* specimens (HUJ 9963 and TAU 14001, both classified as "Lowland"), come from the same locality (Ramat-Ha, Golan). Whether the initial grouping was incorrect, or if these specimens indeed represent "Lowland" (which would be interesting), or whether these have even more eastern affinities (with reference to the suspected distinction of populations in SW Syria and W Jordan), remains to be seen.

When morphometric characters – which reflect morphological structure – are compared individually among all five groups, again a high degree of morphological divergence is apparent as follows (all characters relative to maximum length except for CL itself):

T. antakyensis vs *T. terrestris*. – *Testudo antakyensis* is on the average significantly smaller than *terrestris* (though size without proportional divergence is not considered a very useful taxonomic character). This species differs additionally from *terrestris* by: a smaller maximum (posterior) width; shorter gulars; a narrower anterior shell opening; a longer bridge; a narrower combined humeral scute width; a greater anal width; a shorter nuchal scute (cervical); a longer humeral seam; a shorter femoral seam; a longer anal seam; a narrower plastron across pectorals; narrower 1st, 2nd, 3rd and 4th vertebrals; a shorter second vertebral; longer 4th and 5th vertebrals; a shorter supracaudal and, a greater head width – altogether by 21 significantly divergent characters. ANOVA statistics with Fisher's pairwise comparisons for these and more parameters across all groups are presented in Table 6.

Testudo antakyensis vs *Testudo perses*. – *T. antakyensis* differs from the new species from the Zagros Mountains by: a more diminutive average length; a longer plastron along the midline; a narrower carapace posteriorly; shorter gulars; a higher anterior shell opening; a narrower plastron across humerals and anals; a shorter nuchal scute; a shorter intergular seam; a longer interpectoral; a shorter interanal; narrower 1st, 2nd, 3rd and 4th vertebrals; a longer 5th vertebral; a longer 1st costal; a narrower dorsal surface of the supracaudal; a shorter supracaudal and, a greater head width – a total of 20 significant differences (Table 6).

Testudo antakyensis vs the "Highland" population. – *Testudo antakyensis* shows major divergence from the southern "Hi-group" by: a greater average length; a narrower and lower anterior carapace opening; a narrower plastron across humerals; a narrower nuchal scute; a longer interfemoral seam; a narrower plastron across pectorals; a wider 1st vertebral; a wider 5th vertebral; a shorter first costal; a longer supracaudal and, a narrower head – 12 significant differences in all (Table 6).

Testudo antakyensis vs the "Lowland" group. – *Testudo antakyensis* differs from the "Low-population" by: a longer plastron both maximally and along the midline; a greater shell height; a narrower anterior shell opening; a shorter bridge; a narrower plastron across humerals; a longer and narrower nuchal scute; a longer interanal seam; a longer 3rd vertebral; a shorter 1st costal and, a narrower head – totalling 12 prominent differences (Table 6).

"Highland" vs "Lowland" group. – The Levantine "Highland" population can be discriminated against the southern "Lowland" population by: a small average length; a longer plastron both maximally and along the midline; a shorter bridge; a longer nuchal scute; a longer interanal seam; a ventrally narrower supracaudal and, a shorter supracaudal – totalling 8 major morphometric differences (Table 6).

"Highland" vs Testudo terrestris. – The "Highland" animals are different from *T. terrestris* by: a diminutive average length; a narrower posterior width of the shell; a higher anterior shell opening; a greater width across anals; a shorter nuchal scute; a longer interhumeral seam; a shorter interfemoral; a longer anal seam; narrower 1st, 2nd, 3rd and 4th vertebrals; a shorter 3rd vertebral; a longer 1st costal; a shorter 3rd costal; a shorter supracaudal and, a broader head – adding up to 17 divergent parameters (Table 6).

"Highland" vs Testudo perses. – The "Highlanders" differ from *T. perses* by: a very much smaller average length; a shorter plastron (maximum and midline length); a narrower posterior portion of the shell; shorter gulars; a higher anterior plastron opening; a narrower plastron across anals; a shorter and broader nuchal scute; a shorter intergular seam; a longer interpectoral; a shorter interanal; narrower 1st, 2nd, 3rd and 4th vertebrals; a longer 5th vertebral; a longer 1st costal; a narrower dorsal surface of the supracaudal; a shorter supracaudal and, a wider head – 21 discriminative characters in all (Table 6).

Testudo perses vs *Testudo terrestris*. – The new species is different from *T. terrestris* by 15 characters, namely by having: a greater average length; a longer plastron both maximally and along the midline; a narrower anterior plastron opening; a longer bridge; a greater plastron width across anals; a narrower nuchal scute; a longer intergular seam; a shorter interpectoral; a shorter interfemoral; a longer interanal; a wider 4th vertebral; a shorter 5th vertebral; a shorter 1st costal and, a broader dorsal surface of the supracaudal (Table 6).

Testudo perses vs "Lowland". – *Testudo perses* is distinguished from the "Lowlanders" by 22 characters: a prominent average length; a greater plastron length (maximal and along midline); longer gulars; a narrower and lower anterior carapace opening; a greater width across anals; a longer and narrower nuchal scute; longer gulars; a shorter pectoral (interpectoral) seam; a longer interanal; broader 1st, 2nd, 3rd and 4th vertebrals; a longer 3rd vertebral; a shorter 5th vertebral; a shorter 1st costal; a wider dorsal surface of the supracaudal; a longer supracaudal and, a narrower head (Table 6).

Testudo terrestris vs "Lowland". – *T. terrestris* differs from the Levantine "Lowland" population by: a greater average length; a greater plastron length (maximum and midline); a lower anterior shell opening; a narrower plastron across anals; a longer nuchal; a longer interfemoral seam; a shorter interanal; wider 1st, 2nd and 3rd vertebrals; a longer 3rd vertebral; a shorter 1st costal; a longer 3rd costal; a longer supracaudal and, a narrower head – 16 divergent characters altogether (Table 6).

Descriptive statistics for males among all groups discussed herein, inclusive of *T. ibera* and *T. zarudnyi*, are presented in Table 7. Table 8 features descriptive statistics for *T. perses* females, as well as *T. perses* males with respect to characters not included in male comparisons across all groups.

Differences. – It is not within the scope of this paper to characterize the four remaining populations (*perses* was described earlier) in any great detail. This is to be accomplished in forthcoming publications and inclusive of females. Without going into detail it can be noted however that, basic coloration of shell, head and extremities of animals from within the Levant proper, and additionally with regard to *terrestris*, can vary greatly from a bright yellow ground colour to almost black in every population, depending on individual, ontogenetic stage, and, as it seems, geography. The geographical aspect is of interest because it may have a further taxonomic dimension. For example, *antakyensis* hatchlings or post-hatchlings, which feature typically a yellowish-orangy ground colour, are dark grayish-brown in the Golan, much like the adults (Fig. 9). This indicates a genetic fixation. However, strictly morpho-anatomically these animals fall within the overall limits of *T. antakyensis* with the exception of a few characters – such as anterior narrowing of the first vertebral among others – which are here considered to represent clinal effects until further evidence surfaces. The earlier example is not an isolated case relative to geographically linked colour patterns, and this subject requires further study. Markings are, at least superficially, identical among all groups (in adults): Dark blotches on vertebral and costal (and sometimes marginal) areolae are typical of animals in every population. Many characters pertaining to other features than colour are also highly convergent. *Testudo antakyensis* has on average (with exceptions) the 5th vertebral broader than any other, as noted in the description (Perälä, 1996) - but this turned out to apply to many males in other strictly Levantine populations as well (especially the coastal "Lowland" population). Fifth vertebral width is thus not a very useful character among Levantine populations (but very good with respect to Turkish "*ibera*", or *terrestris*). However, there are a few morphological peculiarities by which to distinguish between undissected animals, enabling classification according to population (subject to individual variation and pertaining to males unless stated otherwise). The supracaudal in adult *T. antakyensis* is usually ventrally incurved, and it protrudes heavily towards the rear (caudally) in most cases. It also forms a distinct hump in lateral view. Many females feature this character too, which led to an occasional mix-up of sexes in Perälä (1996). Such a distinct supracaudal is usually not found as pronounced in the "Highland" population, and the feature is much weaker in "Lowland". Among the "Lowlanders" which are essentially bulky and tank-like animals, the posterior carapace rim is gently V-shaped in dorsal (and ventral) view because the posterior marginals are hardly flared nor strongly serrated, and the supracaudal is more or less in line with the angle of the posterior arch (in lateral view). The supracaudal is not much, or not, incurved. The fifth vertebral is extremely well visible in dorsal view in males of *T. antakyensis* and the "Lowland" tortoises due to a (laterally) gently curved posterior carapace slope. This slope is much more abruptly descending in members of the "Highland" population. The first vertebral in *antakyensis* is anteriorly elongated towards the relatively narrow nuchal scute (Fig. 10), heavily widened towards the anterior in northern populations, but this lateral angle decreases towards the south. Animals with a rounded or close to round V1 are a true rarity among *antakyensis*, but these are frequently encountered in especially the "Lowland" population. Among the "Highlanders", the first vertebral is typically more or less box-shaped, and not much elongated anteriorly (elongate box-shaped in some "Lowlanders). Males of the "Lowland" population have mostly a short nuchal scute, a very short plastron leaving the long and massive, but strikingly conically-shaped tail well exposed in ventral view (Fig. 11). Members of *antakyensis* and "Lowland" have a big tail tubercle (twin-scale) (Fig. 12) at the tip of tail, but this character is found, although not as prominently, in tortoises throughout the Middle East (and it is more pronounced in males than in females in the other groups). In *T. terrestris*, the interanal is typically shorter than the interfemoral, and 1st through 4th vertebrals are very wide in comparison. In other Levantine groups 1st, 2nd, 3rd and 4th vertebrals are rather narrow, and the interanal is normally longer than the interpectoral (Figs. 13-14). All populations can be identified by their skulls. More features, characters pertaining to osteology and better definitions will be given in subsequent papers, but some useful characters have already been used in a phylogenetic analysis, for which data are presented elsewhere in this volume (Perälä, 2002).

Geographical aspects. – (Detailed information on locality records are found in the Appendix.) *Testudo perses*, with an amazingly large distribution, seems to be largely restricted to the Zagros Mountains and adjacent regions. *T. perses* is potentially fully isolated from *Testudo zarudnyi* by the Dasht-e Lūt and the Kavir deserts on the Iranian Plateau with vast areas of salt marshes, most likely inappropriate habitats for tortoises to live in. The westernmost record for *perses* is at a relatively low elevation in Mosul, Iraq (NMW 18668:1, female), where *perses* is found in sympatry with *terrestris* (NMW 1411, female). The river Tigris seems to be delimiting the distribution of *terrestris* effectively in its norththeastern (Diyarbakir) and eastern parts (Mosul), thus it is possible that the specimens quoted above were collected from the opposite banks of Tigris, and the populations do not occur strictly syntopically. This is pure speculation, however. In the north, *T. terrestris* is possibly delimited by the East Anatolian highland (northernmost records from Gaziantep and Şanlıurfa) but it is found at least at an altitude of 1000m (Gaziantep), and potentially in the west by the northernmost remains of the Levantine Trans-rift chain east of the Amanos Mountains and, desert areas west and south of Aleppo. *T. terrestris* and *T. antakyensis* seem to be fully allopatric. Tortoises found in the Amouk Plain are *Testudo antakyensis*. Whether tortoises near Adana, in Tarsus and e.g. Silifke at the eastern foot of Taurus mountains belong to *terrestris*, *antakyensis* or something else, is still under investigation. The distribution of *T. g. anamurensis* Weissinger, 1987 – a very distinct taxon (most certainly a full species by all standards) – does not stretch this far east, according to field and museum work, as opposed to information given by Weissinger (1987). Before continuing with the three strictly Levantine groups, the Levant as a region of zoogeographical importance is discussed briefly.

The manifold geomorphology of the Levant – consisting basically of four north-south oriented topographical features, the coastal plain, the western (Cis-rift) and eastern (Trans-rift) mountain chains, with a rift-valley between the two last mentioned (Por, 1975) – and the region's relatively great variety of habitats and distinct biogeographical zones are expressed by an extraordinary diversity of faunal elements with different zoogeographical origins, a situation largely neglected, or generally not well understood by researchers from outside the area (Haas, 1952; Kosswig, 1955; Wolfart, 1987; Werner, 1987, 1988). This zoogeographical heterogeneity, probably as important as that of, e.g., Central America or Wallacea, can be highlighted by the fact that Israel and Jordan together, countries with relatively small areas, are occupied by more reptile species than nearby located Turkey or Egypt (Haas, 1952). The herpetofauna of Israel alone consisted of at least 102 taxa by 1985, 15 of which were not known to occur in neighbouring Jordan (Werner, 1988). The Levant is characterized by a rich terrestrial faunal composition and exchange of northern, eastern and southern elements, and Por (1987) regards the Levantine landbridge as a historical biogeographical filter, going as far as describing it as the most important crossroads of biotic exchange on the globe. Blondel & Aronson (1999) describe the Levant as the "crossroads of crossroads". Taking these aspects into consideration, the relatively high diversity of terrestrial chelonians found in the Levant ought not to be too surprising.

Testudo antakyensis spreads at least from the Amouk Plain, and mountains east of Antakya and, Iskenderun region and southern parts of the Amanos mountains (Çevlik near Samandağı) in the north, southwards through western Syria (Homs), Lebanon (Halba, and Beka'a valley at 900m), Upper (Qiryat Shmona) and Lower Galilee (Ramat Hadasa), Mt. Hermon and Golan in Israel, and to northern Jordan (Ramtha area). Whether the relatively southern locality Tel Aviv for a *T. antakyensis* specimen (NMW 19001:2) is correct, or if it was collected elsewhere and the data reflect merely the place of residence of the donator (Mendelssohn), is unknown. (The locality "Zaoutor el Charque" in Lebanon cannot be found on any map consulted, and additional information would be much appreciated.) The range of the "Lowland" population is restricted to the Levantine coastal plain and lowland areas more inland in at least Israel and Lebanon, between the vicinities of Be'eri and Nirim near Gaza in the south, Tel Aviv, Caesarea etc. in Central Israel, Sha'ar Ha'Amakim (Plain of Esdraelon) in Galilee, and Beirut (Lebanon). However, "Lowlanders" can apparently be found at somewhat higher elevations too (e.g., Kefar Uriya, west of Jerusalem). Based on fieldwork, the present author is fairly confident that the "Lowland" population is spread also further north along the coast, possibly as far as into Turkey. *T. antakyensis* and the "Lowlanders" occur in sympatry in at least Galilee, if not further north at relatively low altitudes. The "Highland" population is spread from near Gaza, Kerem Shalom, and areas near Be'er Sheva and Dimona in northern Negev along the Judean hills to Galilee, and also entering Golan (even Mt. Hermon), and possibly (South?) Lebanon (MNHN-P, uncatalogued, Tables XV A and XVI A in Gmira, 1995; and confiscated animals said to be from Lebanon). Thus this population is spread much over whole of Israel (and without doubt the West Bank, but there are no data / specimens: A. Ezzughayyar of Birzeit University, pers. comm.), though it is generally confined to mountainous areas. The "Highlanders" seems to occur more or less between what are called the Bodenheimer line (northern Negev) and the Nehring line (Upper Galilee / Israel-Lebanon border area), the latter being a rough dividing region where northern faunal elements start decresing rapidly towards the south (Por, 1975). The southernmost record is from Hazeva in the Arabah, eastern Negev (TAU 12568, adult, deformed female). This population shows a degree of sympatry with both *T. antakyensis* (Galilee, Golan), and the "Lowland" group (at least near Gaza and in Galilee, possibly at the southern foot of Judean hills).

The taxonomic status of tortoises occurring along the Trans-rift chain in SW Syria and much of W Jordan is under investigation.

There is no indication of hybridization between any of the discussed populations. Previous field accounts (sightings) of alleged wild hybrids between *ibera* (sensu Mertens, 1946) and *terrestris* (sensu Wermuth, 1958) in Turkey (Eiselt & Spitzenberger, 1967) are likely to be based on typical representatives of those various natural tortoise populations occurring in Asia Minor and the Levant, some of which still lack detailed analysis (as yet unpublished evidence suggests that true *ibera* is confined to Caucasus only).

Taxonomic rank. – Taken the bewildering morphological variation found among the five populations into account, and to think that these five groups together (with the exception of easternmost samples contained herein) have been taken to represent one subspecies only, according to most authors, is rather hilarious. It is evident that morphological divergence alone among these five homogenous populations is so great as to suggest independent evolutionary histories for each and every one, and thus a full species status irrespective of species concept used. Though its theoretical framework is considered flawed, aspects of sympatry are of additional interest with respect to the Biological Species Concept. All five groups are considered to be evolutionary (and biological, for that matter) species, some of which have an uncertain taxonomic identity, as will be discussed below.

Taxonomy. – The resurrection of the name *Testudo terrestris* Forsskål, 1775 for Middle Eastern tortoises may not have been the most appropriate of taxonomic actions (Wermuth, 1958), but the name is currently valid. The sole descriptive account in the original paragraph naming *terrestris* indicates that the land tortoise attains a length of one foot (Forsskål, 1775), eliminating effectively Anderson's (1896) view that *T. kleinmanni* could have been meant. Tortoises do not occur in Al Luhayyah in Yemen, the primary locality mentioned for *T. terrestris* (Forsskål, 1775), excluding Forsskål himself, who died in Yemen, from being behind the name. It does not invalidate the name however that, as it seems, the description is based on Niebuhr's subsequent work in the Levant, and which work he chose to publish under Forsskål's name along Forsskål's original data. As Niebuhr's role is not explicit in the original publication (Forsskål, 1775), the authorship of the name remains with Forsskål (ICZN, 1999: Art. 50.1.1.). As for a type, Niebuhr could have taken additional specimens back to Copenhagen after the majority of (i.e. Forsskål's) material had been shipped from Bombay. It is unlikely that he would have gone home empty-handed. A lot of material in the Forsskål collection in Copenhagen was destroyed in bombings by the British in 1807 (Nielsen, 1993). In any case, the type is untraceable, or it has never even existed (which does not affect the availability of the name). As the name *T. terrestris* Forsskål, 1775 is valid, and the reference to the tortoises' relatively great size applies to the Levantine population occurring in Aleppo exclusively, it is concluded that Bour's (1989) emended type locality is the only one possible out of those localities mentioned in the description, and thus correct and valid. To clarify the taxonomy of Middle Eastern tortoises, and to fix the status of *T. terrestris* Forsskål, a neotype, based on a specimen from Aleppo, will be designated in a forthcoming publication (Bour & Perälä, in prep.).

As for the southern populations, Werner's (1988) comment on the Israeli situation, as quoted in the Introduction, could not have been more accurate. The taxonomic status of *T. antakyensis* does not pose problems. These are the tortoises of Werner (1988) from the Golan, and basically more northern regions. But two additional tortoise species (excluding *T. kleinmanni* s. l.) exist in the southern Levant, the "Highland" and the "Lowland" populations (Figs. 15-16). These must be attached to names. Ernst et al. (2000) do not consider *T. floweri* as being a valid (available) name, but instead a nomen nudum. There are three alternatives to proceed. One would be not to accept *T. floweri* in the sense of ICZN Article 13.1.1. (ICZN, 1999), and to describe a new taxon but to retain the name (as a new name) with new authorship for one of the two southern populations, or, as the second option, to describe both populations as new species. The first alternative would be fair to the name *T. floweri*, but not to its original author Bodenheimer. The second alternative would betray both. Therefore, a third option is favoured. It is in the interest of the zoological community, and to maintain stabile nomenclature, to accept Crumly's (1988) view that the adjective "tiny" in Bodenheimer (1935) constitutes a description. Indeed, southern tortoises are characterized by a small size. Additionally, *T. floweri* was first listed in the Zoological Record in 1937, and it has been considered valid by Israeli herpetologists for a long time. The problem is that there is no existing type. Both southern populations live in sympatry in the vicinity of Gaza, the type locality of *T. floweri*, as emended by Bour (1989). Flower's (1933) "South Palestine form", as judged by BMNH 1933.9.3.4, represents the "Highland" population which occurs in, but is not confined to, the area "between Hebron and Be'er Sheva" and which is found also near Gaza. The single specimen in any collection labeled *T. g. floweri* is TAU 13022 (adult male) from Nirim close to Gaza. This specimen is a member of the "Lowland" population, confined basically to the coastal plain. The "Lowlanders" represent those animals which the Israeli herpetologists attribute to *floweri*, and which population is not necessarily characterized by a pale yellow coloration, and which is not restricted to northern Negev near Gaza, as opposed to statements by Buskirk (1985), and Bringsøe & Buskirk (1998). There is an overall clinal effect for a paler appearence towards the south, but this applies to the "Highland" population as well, and dark specimens are no rarity. Tortoises found on sandy soils tend to be paler, too. Because local herpetologists, who are after all the ones who should know best, attribute the coastal ("Lowland") species to *T. floweri* Bodenheimer, this stand is also taken here. In consequence, it is a necessity to designate a neotype for *T. floweri* to fix the name, whereas the "Highland" species awaits description. These tasks will be tackled in a subsequent publication.

Suggested trivial names. – *T. zarudnyi*: Zarudny's tortoise. *T. floweri*: Flower's tortoise (Fig. 17). *T. antakyensis*: Antakyan tortoise. *T. terrestris*: Mesopotamian tortoise.

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Specimens examined

Testudo antakyensis

BMNH 1971.1860, Homs, Syria; BMNH 1998.70, Turkey: Antakya, mountains E of the city, near St. Peter's cave church (holotype of *T. antakyensis*); FMNH 25356, 25358-9 (3 spec.), NW Syria: Hatay, Amouk Plain (= Turkey); FMNH 74503, Lebanon; FMNH 166441-45 (5 spec.), Lebanon: Zaoutor el Charque; FMNH 166449-50 (2 spec.), Lebanon; FMNH 206138-61 (23 spec.), Lebanon; MTKD D 40200, Hattay, Cevlik; HUJ 16012, Golan: Bab el Hawa; JP 96.6.5, Antakya, mountains E of the city, near St. Peter's cave church; JP-F 95.10.1-3, 7, 8, 11, 14 (7 spec.), Turkey: Antakya, Mountains E of the city; JP-F 96.6.7, Cevlik, N of Samandag, Turkey; JP-F 97.3.26+33, Antakya: mountains near St. Peter's church; JP-F 97.3.28-29, 31-32 (4 spec.), Cevlik, a few km N of Samandag, Turkey; JP-F 98.4.8, JP-F 98.4.46, JP-F 98.4.48-50, Golan: Kuneitra viewpoint, lower E slopes of Mt. Avital, Israel; JP-F 98.4.11, Golan: Lake shore ca 2 km NE Merom Golan, Israel; JP-F 98.4.14 and 15, Golan: Odem Forest (= Ha'ayalim Forest), road 978 to Mas'ada, Israel; MG 42006114 (ex 120), Antioche, Syrie; NMW 18517:1, Antakya, St. Petrus-Felsenkirche, Türkei; NMW 18517:4, Strand von Samandag bei Antakya, Türkei; NMW 18519:1, Antakya, Türkei; NMW 18670:3, Türkei: Iskenderun; NMW 18670:4, Türkei: Esentere bei Iskenderun; NMW 19001:2, Israel: Tel Aviv; SMNS 3889, Djeba, Libanon; SMNS 3892, Guvens am Ost-Fuss des Amanus, Anatolien; TAU 4887, Qiryat Shmona; TAU 8591, Masada (= Mas'ada, Golan); TAU 9039, Golan: Kuneitra; TAU 9040, Ramat Hadasa; TAU 9462, Hermon, 1400m; TAU 9963, Ramat-Ha, Golan; TAU 11501, Hermon, 1500m, near Mary Mahn; TAU 12585, Baka'a, 15 km S of road Beyroot-Damaskus at 900m; TAU 13124, Lebanon; TAU 14001, Ramat Ha Golan - Shaar Ha Golan; UJZM without number (164.0 CL), Ramtha area, Jordan (specimen bag marked "A" by J. P.)

Testudo buxtoni

BMNH 1947.3.5.16 (ex 1920.8.6.1), Manjil, N Persia (= Mandjil, N Iran), Pres. Bombay Nat. Hist. Soc., holotype of *Testudo buxtoni.*

Testudo floweri

BMNH 1933.9.3.3, no detailed locality data (S. Flower, don.); HUJ 932, Kefar Uriya; HUJ 942, Coastal Plain: Dunes of Caesarea; HUJ 972, 1 km S to Kefar Shemaryahu near Herzliya, HUJ 988, Caesarea; JP-F 98.4.21, Bitronot Be'eri Nature Reserve, off road 232 near Gaza Strip, Israel; MCZ 42206, Beyrooth, Syria (= Beirut, Lebanon); TAU 7935/7936, Pardes Hana; female (2 catalogue numbers; card file: 7935, tag: 7936); TAU 9285, Btw Lachish & Amazia; TAU 9924, Sha'ar Ha-Amakim; TAU 12756, Be'eri area; TAU 13022, Nirim; UF 13991, Givatyim; UF 13931, Israel, 1.5 km, 80 deg. E mouth of Yargon River; UF 14842, 5 km, 14 degrees E Hadera;

"Highland" population (= undescribed species)

BMNH 1933.9.3.4, Btw Gaza and Bir Salem near Yaffa; HUJ 899, Bab-el-Wad (on Judean Hills); HUJ 945, Ramat Ha-Shavim; HUJ 967, Bar'am Forest (in Upper Galilee); HUJ 975, Jerusalem; HUJ 982, Eshta'ol: Judean Hills; HUJ 983, Gaza strip, probably Dir al Bolah (= Deir el Balah); HUJ 986, Sedot Mikha, 225m elevation; HUJ 16023, 8 km E SE of Bet-Guvrin; HUJ-R 16180, Jerusalem, Valley of the Cross; HUJ-R 16182, Judean Hills: nr Even Sapir (= SW of Jerusalem); JP-F 98.4.18, Golan: Banias Springs, Israel; JP-F 98.4.19, Upper Galilee: about 2 km W of Bar'am Forest on road 89, Israel; JP-F 98.4.26, Pine forest near Eshkolot, 2 km NE from road 31, S of Lahav, Judean Hills, Israel; JP-F 98.4.31+33, about 2 km S of Lahav Forest off road 325, Judean Hills (pine forest), Israel; JP-F 98.4.37, JP-F 98.4.40, Switzerland Forest near Poriya, SW of Lake Kinneret, Lower Galilee, Israel; JP-F 98.4.56, Btw Judeida & Tel Al, 2 km E of road 70, Galilee (E of Akko), Israel; MNHN 1988-2098, Bet Shemesh, 20 km W Jerusalem sur la route de Tel Aviv, Israel; MNHN-P uncatalogued female, Lebanon (Gmira, 1995: plates XV A, XVI A); SMNS 3888, Am See Tiberias; TAU 4877, Nirim; TAU 5190, Dimona; TAU 5247, Tidhar; TAU 9041, Gilboa Mt.; TAU 9461, Hermon, 1400m; TAU 9925, Sha'ar Ha-Amakim; TAU 10221, Ibelin (Adona) (= Jeblin); TAU 12332, Sheffayim; TAU 12356, East of Kerem Shalom; TAU 12396, Nahal Gishron/Nahal Garof; TAU 13683, Dvir, 1km E of (= Devira);

Testudo ibera

MCZ 5302, Russia: Tiflis (= Tbilisi, Georgia); MNHN 9327, Makou (= Baku, Azerbaijan); MNHN 9335, Georgia: Tiflis (= Tbilisi); MTKD D 11164, Tbilissi, Georg. SSR (= Tbilisi, Georgia); USNM 14315, Tiflis, Kaukasus - Tbilisi, Caucasus.

Testudo perses sp. nov.

BMNH 76.11.23.2, Karman, SE Persia, 6500ft (paratype); FMNH 20887, Persia: Yazd-i-Khast; FMNH 21028, Persia: Yazd-i-Khast; FMNH 73483, Iran: Zagheb, between Durud & Khurramabad; FMNH 73484, Iran: Zagheb, between Durud and Khurramabad (paratype); FMNH 73487, Iran: Luristan, Khurramabad; FMNH 73488, Iran: Khurramabad (paratype); FMNH 74504, Iraq: Erbil Liwa, Valley of Bastura R., W Salahedin-Erbil Rd, ca 1700' (paratype); FMNH 74950, Iraq: Erbil Liwa, Nahiyah of Shaklawah, grassy field near village of Sisawah, ca 2500' (paratype); FMNH 130820, West Central Iran: 3mi W village of Lalabad & 25 mi NW Kermanshah, in rocks among bushes, above large spring (holotype of *T. perses*); FMNH 141621, Iran: Isfahan, Galatappeh, hibernating in hole among rocks (paratype); FMNH 141630, Iran: W. Azerbaijan, 23mi SE Rezaiyeh; FMNH 141631, Iran: West Azerbaijan, 23 mi SE Rezaiyeh (paratype); FMNH 207646, Iraq: Erbil Liwa; MCZ 53817, Iran: Luristan, Khurramabad (paratype); MCZ 53818-22 (5 spec.), Luristan, Khurramabad; MCZ 53823, Luristan, Khurramabad; MCZ 53824, Iran: Luristan, between Durud & Khurramabad (paratype); MCZ

53825-29 (5 spec.), Iran: Luristan, between Durud & Khurramabad (paratype); MCZ 53833, Iraq: Havidian village at foot of Jebel Barradort, near Rowanduz; MCZ 53834, Iraq: Havidian village at foot of Jebel Barradort, near Rowanduz (paratype); MCZ 53835, Luristan, Khurramabad; MCZ 53836, Iran: Luristan, Khurramabad (paratype); MCZ 53837, Luristan, Khurramabad; MTKD D 31816, Iran: Yazd, ca. 550 km SO von Teheran, 1000-1500 mNN (paratype); MVZ as yet uncatalogued, field ref. number: TP 26158, Iran: Azerbaijan-e-Gharbi province, 14 km SE Dizaj, by Aj Bulak rd, Urmiyeh; MVZ 10753, Mt. Kuh-e Segoch, btw Sirac and Mahan - Kerman highway, SE Kerman, Iran (paratype); MVZ 11083, Kuh-e Lalezar Mt 5 km Qale-ge Askar, S Kerman, Iran; NMW 18556:6, Türkei: Esendere, Hakkari, (= about 50 km W Lake Urmia at Iranian border); NMW 18668:1, Mosul, Mesopotamien (= Mosul, Iraq); NMW 32897, Iran: 20 km NE Dehbid (NNE Schiraz), 2400 m. Gebirge, Polsterpflanzen (paratype); NMW 32898:2, Iran: 60-70 Km E Neyriz, Kerman, 3 km W d. Naturschutzgebiet (paratype); PCHP 499, Jeh-i-Sheni nr. Kermanshah (skull); USNM 153753, 120 km W Kermanshah; USNM 154515, Iran: Kermanshah, 42 km W (paratype); USNM 158528, Iran: Kurdistan, Sanandaj, 32 km WNW (paratype); additionally 2 living specimens from near Karman, Iran, collected by Papenfuss, May 2000 (as described in Materials and Methods).

Testudo terrestris

BMNH 1935.11.4.170-173, Antep, 3000ft, SE Asia Minor (= Gaziantep, Turkey); MCZ 83201, Near Diyarbakir (= Diyarbakir, Turkey); NMW 1411, Mosul, Mesopotamien (= Mosul, Iraq); NMW 1236, NMW 1900, NMW 1902, NMW 1905, NMW 1906, NMW 1907, NMW 1910, NMW 1912, NMW 1913, NMW 1914, NMW 15089:2, NMW 15089:3, NMW 15089:6, NMW 18663:1-3, NMW 18664:1, NMW 18664:2, NMW 18664:3, NMW 18664:4, NMW 18664:5, NMW 18664:6, NMW 18665:1, NMW 18665:4, NMW 18666:3, NMW 18666:5, NMW 18667:3, NMW 18667:4, NMW 18667:5, NMW 18667:6, NMW 18667:7, NMW 18667:8, NMW 18669:1-10 (10 spec.), Urfa, Mesopotamien (= Şanlıurfa, Turkey); NMW 1908, NMW 18671:2, NMW 18671:5, NMW 18671:6, NMW 18671:7, NMW 18671:8, NMW 18672:2, NMW 18673:1, NMW 18673:2, NMW 18674:1, NMW 18674:2, Syrien: Haleb (= Aleppo, Syria).

Testudo zarudnyi

BMNH 1947.3.5.17, Zirkuch, NE Persia (= Zir Kuh, NE Iran) (paralectotype of *T. zarudnyi*); NMW 1412, Iran: Arusan, Ost-Persien, im Süden der Khorasaner Kawir; NMW 19203, Iran: Arusan, 928 m, am Südrand der Salzwüste Kawir; NMW 19312:2, Iran: Arusan.

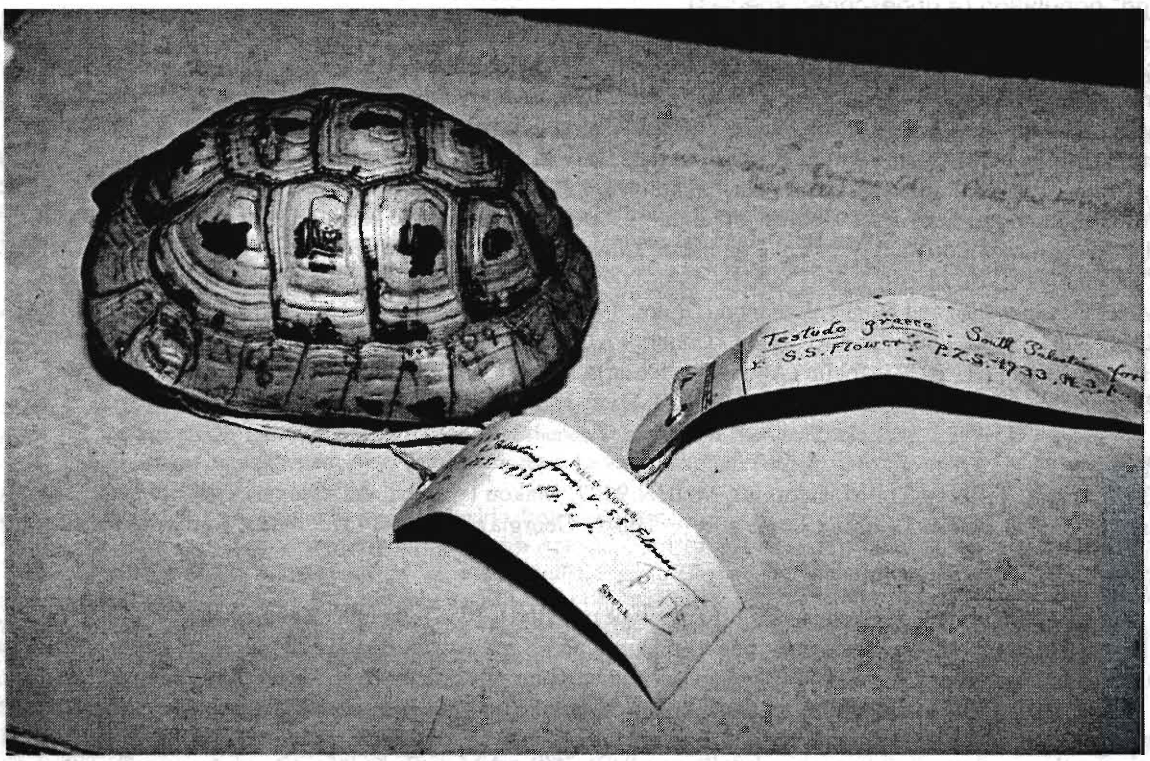


Fig. 1: BMNH 1933.9.3.4, Stanley Flower's South Palestine form.

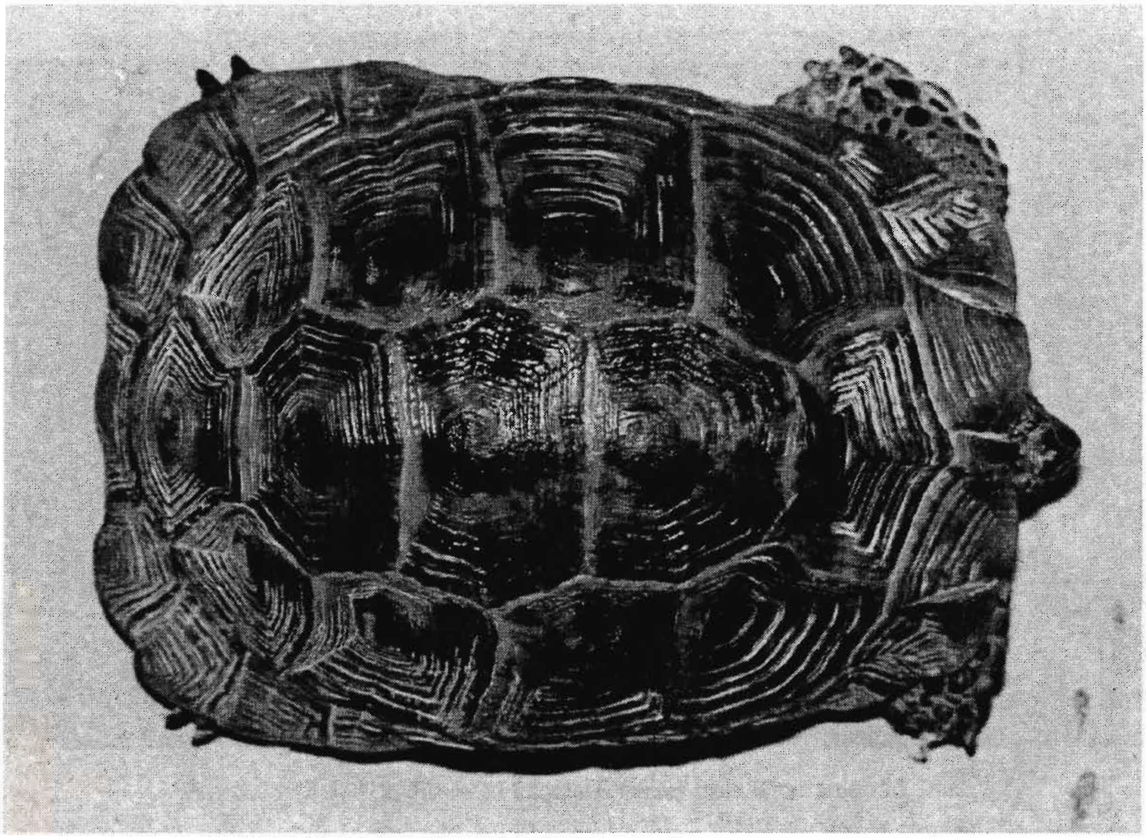


Fig. 2: FMNH 130820, female; holotype of *T. perses* sp. nov., dorsal view.

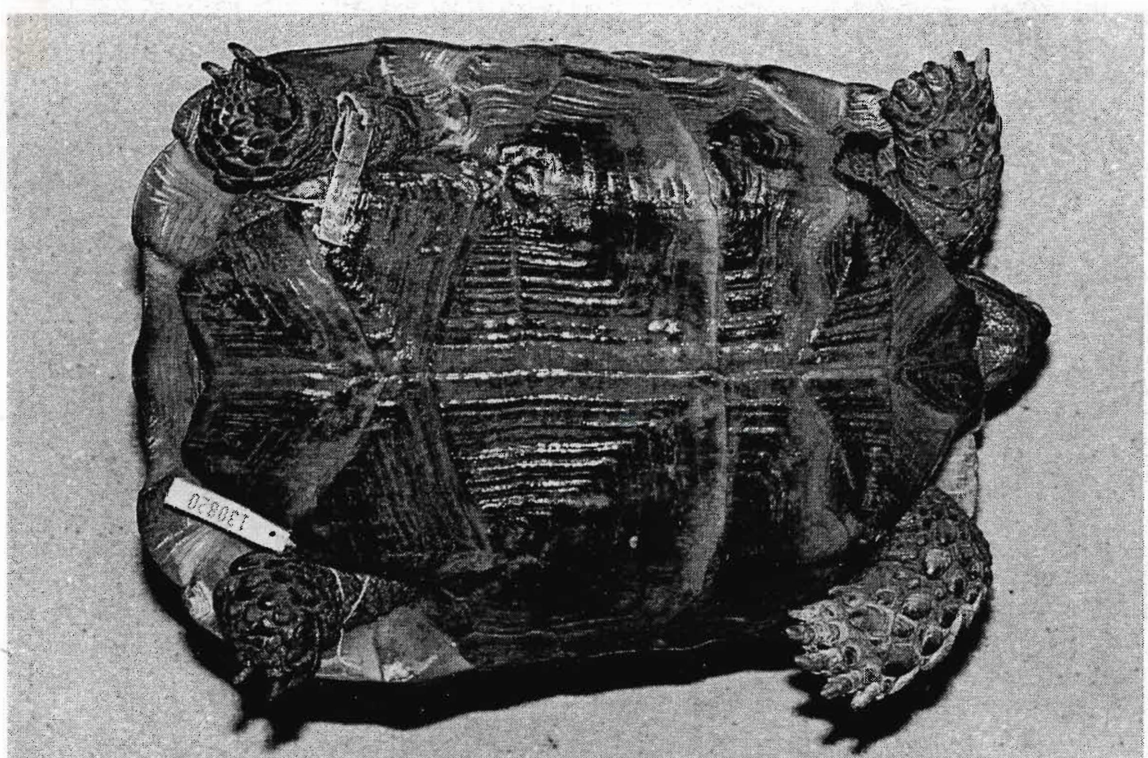


Fig. 3: FMNH 130820, female; holotype of *T. perses* sp. nov., ventral view.

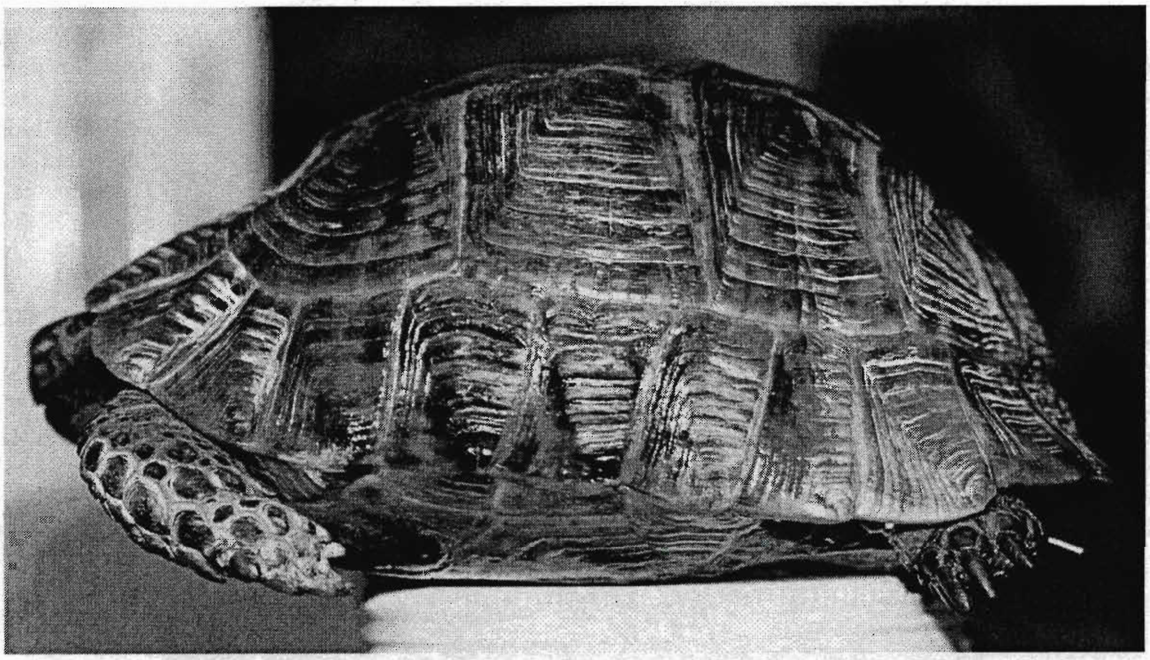


Fig. 4: FMNH 130820, female; holotype of *T. perses* sp. nov., lateral view.

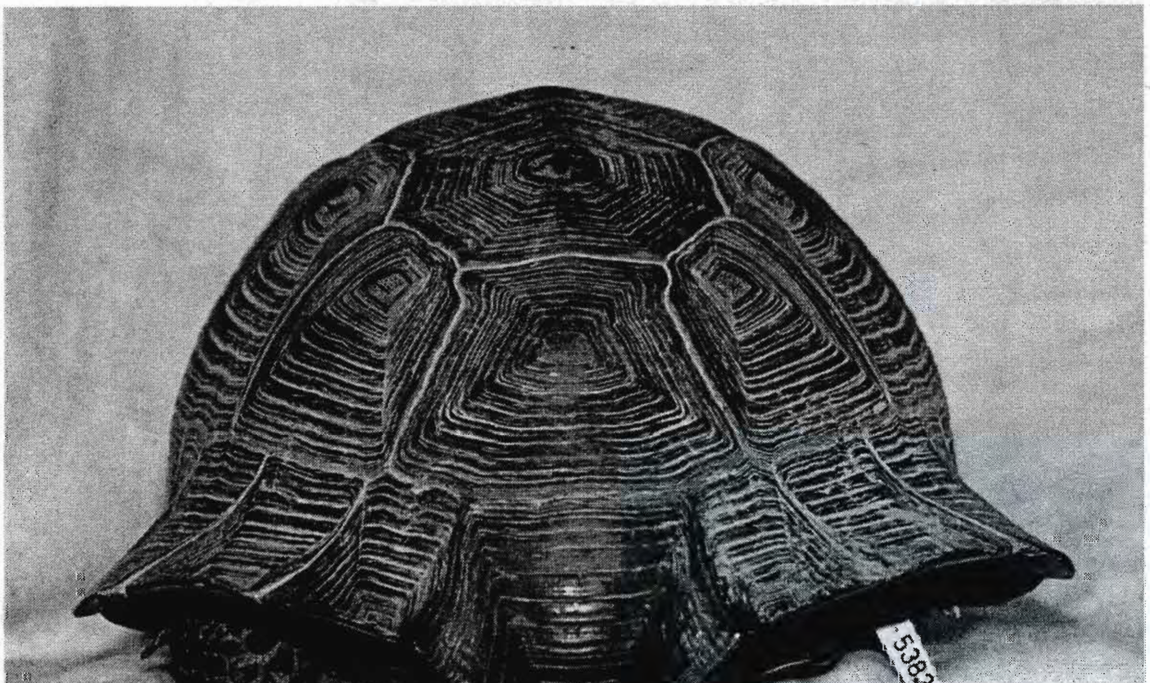


Fig. 5: MCZ 53836, posterior view of male *T. perses* from Khorramābād, Iran (paratype).

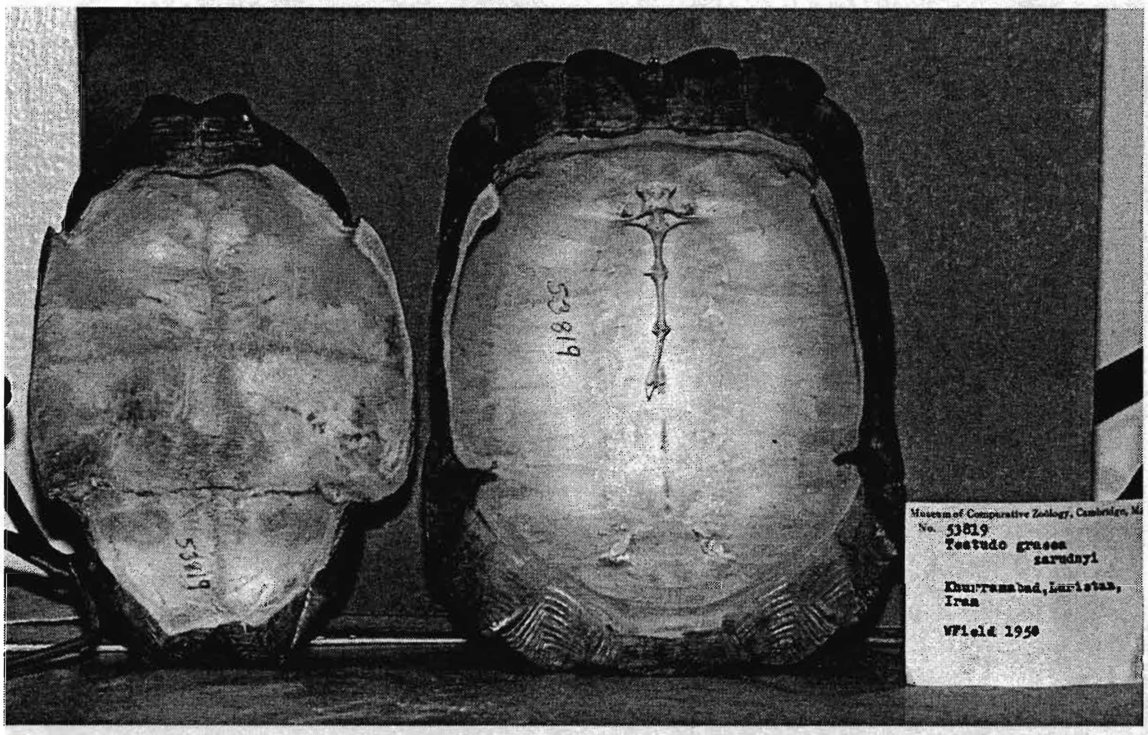


Fig. 6: MCZ 53819, dissected female *T. perses* from Khorramābād, Iran.

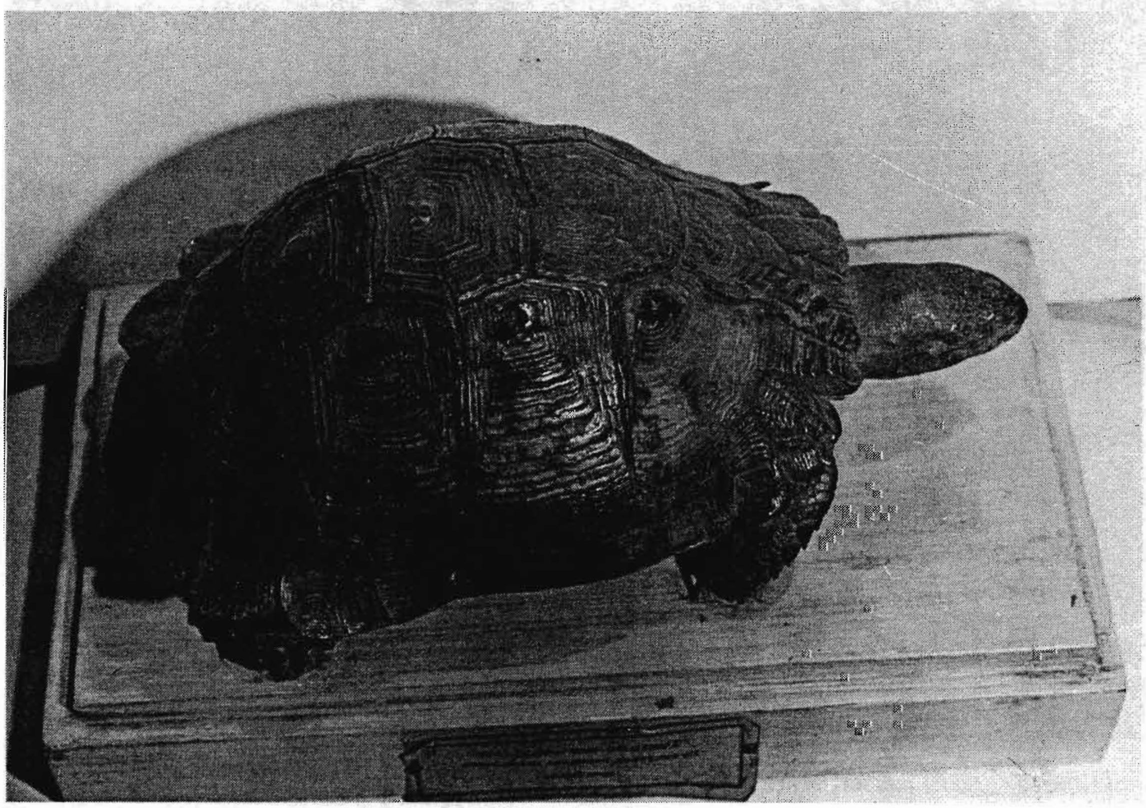


Fig. 7: ZIL 8738, lectotype of *Testudo zarudnyi* from Birjand, E Iran. Photograph courtesy of Boris Tuniyev.

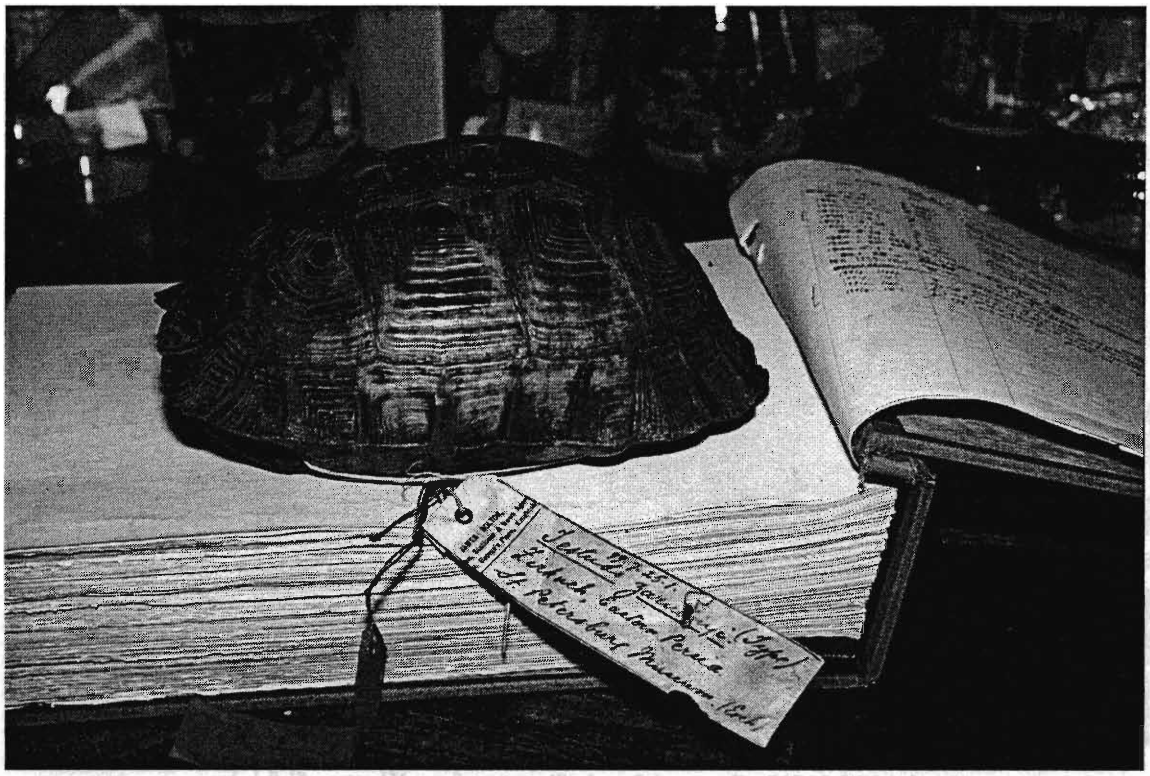


Fig. 8: BMNH 1947.3.5.17, paralectotype of *T. zarudnyi* from Zir Kuh, E Iran.

Fig. 9: *T. antakyensis* from slopes of Mt. Avital (near Kuneitra viewpoint), Golan, Israel.

Fig. 10: *T. antakyensis* from Antakya, Turkey.

Fig. 11: UF 14842, male "Lowlander" i.e. *T. floweri* from near Hadera, Israel.

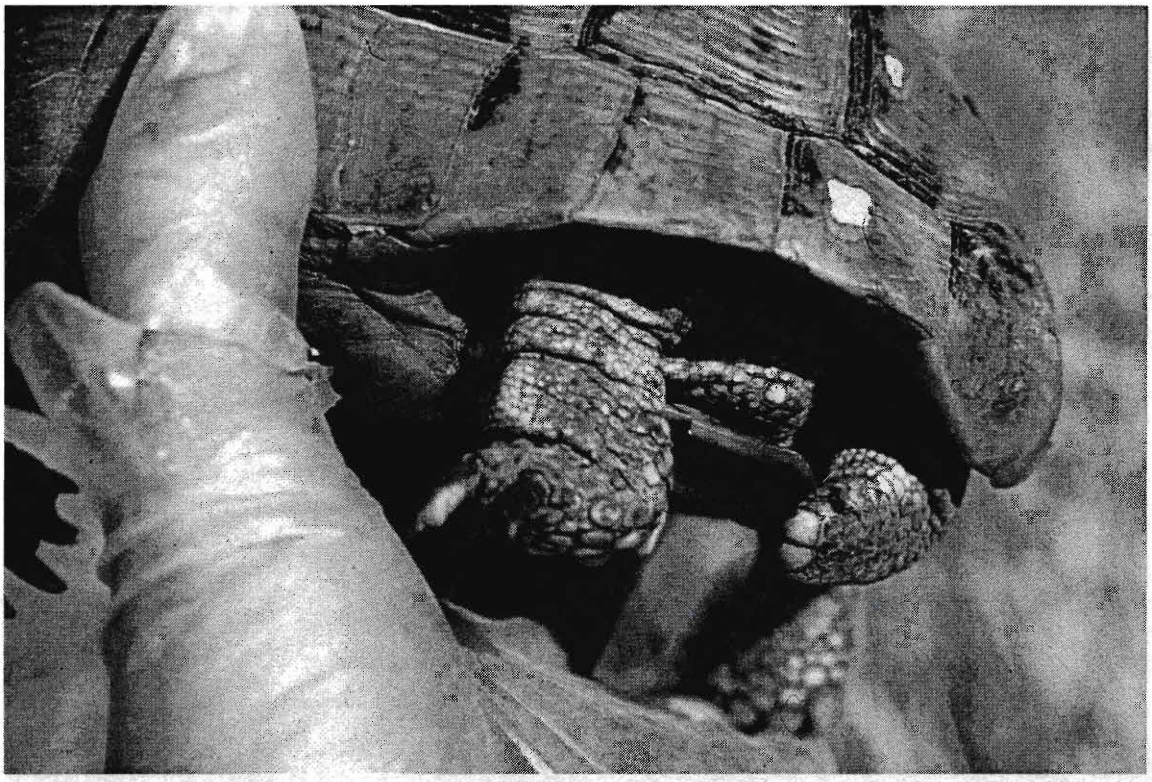


Fig. 12: Tail tubercle in *T. antakyensis* from Antakya, Turkey.

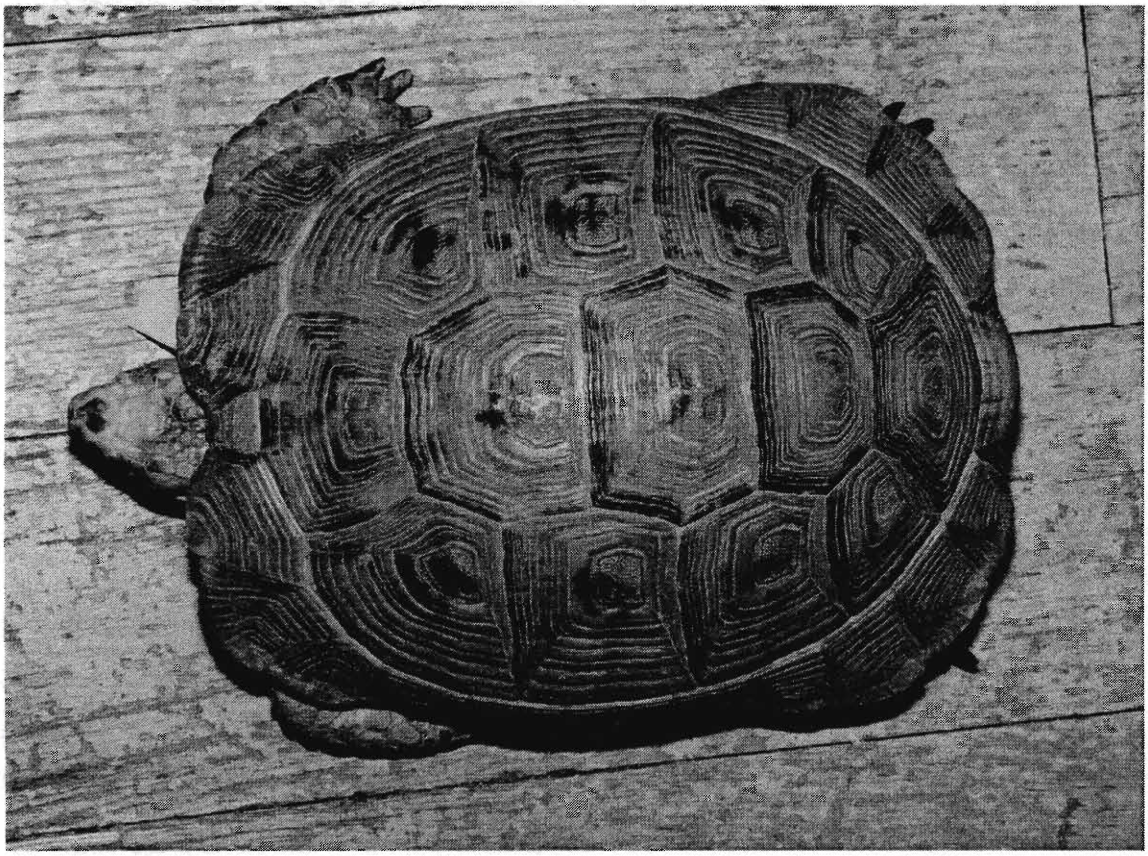


Fig. 13: NMW 18674:2, male *T. terrestris* from Aleppo, Syria.

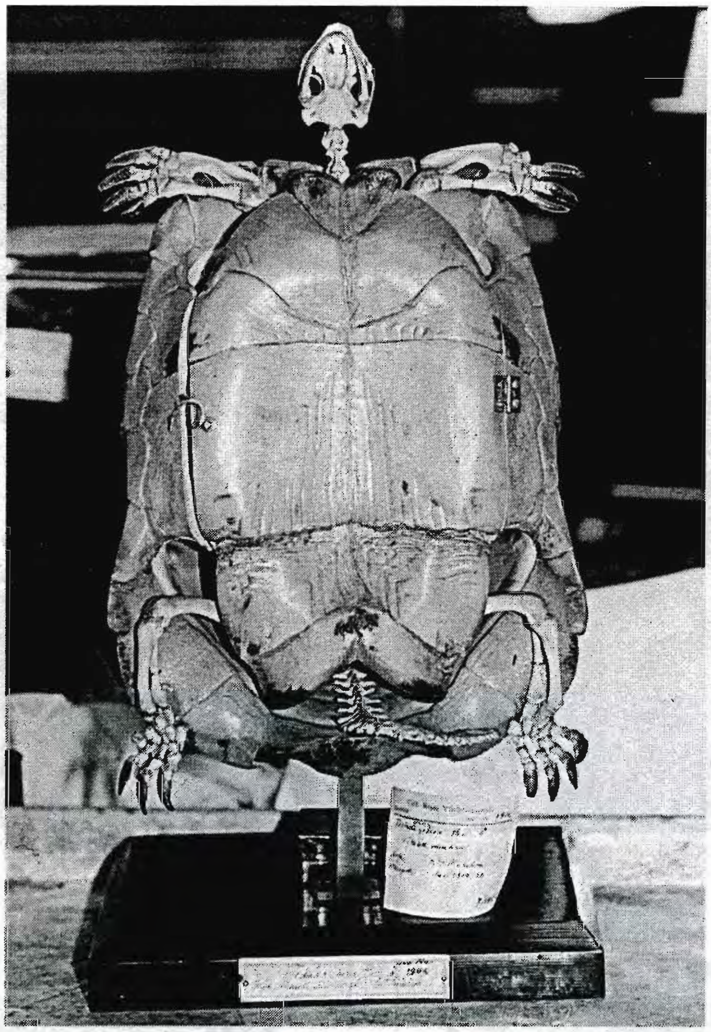


Fig. 14: Mounted skeleton of male *T. terrestris* from Urfa (Şanlıurfa), Turkey (NMW 1902, Siebenrock collection).

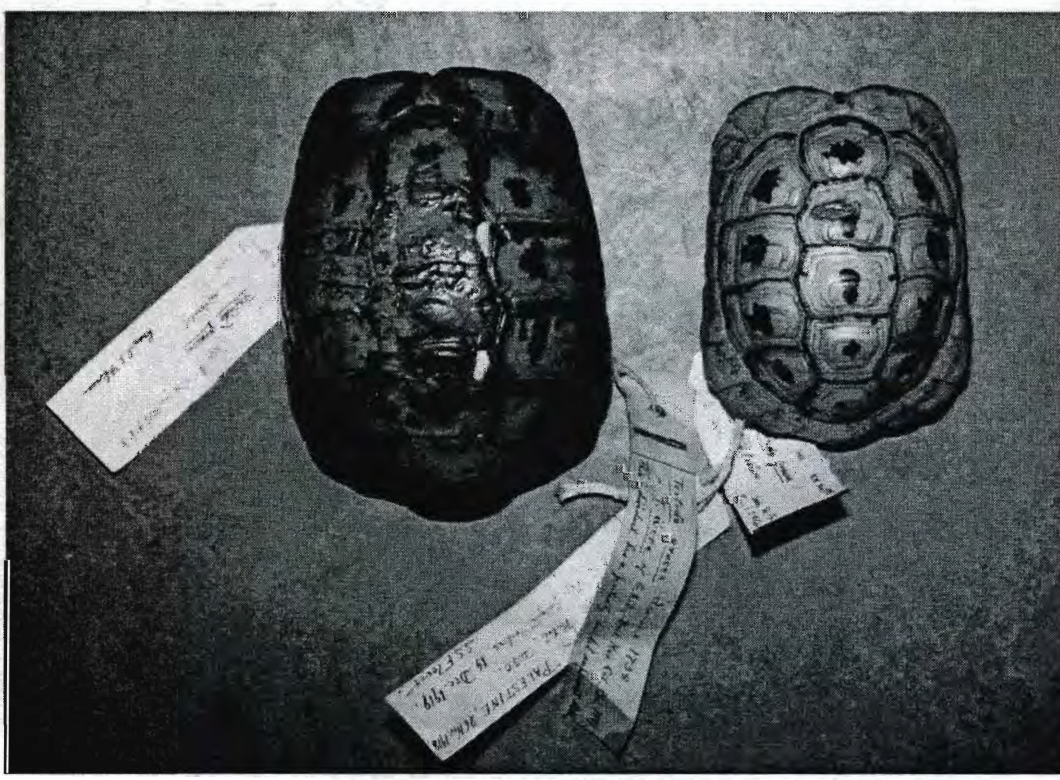


Fig. 15: Dorsal view of BMNH 1933.9.3.3 (*T. floweri*), and BMNH 1933.9.3.4 ("Highland").

Fig. 16: Ventral view of BMNH 1933.9.3.3 (*T. floweri*), and BMNH 1933.9.3.4 ("Highland").

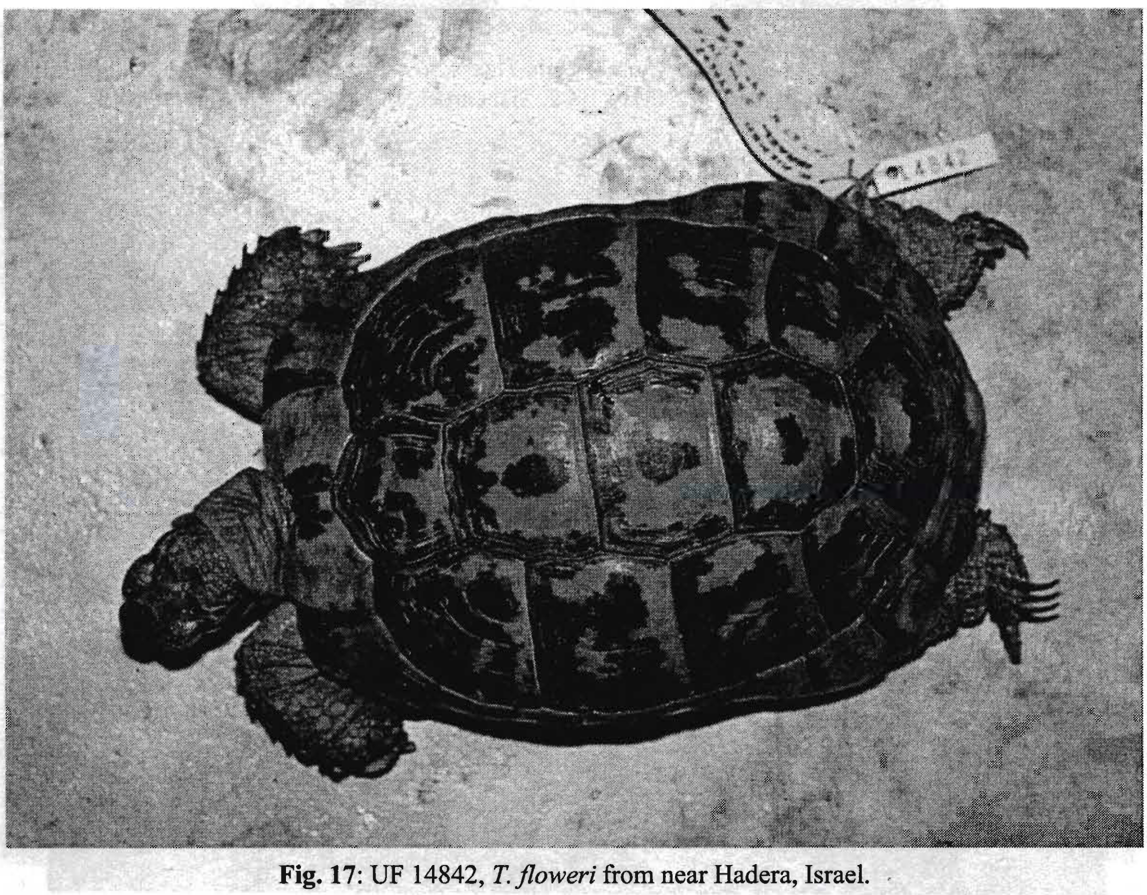
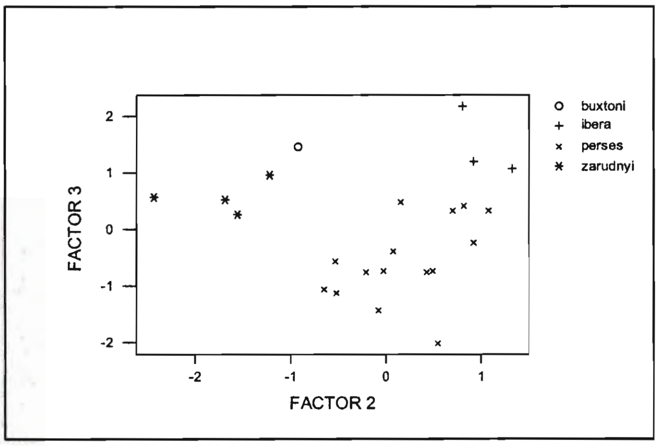
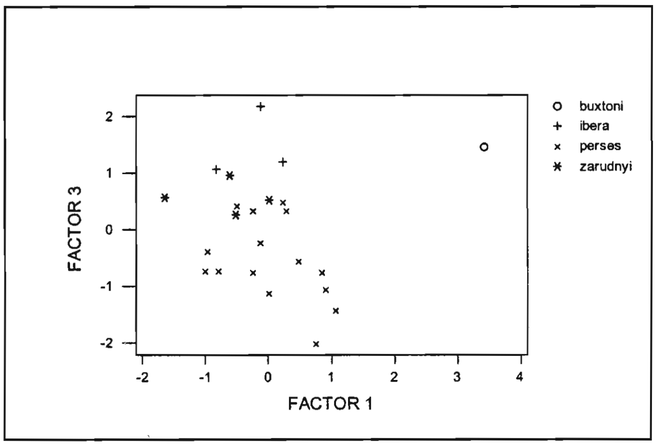


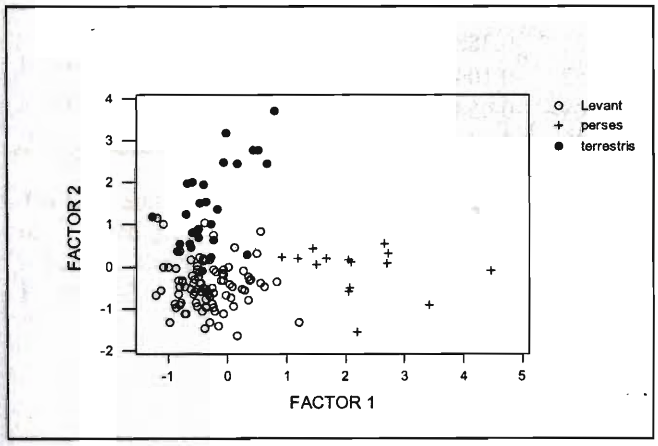
Fig. 17: UF 14842, *T. floweri* from near Hadera, Israel.



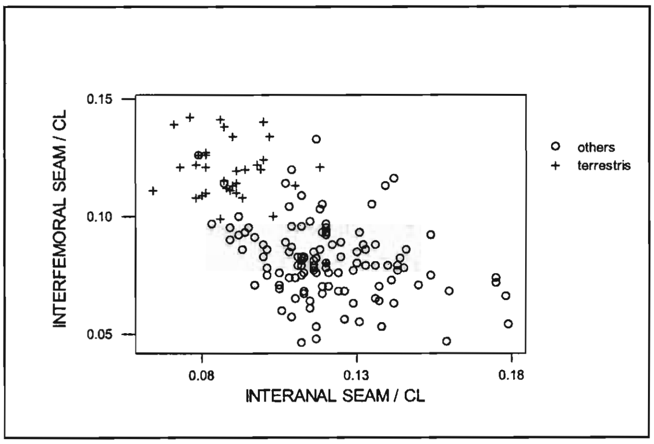
Graph 1: Factor score plot on F2 and F3, with *T. perses*, *T. zarudnyi*, *T. ibera*, and the type of *T. buxtoni*.



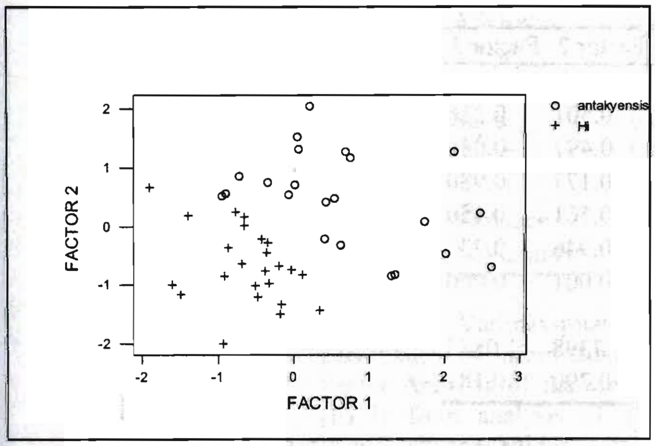
Graph 2: Factor score plot on F1 and F2, with *T. perses*, *T. zarudnyi*, *T. ibera*, and the type of *T. buxtoni*.



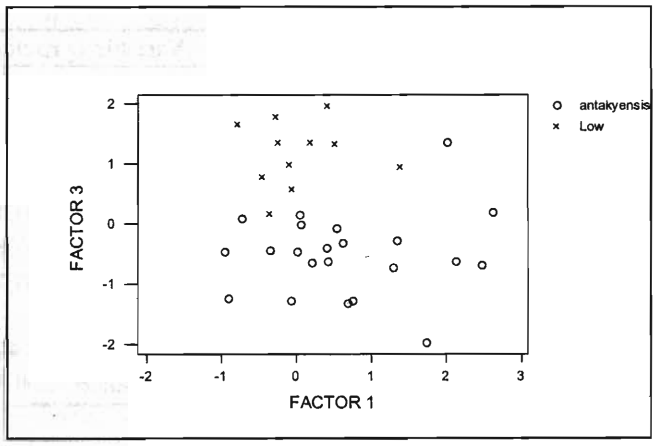
Graph 3: Factor score plot on F1 and F2, with *T. perses*, *T. terrestris* and a pooled Levantine group (combined *T. antakyensis*, "Highland", and "Lowland" populations).



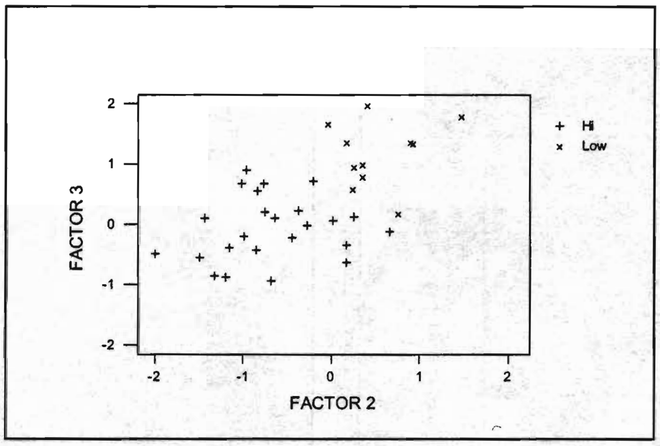
Graph 4: Bivariate plot showing the separation of *T. terrestris* from other groups (combined *T. perses*, *T. antakyensis*, "Highland", and "Lowland" populations).



Graph 5: Factor score plot on F1 and F2 separating *T. antakyensis* and the "Highland" group.



Graph 6: Factor score plot on F1 and F3 separating *T. antakyensis* and the "Lowland" group.



Graph 7: Factor score plot on F2 and F3 separating the "Highland" and "Lowland" populations.

Variable	Factor 1	Factor 2	Factor 3
GU-m	0.391	-0.763	-0.096
HUM-m	0.656	-0.021	-0.388
PEC-m	-0.093	-0.562	-0.104
ABD-m	0.569	-0.809	-0.054
FEM-m	0.869	0.139	-0.040
AN-m	-0.043	-0.885	-0.386
BR	0.587	-0.742	-0.268
ASO-h	0.727	-0.314	-0.125
V5-l	0.790	-0.400	-0.287
V1-w	0.366	-0.481	-0.623
V4-w	0.614	-0.529	-0.586
Variance	3.6805	3.6772	1.2248
% Variance	0.335	0.334	0.111

Table 1: Varimax-rotated Factor loadings, variances and percentages of information captured from Maximum Likelihood Factor Analysis of the correlation matrix for first three Factors (F1-3) from analysis of *T. buxtoni*, *T. ibera*, *T. perses*, and *T. zarudnyi*.

Variable	Factor 1	Factor 2	Factor 3
GU-m	0.721	0.501	0.216
HUM-m	0.667	0.497	-0.036
PEC-m	0.087	0.177	0.980
ABD-m	0.731	0.561	0.150
FEM-m	0.174	0.946	0.231
AN-m	0.955	-0.001	0.060
Variance	2.4491	1.7398	1.0884
% Variance	0.408	0.290	0.181

Table 2: Varimax-rotated Factor loadings, variances and percentages of information captured from Maximum Likelihood Factor Analysis of the correlation matrix for first three Factors (F1-3) from analysis of *T. perses*, *T. terrestris*, and a pooled group (Levant) containing *T. antakyensis*, the "Highland" and "Lowland" populations.

Summary of Classification

Put into Group	....True Group.... Levant	 *perses*	 *terrestris*
Levant	85	0	4
perses	1	18	0
terrestris	6	0	25
Total N	92	18	29
N Correct	85	18	25
Proportion	0.924	1.000	0.862

N = 139
N Correct = 128
Proportion Correct = 0.921

Summary of Classification with Cross-validation

Put into Group	....True Group.... Levant	 *perses*	 *terrestris*
Levant	84	1	4
perses	2	17	0
terrestris	6	0	25
Total N	92	18	29
N Correct	84	17	25
Proportion	0.913	0.944	0.862

N = 139
N Correct = 126
Proportion Correct = 0.906

Squared Distance Between Groups

	Levant	*perses*	*terrestris*
Levant	0.00000	20.29340	8.92140
perses	20.29340	0.00000	28.26460
terrestris	8.92140	28.26460	0.00000

Linear Discriminant Function for Group

	Levant	*perses*	*terrestris*
Constant	-0.3772	-7.7968	-2.9150
Factor 1	-0.9786	7.3991	-1.4880
Factor 2	-0.9694	-0.8074	3.5766
Factor 3	-0.2584	-0.2421	0.9699

Table 3: Summary of classification from Discriminant Function Analysis without and with cross-validation for males of a pooled group containing *T. antakyensis*, "Highland" and "Lowland" populations (= Levant), and *T. perses* and *T. terrestris*. Linear method for response: Populations = groups as above. Predictors: Factor Analysis scores from Factors 1-3.

Variable	Factor 1	Factor 2	Factor 3
CL	0.888	0.438	-0.039
PL	0.881	0.369	-0.264
ASO-w	0.882	0.396	0.104
V5-w	0.681	0.583	-0.110
C1	0.819	0.342	0.011
SC-d	0.301	0.835	-0.035
SC-v	0.666	0.605	0.082
Variance	4.0111	2.0047	0.1022
% Variance	0.573	0.286	0.015

Table 4: Varimax-rotated Factor loadings, variances and percentages of information captured from Maximum Likelihood Factor Analysis of the correlation matrix for first three Factors (F1-3) from analysis of *T. antakyensis*, the "Highland" and "Lowland" populations.

Summary of Classification

Put into Group	....True Group.... *antakyensis*	Hi	Low
antakyensis	19	0	0
Hi	1	24	0
Low	2	0	11
Total N	22	24	11
N Correct	19	24	11
Proportion	0.864	1.000	1.000

N = 57
N Correct = 54
Proportion Correct = 0.947

Squared Distance Between Groups

	antakyensis	Hi	Low
antakyensis	0.00000	9.54491	9.34630
Hi	9.54491	0.00000	9.42357
Low	9.34630	9.42357	0.00000

Summary of Classification with Cross-validation

Put into Group	....True Group.... *antakyensis*	Hi	Low
antakyensis	19	0	1
Hi	1	24	0
Low	2	0	10
Total N	22	24	11
N Correct	19	24	10
Proportion	0.864	1.000	0.909

N = 57
N Correct = 53
Proportion Correct = 0.930

Linear Discriminant Function for Group

	antakyensis	Hi	Low
Constant	-1.4048	-1.2448	-2.2811
Factor 1	1.7637	-1.6689	0.1137
Factor 2	1.7243	-2.1849	1.3184
Factor 3	-1.6491	-0.0003	3.2987

Table 5: Summary of classification from Discriminant Function Analysis without and with cross-validation for males of the strictly Levantine populations (species). Linear method for response: Species = *T. antakyensis*, "Highland" (Hi) and "Lowland" (Low) populations. Predictors: Factor Analysis scores from Factors 1-3.

PARAMETER	ANOVA F	ANOVA P	FISHER'S PAIRWISE DIFFERENCES AT P < 0.05
Max. length (CL)	$F_{4,142} = 55.22$	< 0.0001	HI: < all others; ANT: < PERS, TERR; LOW: < PERS, TERR; PERS: > TERR
Plastron length (PL)	$F_{4,130} = 11.59$	< 0.0001	LOW: < all others; PERS: > HI, TERR
Plastron midline length (PL-m)	$F_{4,110} = 8.50$	< 0.0001	LOW: < all others; PERS: > ANT, HI, TERR
Max. carapax width (MA)	$F_{4,140} = 5,79$	< 0.0001	ANT: < TERR, PERS; HI: < TERR, PERS
Gular length (GU-l)	$F_{4,140} = 4.51$	0.002	ANT: < TERR, PERS; PERS: > HI, LOW
Max. height (HE)	$F_{4,142} = 1.84$	0.125	ANT: > LOW
Anterior shell opening width (ASO-w)	$F_{4,103} = 5.16$	0.001	ANT: < HI, LOW, TERR; PERS: < LOW, TERR
Anterior shell opening height (ASO-h)	$F_{4,125} = 14.08$	< 0.0001	ANT: > PERS; HI: > ANT, TERR, PERS; LOW: > TERR, PERS
Bridge length (BR)	$F_{4,132} = 8.31$	< 0.0001	LOW: > ANT, HI, PERS; TERR: < ANT, HI, PERS
Humeral width (HUM-w)	$F_{4,132} = 3.78$	0.0006	ANT: < all others
Anal width (AN-w)	$F_{4,129} = 7.98$	< 0.0001	PERS: > all others; TERR: < ANT, HI, LOW
Max. nuchal scute length (NU-l)	$F_{4,132} = 6.07$	< 0.0001	LOW: < all others; ANT: < TERR, PERS; HI: < TERR, PERS
Max. nuchal scute width (NU-w)	$F_{4,133} = 4.87$	0.0001	ANT: < HI, LOW; PERS: < HI, LOW, TERR
Gular seam length (GU-m)	$F_{4,137} = 5.96$	< 0.0001	PERS: > all others
Humeral seam length (HUM-m)	$F_{4,137} = 2.29$	0.063	TERR: < ANT, HI
Pectoral seam length (PEC-m)	$F_{4,139} = 8.02$	< 0.0001	PERS: < all others
Femoral seam length (FEM-m)	$F_{4,139} = 38.91$	< 0,0001	ANT: > HI; TERR: > all others
Anal seam length (AN-m)	$F_{4,137} = 49.25$	< 0,0001	PERS: > all others; TERR: < all others; LOW: < ANT, HI
Pectoral width (PEC-w)	$F_{4,109} = 2.26$	0.067	ANT: < HI, TERR
1st vertebral width (V1-w)	$F_{4,132} = 10.24$	< 0.0001	HI: < ANT, TERR, PERS; ANT: < TERR, PERS; LOW: < TERR, PERS
2nd vertebral width (V2-w)	$F_{4,132} = 5.37$	< 0.0001	PERS: > ANT, HI, LOW; TERR: > ANT, HI, LOW
3rd vertebral width (V3-w)	$F_{4,132} = 11.82$	< 0.0001	PERS: > ANT, HI, LOW; TERR: > ANT, HI, LOW
4th vertebral width (V4-w)	$F_{4,131} = 11.05$	< 0.0001	PERS: > all others; TERR: > ANT, HI
5th vertebral width (V5-w)	$F_{4,132} = 2.36$	0.056	ANT: > HI
2nd vertebral length (V2-l)	$F_{4,129} = 2.07$	0.089	ANT: < TERR
3rd vertebral length (V3-l)	$F_{4,129} = 4.15$	0.003	LOW: < ANT, TERR, PERS; HI: < TERR
4th vertebral length (V4-l)	$F_{4,128} = 1.84$	0.125	ANT: > TERR
5th vertebral length (V5-l)	$F_{4,129} = 8.51$	< 0.0001	PERS: < all others; ANT: > TERR
1st costal length (C1)	$F_{4,132} = 11.05$	< 0.0001	PERS: < all others; ANT: < HI, LOW; TERR: < HI, LOW
3rd costal length (C3)	$F_{4,133} = 2.09$	0.086	TERR: > HI, LOW
Dorsal supracaudal width (SUP-d)	$F_{4,116} = 6.33$	< 0.0001	PERS: > all others
Ventral supracaudal width (SUP-v)	$F_{4,103} = 1.84$	0.127	HI: < LOW
Supracaudal length (SUP-l)	$F_{4,102} = 10.52$	< 0.0001	HI: < all others; ANT: < TERR, PERS; LOW: < TERR, PERS
Max. head width (HEAD)	$F_{4,78} = 15.88$	< 0.0001	PERS: < ANT, HI, LOW; TERR: < ANT, HI, LOW; ANT: < HI, LOW

Table 6: Results of univariate analysis of variance (one-way ANOVA) of ratios of 34 morphological characters to maximum carapace length and, maximum length (in mm) among males of *T. antakyensis* (ANT), the S Levantine "Highland" population (HI), the S Levantine "Lowland" population (LOW), *T. perses* sp.nov. (PERS), and *T. terrestris* (TERR), in addition to Fisher's pairwise (post-ANOVA) comparisons between groups showing statistically significant differences at p < 0.05.

TAXON	CHAR	MEAN	SE	s	N	CHAR	MEAN	SE	s	N	CHAR	MEAN	SE	s	N
antakyensis	CL	141.07	2.007	13.61	46	ASO-w	0.481	0.003	0.014	22	NU-w	0.031	0.002	0.012	42
Highland		117.55	1.778	10.37	34		0.495	0.003	0.017	24		0.041	0.002	0.012	33
ibera		178.80	11.62	25.97	5		0.522	0.021	0.037	3		0.032	0.001	0.003	5
Lowland		131.63	2.425	8.40	12		0.503	0.004	0.013	12		0.040	0.005	0.017	11
perses		192.72	5.500	25.21	21		0.486	0.006	0.025	16		0.028	0.002	0.010	18
terrestris		169.97	6.159	33.73	30		0.498	0.003	0.017	30		0.037	0.002	0.012	30
zarudnyi		215.33	3.362	6.72	4		0.450	0.010	0.020	4		0.044	0.004	0.007	4
antakyensis	PL	0.881	0.005	0.031	36	ASO-h	0.161	0.002	0.011	32	GU-m	0.123	0.002	0.014	45
Highland		0.873	0.004	0.021	33		0.177	0.002	0.013	32		0.127	0.001	0.008	33
ibera		0.885	0.011	0.024	5		0.170	0.004	0.007	3		0.136	0.007	0.015	5
Lowland		0.829	0.008	0.029	12		0.169	0.004	0.012	12		0.129	0.003	0.010	12
perses		0.893	0.005	0.024	20		0.153	0.003	0.016	20		0.140	0.003	0.012	18
terrestris		0.873	0.005	0.029	30		0.157	0.003	0.014	30		0.128	0.003	0.014	30
zarudnyi		0.892	0.009	0.019	4		0.140	0.001	0.003	4		0.149	0.008	0.016	4
antakyensis	PL-m	0.798	0.004	0.020	25	BR	0.431	0.003	0.018	37	HUM-m	0.131	0.002	0.015	45
Highland		0.791	0.004	0.019	24		0.436	0.003	0.016	33		0.129	0.003	0.015	33
ibera		0.791	0.016	0.036	5		0.415	0.008	0.017	5		0.120	0.005	0.011	5
Lowland		0.766	0.007	0.023	12		0.415	0.004	0.014	12		0.122	0.005	0.017	12
perses		0.816	0.007	0.031	20		0.432	0.004	0.020	21		0.129	0.004	0.016	18
terrestris		0.788	0.005	0.029	30		0.414	0.003	0.019	30		0.121	0.003	0.019	30
zarudnyi		0.815	0.018	0.035	4		0.427	0.015	0.031	4		0.103	0.014	0.028	4
antakyensis	MA	0.723	0.004	0.027	45	HUM-w	0.438	0.003	0.021	37	PEC-m	0.064	0.002	0.016	46
Highland		0.732	0.003	0.018	33		0.453	0.004	0.024	33		0.070	0.003	0.015	34
ibera		0.808	0.006	0.013	5		0.471	0.011	0.024	5		0.056	0.003	0.007	5
Lowland		0.734	0.005	0.018	12		0.455	0.004	0.012	12		0.069	0.005	0.019	12
perses		0.750	0.009	0.039	21		0.451	0.005	0.023	21		0.046	0.003	0.012	18
terrestris		0.747	0.004	0.024	30		0.454	0.004	0.019	30		0.064	0.003	0.016	30
zarudnyi		0.749	0.010	0.021	4		0.432	0.005	0.010	4		0.053	0.006	0.012	4
antakyensis	GU-l	0.143	0.002	0.014	45	AN-w	0.369	0.003	0.019	37	FEM-m	0.084	0.002	0.015	46
Highland		0.147	0.002	0.009	33		0.368	0.003	0.016	33		0.076	0.003	0.019	34
ibera		0.165	0.007	0.017	5		0.370	0.005	0.011	5		0.103	0.005	0.010	5
Lowland		0.146	0.003	0.011	12		0.371	0.005	0.017	12		0.081	0.005	0.018	12
perses		0.157	0.002	0.011	21		0.385	0.003	0.013	18		0.078	0.003	0.011	18
terrestris		0.150	0.003	0.014	30		0.358	0.003	0.014	30		0.119	0.003	0.014	30
zarudnyi		0.163	0.007	0.013	4		0.396	0.011	0.023	4		0.051	0.007	0.014	4
antakyensis	HE	0.509	0.005	0.031	46	NU-l	0.078	0.002	0.011	41	AN-m	0.116	0.002	0.016	45
Highland		0.499	0.004	0.022	34		0.079	0.002	0.009	33		0.119	0.003	0.015	33
ibera		0.485	0.009	0.019	5		0.077	0.008	0.019	5		0.105	0.014	0.031	5
Lowland		0.491	0.006	0.019	12		0.069	0.002	0.008	11		0.105	0.005	0.019	12
perses		0.499	0.007	0.030	21		0.086	0.002	0.010	18		0.152	0.004	0.015	18
terrestris		0.505	0.004	0.019	30		0.085	0.002	0.012	30		0.091	0.002	0.012	30
zarudnyi		0.468	0.010	0.020	4		0.090	0.010	0.021	4		0.180	0.008	0.015	4

Table 7 : Descriptive statistics for males of *T. antakyensis*, the S Levantine "Highland" population, *T. ibera*, the S Levantine "Lowland" population, *T. perses* sp.nov., *T. terrestris*, and *T. zarudnyi* (including BMNH 1947.3.5.17: female). Character abbreviations as listed in Materials and Methods. Characters were standardized for maximum carapace length, except for CL (= in mm). CHAR = character, MEAN = mean value, SE = standard error, s = standard deviation, N = sample size.

TAXON	CHAR	MEAN	SE	s	N	CHAR	MEAN	SE	s	N	CHAR	MEAN	SE	s	N
antakyensis	PEC-w	0.622	0.004	0.019	23	V2-l	0.186	0.002	0.012	36	SUP-d	0.160	0.004	0.022	31
Highland		0.640	0.004	0.021	24		0.191	0.004	0.021	32		0.150	0.004	0.021	24
ibera		0.659	0.022	0.048	5		0.182	0.003	0.007	5		0.174	0.008	0.019	5
Lowland		0.637	0.006	0.022	12		0.186	0.003	0.011	11		0.166	0.004	0.014	11
perses		0.632	0.005	0.024	21		0.192	0.003	0.012	21		0.185	0.008	0.038	21
terrestris		0.639	0.005	0.028	30		0.195	0.002	0.012	30		0.162	0.003	0.019	30
zarudnyi		0.604	0.014	0.029	4		0.194	0.005	0.010	4		0.169	0.011	0.021	4
antakyensis	V1-w	0.232	0.004	0.022	38	V3-l	0.181	0.002	0.012	36	SUP-v	0.293	0.005	0.022	22
Highland		0.221	0.003	0.017	33		0.179	0.002	0.009	32		0.289	0.004	0.018	24
ibera		0.232	0.005	0.012	5		0.166	0.006	0.013	5		0.306	0.010	0.021	4
Lowland		0.227	0.004	0.012	11		0.173	0.003	0.010	11		0.304	0.005	0.016	11
perses		0.250	0.005	0.022	21		0.183	0.003	0.014	21		0.291	0.005	0.021	17
terrestris		0.245	0.003	0.017	30		0.187	0.002	0.009	30		0.298	0.003	0.015	30
zarudnyi		0.225	0.006	0.012	4		0.187	0.005	0.010	4		0.275	0.016	0.032	4
antakyensis	V2-w	0.244	0.004	0.022	38	V4-l	0.201	0.002	0.013	35	SUP-l	0.160	0.003	0.012	21
Highland		0.249	0.003	0.015	33		0.199	0.001	0.007	32		0.153	0.003	0.014	24
ibera		0.248	0.002	0.005	5		0.182	0.004	0.008	5		0.165	0.004	0.009	4
Lowland		0.244	0.004	0.013	11		0.197	0.003	0.010	11		0.161	0.003	0.010	11
perses		0.262	0.003	0.016	21		0.200	0.002	0.009	21		0.171	0.003	0.014	17
terrestris		0.258	0.003	0.016	30		0.193	0.003	0.018	30		0.172	0.002	0.010	30
zarudnyi		0.263	0.006	0.011	4		0.194	0.010	0.020	4		0.175	0.009	0.018	4
antakyensis	V3-w	0.277	0.003	0.021	38	V5-l	0.241	0.003	0.018	36	HEAD	0.153	0.002	0.007	16
Highland		0.281	0.002	0.014	33		0.240	0.003	0.018	32		0.162	0.002	0.008	21
ibera		0.278	0.003	0.006	5		0.225	0.009	0.021	5		0.145	0.008	0.019	5
Lowland		0.274	0.004	0.012	11		0.236	0.005	0.018	11		0.161	0.002	0.007	9
perses		0.303	0.004	0.018	21		0.217	0.003	0.012	21		0.141	0.004	0.009	4
terrestris		0.295	0.003	0.015	30		0.233	0.003	0.017	30		0.146	0.002	0.009	29
zarudnyi		0.293	0.007	0.013	4		0.191	0.004	0.009	4		0.122	*	*	1
antakyensis	V4-w	0.254	0.003	0.019	37	C1	40.844	0.613	3.780	38					
Highland		0.251	0.002	0.011	33		35.639	0.510	2.932	33					
ibera		0.251	0.008	0.017	5		51.040	2.502	5.594	5					
Lowland		0.255	0.004	0.013	11		40.000	0.818	2.713	11					
perses		0.276	0.002	0.010	21		53.298	1.551	7.108	21					
terrestris		0.262	0.003	0.014	30		48.913	1.421	7.785	30					
zarudnyi		0.248	0.007	0.015	4		58.550	1.859	3.719	4					
antakyensis	V5-w	0.304	0.004	0.023	38	C3	0.197	0.003	0.016	38					
Highland		0.286	0.004	0.023	33		0.202	0.003	0.017	33					
ibera		0.303	0.007	0.017	5		0.201	0.008	0.019	5					
Lowland		0.301	0.006	0.020	11		0.192	0.004	0.012	11					
perses		0.295	0.005	0.025	21		0.199	0.002	0.011	21					
terrestris		0.294	0.006	0.031	30		0.199	0.002	0.012	30					
zarudnyi		0.279	0.006	0.012	4		0.214	0.008	0.016	4					

Table 7: (continued)

CHAR	MEAN	SE	s	N	CHAR	MEAN	SE	s	N	CHAR	MEAN	SE	s	N
CL	161.34	8.254	39.59	23	NU-l	0.085	0.002	0.010	21	V1-l	0.213	0.003	0.015	23
PL	0.918	0.006	0.027	23	NU-w	0.035	0.002	0.011	23	V2-l	0.211	0.002	0.010	23
PL-m	0.865	0.007	0.034	23	GU-m	0.140	0.002	0.011	23	V3-l	0.201	0.002	0.010	23
MI	0.747	0.007	0.034	23	HUM-m	0.131	0.004	0.019	23	V4-l	0.205	0.003	0.012	23
MA	0.757	0.007	0.036	23	PEC-m	0.055	0.003	0.014	23	V5-l	0.203	0.004	0.019	23
GU-l	0.154	0.002	0.011	23	ABD-m	0.314	0.004	0.020	23	C1	0.296	0.004	0.020	23
GU-w	0.185	0.004	0.018	23	FEM-m	0.072	0.005	0.025	23	C2	0.227	0.003	0.015	23
GU-h	0.107	0.003	0.012	23	AN-m	0.176	0.005	0.024	23	C3	0.211	0.002	0.009	23
HE	0.510	0.006	0.029	23	PEC-w	0.659	0.007	0.033	23	C4	0.184	0.003	0.012	23
ASO-w	0.509	0.006	0.025	19	ABD-w	0.670	0.005	0.025	23	SUP-d	0.163	0.004	0.018	23
ASO-h	0.159	0.003	0.012	23	V1-w	0.258	0.004	0.019	23	SUP-v	0.254	0.004	0.021	23
BR	0.463	0.005	0.023	23	V2-w	0.288	0.004	0.020	23	SUP-l	0.140	0.003	0.012	23
HUM-w	0.466	0.005	0.023	23	V3-w	0.326	0.004	0.020	23	HEAD	0.159	0.007	0.023	11
FEM-w	0.477	0.005	0.024	23	V4-w	0.277	0.004	0.017	23	EYE-TY	0.055	0.002	0.007	9
AN-w	0.355	0.004	0.020	23	V5-w	0.284	0.004	0.019	22	EYE-NO	0.049	0.002	0.005	11

Male characters not used in Table 7.														
MI	0.704	0.006	0.029	21	ABD-m	0.282	0.003	0.014	18	C4	0.193	0.003	0.012	21
GU-w	0.184	0.006	0.028	21	ABD-w	0.639	0.005	0.021	21	EYE-TY	0.044	0.002	0.002	2
GU-h	0.101	0.003	0.014	21	V2-l	0.192	·0.003	0.012	21	EYE-NO	0.046	0.003	0.005	3
FEM-w	0.467	0.004	0.019	20	C2	0.199	0.002	0.011	21					

Table 8: Descriptive statistics for *T. perses* sp. nov. Upper section: females. Lower section: males, with respect to characters not listed in Table 7. Character abbreviations as listed in Materials and Methods. Characters were standardized for maximum carapace length, except for CL (= in mm). CHAR = character, MEAN = mean value, SE = standard error, s = standard deviation, N = sample size.