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The diverse fossil chelonians from Milia (Late Pliocene, Grevena, Greece) with a new species of *Testudo* Linnaeus, 1758 (Testudines: Testudinidae)

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*Institutional abbreviations*. AMNH, American Museum of Natural History; CRI, Chelonian Research Institute (P. Pritchard), U.S.A.; FRANK, Natural History Museum of Frankfurt, Germany; LGPUT, Laboratory of Geology and Paleontology of University of Thessaloniki; NHMW, Naturhistorisches Museum, Vienna, Austria; MNCN, Museo National de Ciencias Naturales, Madrid, Spain; MNHN, Muséum National d’Histoire Naturelle, Paris, France; NWS, Naturmuseum Winterthur, Switzerland; PIMUZ, Paläontologische Institut und Museum, University Zurich, Switzerland; REP, Comparative Anatomy Collection, MNHN, Paris; STUS, Sala de las Tortugas de la Universidad de Salamanca, Spain; UCMP, University of California Museum of Paleontology, U.S.A.; USNM, Smithsonian Museum of Natural History, U.S.A; ZIN, Zoological Museum of the Russian Academy of Sciences, Moscow, Russia.

**DESCRIPTION OF SPECIMENS**

*Testudo brevitesta* sp. nov.

MIL 255 (Fig. 4X-U): It is fragment of the shell of a tortoise. By the curvature we can assume that it belongs to the carapace. Further identification is not possible.

MIL 256a (Fig. 4A-C): This specimen corresponds to an almost complete neural. Viscerally we notice the attachment for the corresponding vertebra. The neural is quadrangular with rounded edges, wider than long. Dorsally it is crossed by the vertebral sulcus, which is strongly convex anteriorly.

MIL 256c (Fig. 4G-I): This specimen corresponds to a fragment of the pygal region, preserving the pygal and part of the left peripheral 11. The pygal is trapezoid, with wider anterior side. The pygal, along with the peripheral, are strongly flared posteriorly. Dorsally, it is crossed by the vertebral sulci. No marginals 12 are noted, therefore the presence of a supracaudal is assumed.

MIL 495 (Fig. 2): This specimen corresponds to the medial and posterior part of the carapace. The surface of the carapace is fragmented and eroded in some parts. The limits between the plates and the scutes can be observed in most of the surface of the carapace. The shell is rounded in outline and tall in height. The medial and posterior part of the neural series can be described. The neural 4 is octagonal, as long as wide. The neural 5 is quadrangular, wider than long. The neural 6 is roughly octagonal, slightly wider than long. The neural 7 is hexagonal, with short anterior lateral sides. Most probably the neural 8 is present, being quadrangular with rounded edges. It seems that only one suprapygal is present, being trapezoid with narrow anterior and wider posterior part. The costal plates preserve the typical alternating pattern of the testudinids, showing costals that are medially short and laterally long to be alternated with costal that are medially long and laterally short. From the peripheral series, those from the right bridge and the entire posterior rim are preserved. The bridge peripherals are tall and short. The peripherals of the posterior rim are moderately long and posteriorly flared, including also the pygal region. The pygal is trapezoid in shape, with slightly narrow anterior and wider posterior side, thus showing lateral sides that slightly diverge posteriorly. The imprints of the scute sulci are clearly visible as they are deeply pronounced on the plates. The vertebrals are slightly longer than wide, but still narrower than the pleurals. The vertebral sulci cross transversely the neural 3, neural 5, and the last neural plate. In the crossing of the sulci on the neurals, significant dorsal bumps are noted. The pleurals are rectangular, wide and short, crossing the costals 2, 4, and 6 transversely. The marginals are long and narrow, crossing the peripherals. The marginals 12 are fused into a supracaudal. In the preserved part there is good coincidence between the costo-peripheral suture and the pleuro-marginal sulci.

MIL 982d (Fig. 4S-U): This specimen corresponds to a fragment of the left hyoplastron. The specimen is rather flat and small in size. Ventrally, we notice a part of a sulcus, most probably of the humero-pectoral sulcus.

MIL 1168 (Fig.4J-L): It is a fragment of the left anterior lobe, preserving the entire left epiplastron, part of the entoplastron and the anterior part of the left hyoplastron. Dorsally, it is marked by the presence of a thick convex epiplastral lip, which creates a strong gular pocket. Ventrally, the gulars are rather short, restricted in the anterior part of the lobe and overlapping the anterior part of the entoplastron. The remaining part is covered by the humeral scutes that are long. Gular protrusion is absent.

MIL 1396: It is a fragment of the left hyoplastron. Ventrally, it is crossed by the humero-pectoral and the pectoro-abdominal sulci. Pectorals are very short and wide.

MIL 1592: It is a fragment of a peripheral bone. The outer surface is eroded and the identification of the sulci is rather difficult. Only in ventral view a marginal sulcus is noted. This plate is long and flared, consistent with the morphology of the marginated tortoise. By using MIL 495 as comparative material we can identify this plate as a fragment of the right 11th peripheral, but the preservation of the specimen does not allow a clear identification.

MIL 1633: It is a small shell fragment. Further identification is not possible.

MIL 1638: It is fragment of the shell of a tortoise and it is crossed by a sulcus. By the curvature we can assume that it belongs to the carapace. Further identification is not possible.

MIL 1753 (Fig. 3; Table 1 for measurements): This specimen corresponds to the left part of a plastron that is preserved in four fragments. MIL 1753a represents the epiplastron, partial entoplastron and hyoplastron. MIL 1753b represents the anterior part of the hypoplastron. MIL 1753c represents the end of the left bridge, whereas MIL 1753d is a fragment of the hypoplastral region. The anterior lobe of the plastron is short and wide, with a rounded rim. The epiplastra are short and wide, forming a thick convex epiplastral lip viscerally. A deep gular pocket is noted. The entoplastron is longer than wide, roughly hexagonal. The hyo- and hypoplastra are long and wide, showing a moderate concavity ventrally. This suggests that the specimen is probably a male individual. The preserved part of the left bridge shows that the peripherals were tall and short, being moderately flared posteriorly. The gulars are long and narrow, covering the epiplastra and overlapping the anterior part of the entoplastron. The humerals are long, compared to the short pectorals. The humero-pectoral sulcus is laterally convex and medially slightly concave. It is situated on the hyoplastra, posterior to the end of the entoplastron. The pectoro-abdominal sulcus is curved, being concave medially and convex laterally. The abdominals cover the posterior half of the hyoplastra and all the preserved part of the hypoplastra, suggesting a rather long covering of the abdominals. This morphology, together with the thickened plate on the preserved part of the bridge resembles the morphology of the plastra with a movable posterior lobe.

MIL 1937 (Fig. 4D-F): This specimen corresponds to an almost complete costal, missing only the lateral part. The costal is medially short with a single rounded sutured side and laterally is long. Therefore, it presents the typical alternating pattern of the testudinids with costal medially short and laterally long alternating with costals being medially long and laterally short. Viscerally we notice the inserted rib. Dorsally, the vertebrals cover the medial part of the costal and it is crossed transversely by a curved pleural sulcus.

MIL 1938 (Fig.4M-O): This specimen corresponds to the anterior part of the left hypoplastron. The hypoplastron is flat. In the posterior part we notice the presence of a strongly curved abdomino-femoral sulcus.

*Titanochelon* sp.

MIL 1511: This specimen corresponds to the proximal part of the right coracoid. The proximal part MIL 1511 (Fig. 6): This specimen corresponds to the proximal part of the right coracoid. It is large and wide, triagonal in cross-section*,* and it shows a shallowly concave articular surface for the humeral head, whereas the symphyseal area with the scapula is broken. The coracoid shows a narrow and long neck, leading to the medial part of the bone, which is flattened and with elliptical cross-section.

MIL 1834: This specimen corresponds to a fragment of a porous, flat and rounded element. Based on the available material and the structure of the broken inner surface, this specimen can be attributed to a rounded osteoderm of a giant tortoise.

*Mauremys* sp.

MIL 818 (Fig. 7M-O): The specimen corresponds to a fragment of the right hypoplastron. The posterior side corresponds to the slightly convex suture with the xiphiplastron. Viscerally, there is a wide covering of the femoral scutes. Ventrally, no sulci are noted indicating that the preserved surface was covered only by the femorals.

MIL 981 (Fig. 7J-L): This specimen corresponds to a complete left long and narrow epiplastron. . Viscerally, a long lip is formed, being concave medially. The gular scutes are wide and long, overlapping the anterior part of the entoplastron. The gularo-humeral sulcus is slightly curved. The length of the medial suture of the epiplastra is 21 mm, the maximum width is 44 mm.

MIL 1847 (Fig. 7D-F): This specimen corresponds to a complete left long and rather narrow epiplastron. . Viscerally, a long lip is formed, being concave medially and convex laterally. The gular scutes are narrow and long, overlapping the anterior part of the entoplastron. The gularo-humeral sulcus is slightly convex, and causes a slight constriction in the anterior part of the lobe. Therefore, the anterior part of the lobe is protruding. This specimen shows a remarkable size. The length of the medial suture of the epiplastra is 34 mm, the maximum width is 54 mm. This suggests that the width of the anterior lobe could reach 11 cm, making this terrapin among the largest known.

MIL 1927 (Fig. 7P-R): This specimen corresponds to a fragment of the right hyoplastron. Ventrally, part of a sulcus is noted, probably of the humero-pectoral sulcus.

MIL 1928 (Fig. 7G-I): This specimen corresponds to an almost complete left long and narrow epiplastron. The gular scutes are narrow and long, overlapping the anterior part of the entoplastron. The gularo-humeral sulcus is almost straight. The length of the medial suture of the epiplastra is 21 mm.

MIL 1939 (Fig. 7A-C): This specimen corresponds to an almost complete neural that is hexagonal in shape, with short anterior lateral processes. The anterior part of the neural is wider than the posterior one. It is not crossed by any sulci.

MIL 1940 (Fig. 7S-U): This specimen corresponds to a fragment of the left hyoplastron. No sulci are noted in the preserved part and further description is not possible.

**ANALYSED MATERIAL**

*The outgroup taxa*. As outgroup taxa two extant representatives within Testudinoidea have been used, the emydid *Chrysemys picta* and the geoemydid *Mauremys caspica*. For the scoring, photographs of several specimens have been used, for *C. picta* (AMNH 75250; FMNH 22224; USNM 63078) and for *M. caspica* (USNM 167562).

*The ingroup extant taxa*. Many extant representatives of testudinids have been used in this analysis, trying to include most of the diversity in this clade. Photographs and direct observations were used. *Manouria impressa* (UCMP 136588; REP 63); *Geochelone elegans* (USNM 167557); *Stigmochelys pardalis* (UCMP 119051); *Indotestudo elongata* (UCMP 119050, 520645; ZIN 6978); *Indotestudo forstenii* (FRANK 73267); *Centrochelys sulcata* (MNCN 58823; REP 179, 180); *Agrionemys horsfieldii* (Mlynarksi, 1966 and information on digimorph.org for the cranium); *‘Testudo’ hermanni* (REP 3, 26; USNM 102222; ZIN 29; specimens in LGPUT uncatalogued); *Testudo graeca* (ZIN 15727, 18242; USNM 76506; FRANK 67588; REP 73; specimens in LGPUT uncatalogued); *Testudo marginata* (USNM 499029; ZIN 3941; specimens in LGPUT uncatalogued); *Testudo kleinmanni* (ZIN 9446; information in Delfino et al. 2009); *Kinixys erosa* (USNM 63483, 109687, 109696); *Gopherus agassizii* (UCMP 119060, 119066, 222094); *Gopherus polyphemus* (AMNH 73053; USNM 61059, 167526); *Astrochelys radiata* (USNM 167657); *Chelonoidis chilensis* (MPEF specimens); *Chelonoidis nigra* (VCCDRS 860-875; MNHN 1883-230); *Chelonoidis denticulata* (CRI 284, 287, 2489, 6374, 7702; UCMP 138687; USNM 73932); *Chelonoidis carbonaria* (AMNH 7042, 7043, 62583-62590; UCMP 119049, 119049, 137990). Information from the drawings, photographs and descriptions of Crumly (1982; 1984), Amiranashvili (2000), Meylan and Sterrer (2000), Gerlach (2001), Claude and Tong (2004), Joyce and Bell (2004), Lapparent de Broin *et al.* (2006), Pérez-García and Vlachos (2014), consisting of 81 characters from skull, shell and appendicular elements and 37 taxa (21 extant and 16 extinct; see suppl. material for further information). Please note that list of the above mentioned works is not exhaustive, as several summarize the anatomy and character definitions from numerous previous papers (e.g. references in: Crumly 1982; 1984, Meylan and Sterrer 2000; Claude and Tong 2004; Joyce and Bell 2004).

The ingroup fossil taxa: For *Titanochelon bolivari* material from MNCN and STUTS (presented in Pérez-García and Vlachos, 2014, see their supplementary information for detailed numbers). For *Ti. bolivari* Luján et al. (2014) is also used. For *Ti. bacharidisi* LGPUT material in Vlachos et al. (2014) and Vlachos (2015). *Titanochelon perpiniana* (Perpignan, MNHN 1887-26, Late Pliocene). *Titanochelon schafferi* (Samos; NHMW 2009z0103/0001, NHMW 1911/0005/0275, MN12-13). *Testudo antiqua novitensis* (Roggendorf; NHMW A-3602, MN6-8?). *Titanochelon vitodurana* (holotype, Wintethur; NWS 13758, MN6). *Titanochelon vitodurana* (Zurich; PIMUZ A/III 661, MN6). “*Testudo*” *picteti* (holotype, Winterthur; NWS 14900, MN6). For *Cheirogaster maurini* and ‘*Ergilemys’* *bruneti* the information in de Broin (1977) is used. For *Gigantochersina ammon* Andrews (1906) is used. For “*Testudo*” *gigas* direct observation on the holotype specimen in MNHN are made. For *Namibchersus namaquensis* Lapparent de Broin (2003; 2008) is used. For '*Paleotestudo canetotiana’* group Lapparent de Broin (2000) and Pérez-García and Murelaga (2013) are is used. For *‘Testudo’ antiqua* Corsini et al (2014) is used. For *Impregnochelys pachytestis* Meylan and Auffenberg (1986) is used. For ‘*Achilemys’* *cassouleti* Claude and Tong (2004) is used.

**CHARACTERS**

Carapace Characters

[1] NUCHAL 1: Shape of the outline of the nuchal plate (see Amiranashvili 2000:1). Coding: hexagonal (0); octagonal (1).

[2] NUCHAL 2: General shape of the nuchal plate (see Pérez-García and Vlachos, 2014:2). Coding: markedly wider than long (0); slightly wider than long or as long as wide (1); markedly longer than wide (2).

[3] NUCHAL 3: Overlapping of the first pleural on the nuchal plate (see Amiranashvili 2000:4). Coding: first pleural overlaps postero-lateral parts of the nuchal (0); first pleural touches, but it does not overlap the nuchal (1); first pleural is not in contact with the nuchal (2).

[4] NUCHAL 4: Nuchal notch (see Pérez-García and Vlachos, 2014:1). Coding: absent (0); shallow (1); deep (2); significant medial protrusion present (3).

[5] CERVICAL: Presence of a cervical scute on dorsal side of the carapace (see CVS, Crumly, 1984; Takahashi et al., 2003:15; Joyce and Bell, 2004:40; Pérez-García and Vlachos, 2014:14). Coding: dorsally present (0); absent (1).

[6] NEURAL NUMBER: Number of neural plates (see Amiranashvili, 2000:7; Lapparent de Broin et al., 2006:5; Pérez-García and Vlachos, 2014:3). Coding: nine neurals (0); eight neurals (1); seven neurals or less (2).

[7] NEURAL 1: Shape of the first neural (see Pérez-García and Vlachos, 2014:6). Coding: hexagonal, short sides positioned posteriorly (0); rectangular (1).

 [8] NEURAL 2: Shape of the second neural (see Joyce and Bell, 2004:37; Pérez-García and Vlachos, 2014:7). Coding: rectangular (0); hexagonal, short sides positioned anteriorly (1); hexagonal, short sides positioned posteriorly (2); octagonal (3).

[9] NEURAL 3: Shape of the third neural (see Joyce and Bell, 2004:38; Pérez-García and Vlachos, 2014:8). Coding: hexagonal (0); rectangular (1); octagonal (2).

[10] NEURAL 4: Shape of the fourth neural (see Pérez-García and Vlachos, 2014:9). Coding: rectangular (0); hexagonal (1); octagonal (2).

[11] NEURAL 5: Shape of the fifth neural (see Pérez-García and Vlachos, 2014:10). Coding: hexagonal (0); rectangular (1).

[12] COSTAL: Medial contact of the seventh and/or eighth costal plates (see Joyce and Bell, 2004:39). Coding: absent (0); present (1).

[13] SUPRAPYGAL: Number and shape of the suprapygal bones (see PYP, Crumly, 1984; Amiranashvili, 2000:12; Lapparent de Broin et al., 2006:6, 7; Pérez-García and Vlachos, 2014:11). Coding: two, the contact between the suprapygals is straight and perpendicular to the axial plane (0); two, the two suprapygals together constitute one trapeze and the first suprapygal embraces the lenticular second one (1); one, suprapygals fused, constituting one trapeze (2).

[14] PYGAL: Pygal shape (see Lapparent de Broin et al., 2006:8). Coding: quadrangular (without small latero-anterior borders) (0); quadrangular or hexagonal with small latero-anterior borders (1).

[15] VERTEBRAL 1: Width of the vertebrals in respect with the pleurals (see Amiranashvili, 2000:15, 16; Lapparent de Broin et al., 2006:14). Coding: wide vertebrals, wider than the pleurals (0); wide vertebrals, almost equal to the pleurals (1); narrow vertebrals, narrower than the pleurals (2).

[16] VERTEBRAL 2: Overlapping of fifth vertebral on suprapygal (see Lapparent de Broin et al., 2006b:6). Coding: the posterior sulcus of the fifth vertebral overlaps the anterior part of the pygal (0); the posterior sulcus of the fifth vertebral crosses the suprapygal transversely (1); the posterior sulcus of the fifth vertebral coincides with the suprapygal-pygal suture (2).

[17] SUPRACAUDAL 1: Fusion of twelfth marginals into a supracaudal, dorsally (see SSP, Crumly, 1984; Amiranashvili, 2000:18; Takahashi et al., 2003:27; Joyce and Bell, 2004:49; Lapparent de Broin et al., 2006b:15, 16; Pérez-García and Vlachos, 2014:19). Coding: two twelfth marginals present dorsally (0); twelfth marginals fused into a single supracaudal dorsally (1).

[18] SUPRACAUDAL 2: Fusion of twelfth marginals into a supracaudal, viscerally (see previous character). Coding: two twelfth marginals present viscerally (0); twelfth marginals fused into a supracaudal viscerally (1).

[19] COINCIDENCE: Coincidence between the costo-peripheral suture and the pleuro-marginal sulcus, in the anterior peripherals (1-4) (see Amiranashvili, 2000:19; Lapparent de Broin et al., 2006:4; Pérez-García and Vlachos, 2014:15). Coding: absent (0); present (1).

[20] PERIPHERAL: Protrusions on the peripherals, at the limit with the sulci between the marginal (Pérez-García and Vlachos, 2014:12,13). Coding: absent or poorly developed (0); well developed (1).

[21] MARGINAL 1: Contact of the second marginals with the lateral margin of the nuchal (Pérez-García and Vlachos, 2014:16). Coding: absent (0); present (1).

[22] MARGINAL 2: Contact of the second marginals with the first vertebral scute (Joyce and Bell, 2004:47; Pérez-García and Vlachos, 2014:17). Coding: absent (0); present (1).

[23] MARGINAL 3: Contact of the fourth marginals with the second pleural scutes (Pérez-García and Vlachos, 2014:18). Coding: absent (0); present (1)

[24] MARGINAL 4: Contact of the sixth marginals with the third pleural scute. Coding: absent (0); present (1)

[25] CARAPACIAL HINGE: presence of a carapacial hinge (CRH, Crumly, 1984). Coding: absent (0); present (1).

[26] BORDER: shape of the posterior shell border (see Lapparent de Broin et al., 2006:2). Coding: posterior border curved inwards (0); posterior border posteriorly flared (1).

Plastron

[27] ANTERIOR LOBE: Shape of the anterior lobe (Amiranashvili, 2000:22; Pérez-García and Vlachos, 2014:21). Coding: subrounded to straight (0); medially notched (1); trilobed (2); triagonal (3).

[28] GULAR PROTRUSION: Well-developed gular protrusion, caused by constriction in the gularo-humeral sulcus (see PLC, Crumly, 1984; Pérez-García and Vlachos, 2014:22). Coding: absent (0); present (1).

[29] EPIPLASTRON 1: Presence of an epiplastral lip (Amiranashvili, 2000:23; Takahashi et al., 2003:28; Joyce and Bell, 2004:59; Lapparent de Broin et al., 2006b:9). Coding: absent or poorly developed (0); present (1).

[30] EPIPLASTRON 2: Shape of the dorsal lip of the epiplastra (Pérez-García and Vlachos, 2014:23). Coding: concave (0); convex to flat (1).

[31] GULARS 1: Gulars in contact with the entoplastron or covering this plate (see GSE, Crumly, 1984; Amiranashvili, 2000:25; Takahashi et al., 2003:29; Pérez-García and Vlachos, 2014:24). Coding: not in contact (0); in contact with the anterior margin (1); covering the anterior area (2).

[32] GULARS 2: Angle between the sagittal axis and the gular–humeral sulcus (see GSE, Crumly, 1984; Pérez-García and Vlachos, 2014:28). Coding: 45º or more obtuse (0); more acute (1).

[33] HUMERALS: Median length of humerals, compared to the median length of gulars (Amiranashvili, 2000:28) Coding: humerals equal or smaller than the gulars (0); humerals longer than the gulars (1).

[34] HUMERO-PECTORAL 1: Position of the humero-pectoral sulcus relative to the entoplastron (Amiranashvili, 2000:32; Joyce and Bell, 2004:60). Coding: posterior to the entoplastron (0); coinciding medially with the posterior suture of the entoplastron (1); crossing the entoplastron (2).

[35] HUMERO-PECTORAL 2: Humero-pectoral sulcus shape (see PEC, Crumly, 1984; Amiranashvili, 2000:34, Takahashi et al., 2003:30; Pérez-García and Vlachos, 2014:25). Coding: not perpendicular to the axial plane, rounded or forming a wide angle (0); perpendicular to the axial plane, relatively straight throughout its width (1); perpendicular to the axial plane, with a well-developed lateral change of curvature (2).

[36] PECTORALS: Medial length of pectorals (see Amiranashvili, 2000:33; Pérez-García and Vlachos, 2014:26). Coding: long (0); short (1).

[37] PLASTRAL HINGE: Presence of a hypo-xiphiplastral hinge in the posterior lobe (see PPH, Crumly, 1984; Amiranashvili, 2000:40; Lapparent de Broin et al., 2006:3; Pérez-García and Vlachos, 2014:27; closely related morphological characters Amiranashvili 2000:37, Amiranashvili 2000:39, Lapparent de Broin et al., 2006b:11). Coding: absent (0); present, between hyoplastra and hypoplastra (1); present, between hypoplastra and xiphiplastra (2).

[38] FEMORO-ANAL: Shape of the femoro-anal sulcus (Amiranashvili, 2000:42). Coding: forms an acute angle with the axial plane (0); it is straight or slightly rounded, developed mainly perpendicular with the axial plane (1); forms S-shaped curve laterally (2).

[39] MEDIAN LENGTH OF ANAL SCUTE: (see Amiranashvili, 2000:44). Coding: shorter than the median length of femoral (0); longer than the medial length of femoral (1).

Cranium

[40] FRONTAL 1: Frontal participation to the orbital rim (Gerlach, 2001:1; Joyce and Bell, 2004:3). Coding: frontal participates to the formation of the orbital rim (0); frontal excluded from the orbit (1).

[41] FRONTAL 2: median length of frontals, compared to the prefrontals (Gerlach, 2001:4). Coding: frontals longer than prefrontals (0); prefrontals longer than frontals (1).

[42] INFERIOR DESCENDING PROCESSES OF THE FRONTAL: Modified by Joyce and Bell (2004:2) regarding the ventral closure of the processes (Gerlach, 2001:3, see below). Coding: absent, or very small (0); present, well-developed (1)

[43] SULCUS OLFACTORIUS: (Gerlach, 2001:3). Coding: ventrally open (0); ventrally nearly closed (1).

[44] FOSSA ORBITALIS: Position of fossa orbitalis (A), relative to the total length (B) of the cranium, from the anterior tip to the end of the condylus occipitalis (Pérez-García and Vlachos, 2014:31). Coding: placed on the anterior half (0); placed on the posterior half (1).

[45] LOWER TEMPORAL EMARGINATION: (Pérez-García and Vlachos, 2014:32). Coding: small (0); extensive (1).

[46] MAXILLA-PREMAXILLA SYMPHYSIS HEIGHT: Height of the symphysis of the maxilla/premaxilla compared to the height of the fossa nasalis (see Gerlach, 2001:10). Coding: short, shorter than the height of fossa nasalis (0); short, shorter than the height of fossa nasalis, but with the development of a dorsal projection (1); high, taller than the height of fossa nasalis (2).

[47] PREMAXILLA RIDGE: Presence of a longitudinal ventral ridge along premaxillary symphysis (Gerlach, 2001:11). Coding: absent (0); present (1).

[48] PREMAXILLARY PIT: Presence of a premaxillary pit on the ventral part of the premaxillae that could be circular or elliptical. Coding: absent (0); present (1).

[49] PREMAXILLA-MAXILLA RIDGE: Presence of a longitudinal ventral ridge along premaxilla-maxilla suture (Gerlach, 2001:12; “transverse ridge” of Takahashi et al, 2003). Coding: absent (0); present (1).

[50] NUMBER OF TRITURATING RIDGES: number of triturating ridges on the maxilla (Takahashi et al., 2003). Coding: one, labial (0); three (1).

[51] EXTENT OF LINGUAL RIDGE: Extent of the lingual ridge on premaxilla (modified by Gerlach, 2001:13). Coding: no, restricted to maxilla (0); yes, extending onto premaxillae (1).

[52] LABIAL RIDGE: Tooth-like tubercles on the labial ridge (modified by Gerlach, 2001:14 and Gerlach 2001:15). Coding: absent (0); present (1).

[53] POSTERIOR MAXILLARY PROCESS: the posterior maxillary process is defined as the posterior elongation of the maxilla below the jugal, forming an extension of the labial ridge (PMP, Crumly, 1984; Takahashi et al., 2003:7). Coding: absent (0); present (1).

[54] MEDIAN MAXILLARY RIDGE: Presence of a median maxillary ridge, between the lingual and the labial ridges on the palate (Takahashi et al., 2003:4; see also TR, Crumly, 1984;). Coding: absent (0); present, restricted to maxilla (1); present, extends to the premaxilla (2).

[55] MAXILLARY RIDGES: Tooth-like tubercles on the maxillary alveolar ridge (Gerlach, 2001:17). Coding: absent (0); present (1).

[56] VOMER RIDGE: presence of a ventral ridge on vomer (Gerlach, 2001:22). Coding: absent (0); present (1).

[57] VOMER: Posterior extent of the vomer till the basisphenoid (modified by Gerlach, 2001:24; based on Takahashi et al., 2003:10). Coding: vomer short, not dividing the palatines (0); vomer dividing the palatines, not the pterygoids (1); vomer diving part of the pterygoids, not reaching the basisphenoid (2); vomer dividing palatines and pterygoids, reaching the basisphenoid (3).

[58] CONTACT PTERYGOID-BASIOCCIPITAL: (see BP, Crumly, 1984; Joyce and Bell, 2004:21). Coding: present (0); absent (1).

[59] FORAMEN PRAEPALATINUM: Position of foramina praepalatina in ventral view (modified by Gerlach, 2001:28). Coding: visible (0); not visible in ventral view - foramina may be concealed by lingual extensions of the maxillary alveolar ridges (1).

[60] EXTENSION OF SQUAMOSALS: Extension of the squamosals in relation with the condylus occipitalis (modified by Gerlach, 2001:38). Coding: not extending (0); extending beyond the condylus occipitalis (1).

[61] CRISTA SUPRAOCCIPITALIS 1: Length of the crista supraoccipitalis, in relation with the condylus occipitalis (modified by Gerlach, 2001:42). Coding: not extending (0); extending beyond the condylus occipitalis (1).

[62] CRISTA SUPRAOCCIPITALIS 2: Presence of horizontal keels in crista supraoccipitalis (Gerlach, 2001:43). Coding: absent (0); present (1).

[63] CRISTA SUPRAOCCIPITALIS 3: Shape of crista supraoccipitalis (Pérez-García and Vlachos, 2014:30). Coding: straight (0); bended inwards (1); elevated posteriorly (2).

* [64] PARIETAL: Contact between the parietal and the quadrate, partially covering the prootic (modified by Gerlach, 2001:45). Coding: absent (0); present (1).
* [65] OPISTHOTIC: degree of expansion of the opisthotic in posterior view (modified by Gerlach, 2001:50). Coding: not expanded, fenestra postotica open (0); expanded, could contact exoccipital (1) expanded, contacting the pterygoid (2).
* [66] PROCESSUS TROCHLEARIS OTICUM: Extension of processus trochlearis oticum (see TP, Crumly, 1984; Gerlach, 2001:54). Coding: absent, or small (0); large (1).
* [67] FORAMEN NERVI TRIGEMINI: Number of foramen nervi trigemini (see Gerlach, 2001:56). Coding: one (0); two (1).

Skeleton

[68] HUMERUS 1: Diaphysis of the humerus (CRE, Crumly, 1984; Pérez-García and Vlachos, 2014:33). Coding: slightly curved (0); well-developed curvature (1).

[69] HUMERUS 2: Shape of the distal end of the humerus (Pérez-García and Vlachos, 2014:34). Coding: symmetric (0); asymmetric (1).

[70] HUMERUS 3: presence of latissimus dorsi scar (LDS, Crumly, 1984;). Coding: absent or reduced (0); present (1).

[71] HUMERUS 4: major trochanter of the humerus, in relation with the humeral head (Takahashi et al., 2003:22). Coding: short, not extending beyond the humeral head (0); long, extending beyond the humeral head (1).

[72] SCAPULA: Glenoid fossa of the scapula (Pérez-García and Vlachos, 2014:35). Coding: relatively short (0); elongated (1).

[73] CORACOID: Shape of the coracoid end (Takahashi et al., 2003:21). Coding: long and narrow (0); fan shaped (1).

[74] FEMUR 1: Angle between the femoral head and the diaphysis of the femur (Pérez-García and Vlachos, 2014:36). Coding: relatively large angle (0); femoral head developed almost perpendicular to the diaphysis (1).

[75] FEMUR 2: Union of the trochanters of the femur in ventral view (Takahashi et al., 2003:26; Lapparent de Broin et al., 2006:17). Coding: not fused (0); fused (1).

[76] CARPALS 1: medial and lateral centrale fusion (CNF, Crumly, 1984). Coding: not fused (0); fused (1).

[77] CARPALS 2: fusion of ulnare and intermedium (FUI, Crumly, 1984). Coding: not fused (0); fused (1).

[78] MANUS: phalangeal number in the manus (PHN, Crumly, 1984). Coding: two phalanges in all digits (0); one phalanx in fifth finger (1); one phalanx in first and fifth fingers (2); one phalanx in second and fifth finger (3).

[79] TARSALS: fusion of calcaneus and astragalus (CA, Crumly, 1984). Coding: not fused (0); fused (1).

[80] PES: fifth phalanx in the pes (FP, Crumly, 1984). Coding: present (0); absent (1).

[81] THIGH SPURS: Presence of thigh spurs, posterior to the femur (HSP, Crumly, 1984) Coding: absent (0); present (1).

MATRIX (in TNT format)

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81 37

Chrysemys\_picta 020001110100200000000000000000210010101110000001010001011101101?00000001110000110

Mauremys\_caspica 00200112010000000000110000?100210210000010000000100000011000101?000??????????0???

Manouria\_impressa 00210102010010120011000000111010101102000000010001001100200111000000000??????[0 1]???

Geochelone\_elegans 1021110212101001111000000010110010210000000001000101111030011100000??????????????

Stigmochelys\_pardalis 00111103121010111111000?00001111102101010100010001010?0120101120101??????????[0 1]???

Indotestudo\_elongata 0013011312101022111100000000112002110100010002000100010120001000000??????????[0 1]???

Indotestudo\_forstenii 00100113121010121110000000001120011101000100010001100101200110000011001010110[0 1]?10

Centrochelys\_sulcata 121211021210?02?111000??00111001102101010100010011011101200011001110011111110[0 1]111

Agrionemys\_horsfieldii 1011021312100011111000000000112102010010010000000100110120000000100??????????[2 3]???

Testudo\_hermanni 101002031210212201110000000011210101001011000000010011012000102011010010101102110

Testudo\_graeca 001102131210[0 1 2]0121111000000[0 1]011211101220000000100010011012?0010211101011110110[0 1 2 3]110

Testudo\_marginata 00100[1 2]13121[0 1][0 2]0121[0 1]11000001[0 1]01121110122?????????????????????????????10111101??2110

Milia\_testudinid ????????12102012111?????010011211001?????????????????????????????????????????????

Testudo\_kleinmanni 0003021312102012[0 1]1100000000011211001201????????????????????????????????????????10

Testudo\_marmorum 020101131210?0121100000?000011211001221??????????????????????????????????????????

Testudo\_antiqua 00[0 1]00[1 2]131[0 1 2]10102211100000000011211001000??????????????????????????????????????????

Kinixys\_erosa 0223110101002010110100001120110010000000110101100000000110011120000??????????????

Gopherus\_agassizii 002001131210100111[0 1]000000031101110010100101011100110110110001000101??????????[0 2]???

Gopherus\_polyphemus 00200113121000011110001100[2 3]1101010000200111010100110110110111010101??????????[0 2]???

Astrochelys\_radiata 0020010312101001110000000001110010110100010000001101110110111000111??????????????

Chelonoidis\_chilensis 0221111301[0 1]0100111100000001111[0 1]010110[0 1]0111000101110111012010102021000011101100010

Chelonoidis\_nigra 1222111301[0 1]0100111100000001011200021020001000101110111112010112021000111111100110

Chelonoidis\_carbonaria 01[1 2]011131210100211100000000111[0 2]01011010011000101110012012000112021???????????????

Chelonoidis\_denticulata 012011131210100211100000000111001021010011000101110112012010110021???????????????

Titanochelon\_bolivari 01101113121010211110001100[0 1 2][0 1]112110210100010001011100110???00112??1?01111111[0 1]0?1?0

Titanochelon\_vitodurana 02101?131210??21??1000110?00112110210?0??????????????????????????????????????????

Titanochelon\_perpiniana 0110111312101021111000?1000011011121010????00??????????????0???????00111111??????

Titanochelon\_bacharidisi ???????????010?11110???1000[0 1]111111210100010111?1???01?0????1111??1?0011111110?1?1

Achilemys\_cassouleti 000001002000002000000000000010001000011??????????????????????????????????????????

Gigantochersina\_ammon 00200103121010111?10000000011?211221010??????????????????????????????????????????

Namibchersus\_namaquensis 022001131210100111100000000011211021000??????????????????????????????????????????

Testudo\_gigas ??021????????0??1?000?00000011211001010??????????????????????????????????????????

Paleotestudo\_canetotiana 00[0 1]001131210102211110000000011210000001??????????????????????????????????????????

Ergilemys\_bruneti 011301131210100110110000000001201021200??????????????????????????????????????????

Hadrianus\_castrensis 01130002110010110?00000000111020020001???????????????????????????????????????????

Cheirogaster\_maurini 02221?131100001???00110?00111?201000010??????????????????????????????????????????

Impregnochelys\_pachytestis ???00???????10?????0??????0111210011010?????????????????????????????????11???????

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