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Eurotestudo, a new genus for the species *Testudo hermanni* Gmelin, 1789 (Chelonii, Testudinidae)

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Abstract

The new genus is created to include the species of the *hermanni* group, which is within *Testudo* s.l., a Palearctic genus, consequently separated from both *Testudo* s.s. and *Agrionemys*. A preliminary cladistic analysis of the osteological characters, including fossil species, demonstrated the splitting of the three lineages, probably since the Oligocene and surely at the Upper Miocene. Diagnosis of the new genus is based on a collection of features. The main stages of evolution leading to the three lineages are provided. We also describe external characters of the extant species that could be considered as diagnostic. However, phylogenetic relationships between genera are not definitively established. **To cite this article: F. de Lapparent de Broin et al., C. R. Palevol 5(2006).**

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Résumé

***Eurotestudo*, nouveau genre pour l'espèce *Testudo hermanni* Gmelin, 1789 (Chelonii, Testudinidae).** Ce nouveau genre est créé pour le groupe d'espèces *hermanni*, le séparant de *Testudo* s.s. et d'*Agrionemys* au sein de *Testudo* s.l., genre paléarctique. Une analyse cladistique des caractères ostéologiques, menée au préalable et incluant des espèces fossiles, a montré la séparation des trois lignées, probablement depuis l'Oligocène et sûrement le Miocène supérieur. La diagnose du nouveau genre est établie sur une conjonction de caractères. Les principales étapes de l'évolution menant aux trois genres sont données. Les caractères externes des espèces actuelles pouvant participer à la diagnose sont examinés. Les relations phylétiques entre les genres ne sont pas établies définitivement. **Pour citer cet article : F. de Lapparent de Broin et al., C. R. Palevol 5(2006).**

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Version française abrégée

Introduction

Un nouveau genre est créé pour le groupe d'espèces *hermanni*, en le séparant de *Testudo* s.s. [20]. Il existe trois lignées distinctes, séparées au sein de *Testudo* s.l. (sensu [17,23,24]), Testudinidae terrestre d'origine paléarctique : (a) *Testudo* s.s., connu en Europe [1,24] depuis le Miocène supérieur au moins [17], et en Afrique sûrement depuis le Pliocène, mais probablement dès le Miocène [15]; (b) *Agrionemys* [12], connu en Afghanistan et en Moldavie au Miocène supérieur [8,17,30], lié ou non à des formes orientales plus anciennes dont « *T.* » *turgaica* du Miocène « moyen » [17,31,34]; (c) la lignée d'*Eurotestudo* n.g., représentée en Europe au plus tard depuis le Miocène supérieur et moyen [5,16,32] de France et d'Allemagne et probablement dès l'Oligocène et actuellement représentée en Europe au moins par « *T.* » *hermanni* Gmelin, 1789 et « *T.* » *boettgeri* Mojsisovics, 1889 [1–3,28]. Des formes du Miocène inférieur [5] peuvent se situer, soit dans cette lignée, soit dans une lignée commune avec celle de *Testudo* s.s., suivant leur point de séparation [20]. La définition du nouveau genre proposée ici est fondée sur des caractères ostéologiques [5,6,9,10,18,19,23,24], grâce à une nouvelle analyse cladistique incluant des espèces fossiles [5,7,16,30–32] et actuelles de *Testudo* s.l., ce qui a permis de polariser les caractères et de faire la part des homoplasies. Certains caractères externes des espèces actuelles peuvent participer à la diagnose [1–4,9,23,24,27].

Systématique (voir la version anglaise)

Eurotestudo n.g.

Espèce type: *Testudo hermanni* Gmelin, 1789

Espèces valides incluses

Le groupe *hermanni*: *Eu. hermanni* (Fig. 1), *Eu. boettgeri* (dont *Eu. hercegovinensis* tend à être séparé [28]), *Eu. pyrenaica*, *Eu. globosa*, *Eu. lunellensis*, *Eu. szalai*. Les espèces actuelles et les fossiles *Eu. pyrenaica* et *Eu. lunellensis*, sont ou peuvent être bien définies. *Eu. globosa* (un seul spécimen, mâle, os épais) se présente comme un représentant de *Eu. hermanni*. *Eu. szalai* (fragments isolés) n'est pas assez préservé pour être diagnostiqué [1–3,5,11,13,21].

Diagnose du genre

Eurotestudo n.g. est caractérisé par la nécessaire combinaison de (1) la série des vertébrales étreécie ;

(2) la fusion des suprapygales en un trapèze à bord postérieur rectiligne (ou l'état de la plus forte tendance à la fusion précédant celui de celle-ci) ; (3) la pygale quadrangulaire tendant à devenir hexagonale, à petits côtés antérieurs (alors souvent chevauchés par les marginales 11) ; (4) la tendance à la division de la supra-caudale, externe (souvent) et interne (moins souvent) ; (5) la surface ventrale des gulaires formant un triangle dirigé postérieurement et souvent saillant ventralement, souvent avec inflexion médiane antérieure du bord, saillant à l'avant, des gulaires. Les caractères 2 à 5 sont indépendamment homoplasiques chez *Agrionemys* et/ou *Testudo* s.s., rarement, et jamais tous ensemble (Fig. 1A, B, C, D).

Caractères externes additifs, non fossilisés (synapomorphies des espèces actuelles potentiellement génériques) : (1) sur la face frontale du bras, distale par rapport aux grandes écailles, une aire antéro-distale limitée, avec, soit des écailles petites et irrégulières (*Eu. hermanni*), soit uniquement de nombreuses écailles très petites (*Eu. boettgeri*), alors que toutes les écailles sont grandes et régulières chez les autres espèces de *Testudo* s.l. ; (2) écaille frontale fragmentée, presque indistincte ; (3) patron de coloration du plastron avec deux bandes foncées parasagittales, entières ou fragmentées [1,3,4].

Matériel référé au genre: tous les spécimens référés à *T. hermanni* et à *Testudo* sp. du Quaternaire d'Europe ayant les caractères donnés dans la diagnose et notamment ceux de l'Escale, Lunel-Viel [10,11] et Soave [33]. Les populations de Lunel-Viel et de Soave représentent de bonnes espèces, suffisamment préservées pour être diagnostiquées.

La lignée hermanni : elle débute avec *Paleotestudo canetotiana* [16,19] par la tendance, plus complète que chez les autres espèces de *Testudo* s.l., à la fusion des trochanters du fémur, puis avec « *T.* » *antiqua* [32] par les tendances conjointes à la division externe de la supra-caudale et à la fusion des suprapygales, enfin avec *Eurotestudo* n.g., où tous les caractères sont menés à leur terme [20].

Comparaisons morphologiques

Étude cladistique préalable. Une étude cladistique préalable, détaillée par ailleurs [20], inclut un nombre significatif de spécimens des espèces des lignées de *Testudo* s.s., d'*Agrionemys* et d'*hermanni* (voir la version en anglais) et certains de ses possibles alliés [5,16], *Paleotestudo canetotiana* et *Testudo promarginata*. Les *outgroups* sont *Manouria impressa*, *Indotestudo elongata* et « *Ergilemys* » [7] (sensu [5]) *bruneti*. Tous par-

tagent des caractères de Testudinidae terrestres [20]. *Testudo* s.l. partage des caractères avec *Indotestudo* et « *Er. bruneti* » et d'autres avec le seul « *Er. bruneti* ». Le genre *Testudo* s.l. est défini, les caractères partagés sont donnés ainsi que des particularités des formes de la lignée d'*Eurotestudo* n.g. [5,10,11,13,16–18,32]. Le point de séparation de *Testudo* s.s. et de la lignée *Eurotestudo* par rapport à *Paleotestudo canetotiana* [16] est examiné, ainsi que l'intégration de « *T.* » *antiqua* [32] dans la lignée.

Caractères externes des représentants actuels pouvant appuyer la séparation générique. Les caractères, mentionnés ci-dessus et retenus, sont examinés, ainsi que d'autres, à écarter de la diagnose, tels les tubercules des cuisses (apomorphie de *Testudo* s.s.), l'éperon caudal présent, mais variable, chez *Agrionemys*, *Eurotestudo* et *T. kleinmanni* et les modes de réduction de la main: réduction à quatre doigts (*Agrionemys*) ou seulement partielle chez *Eurotestudo* (ongle du 1^{er} et/ou du 5^e doigts, éventuellement réduits à absents) [1,3,4,9,23,24,27].

Discussion et conclusion

Les relations phylétiques des trois lignées par les différentes approches (morphologie des actuels ou/et des fossiles [9,23,24], analyse moléculaire [14,22, etc.]), ne peuvent être définies. Il apparaît que, suivant les taxons inclus et en fonction des méthodes utilisées, le groupe actuel *hermanni* (*hermanni* seule ou avec *boettgeri*) peut, soit être rapproché d'*Agrionemys* [9], mais aussi d'*Indotestudo* et d'autres taxons [14,22], soit être le groupe frère d'*Agrionemys* et de *Testudo* s.s. [24]. D'après l'étude sur laquelle est fondée la présente diagnose [20], les trois lignées sont bien séparées, après *Manouria impressa*, *Indotestudo* et «*Er.* » *bruneti*, en un groupe « *Testudo* s.l. ». Soit la lignée d'*Eurotestudo* n.g. est rapprochée de *Testudo* s.s., soit les trois lignées de *Testudo* s.l. sont en irrésolution, si l'on supprime le taxon asiatique fossile « *T.* » *turgaica*, moins bien connu. *Testudo* s.s. et *Eurotestudo* n.g. acquièrent un même mode de recourbement progressif du bourrelet épiplastral dorsal. Le caractère est constamment mené à son terme chez *Testudo* s.s. dès son apparition (présence d'une poche gulaire, recourbement jusqu'à l'entoplastron), moins souvent chez *Eurotestudo* n.g. *Agrionemys* présente le stade le moins avancé du processus évolutif et dans une conformation différente du lobe antérieur plastral (plus large avec bords latéraux plus convergents et entoplastron moins réduit). Il y a hétérochronie dans l'apparition des stades évolutifs de plusieurs caractères homoplasiques dans les deux groupes. Le patron de

coloration commun de la carapace de type « *Testudo* » milite aussi en faveur de l'union de *Testudo* s.s. et *Eurotestudo*. En tout état de cause, le point de séparation de la lignée d'*Eurotestudo* n.g. par rapport aux formes asiatiques originelles remonte à une époque indéterminée, mais antérieure à l'Oligocène.

1. Introduction

The principal aim of this work is to create a new genus *Eurotestudo* for the so-called *hermanni* group of testudinids, because it forms a distinct evolutionary lineage without an available name. Some valid names that seemed available for *Testudo hermanni* Gmelin, 1789 such as *Chersine* Merrem, 1820 and *Medaestia* Wussow, 1916, have *Testudo graeca* Linnaeus, 1758 as type species ([23], A. Rhodin in litt. to J.P.). *Eurotestudo* n.g. is part of *Testudo* s.l. (sensu [17,23,24]). This is a diverse group of terrestrial Palaearctic testudinids which, besides (a) *Eu. hermanni* and affiliated taxa [1–6,10,11,13,16,17,19,24,32] includes (b) the western hinged form *Testudo* Linnaeus, 1758, s.s., type species *T. graeca*, a genus extant in the southern-oriental Mediterranean Basin eastward to the Middle East [1,6,8,9,15,17,24], and (c) *Agrionemys* Khozatsky & Mlynarski, 1966 [13], type species *Testudo horsfieldii* Gray, 1844, a western Central Asiatic extant genus, only represented in Europe as fossil (eastern part). Some recent studies [23–26] have elevated many subspecies to the rank of species within *Agrionemys*, *Testudo* s.s., and '*T.*' *hermanni* Gmelin, 1789, while new species have also been described recently [29]. *T. hermanni* (osteological Fig. 1) was separated from *T. boettgeri* Mojsisovics, 1889 (osteological Fig. in [9] as *T. hermanni*), and the name *T. hercegovinensis* Werner, 1899 was resurrected for a population previously attributed to *boettgeri* [28] (not included in the analysis in [20]). The taxon of upper rank (according to the ICZN) to unite the extant and fossil species in the *hermanni* complex is a genus, necessary in accordance with previous opinions [16,17,23,24], that agree with the various hypotheses about phylogenetic relationships among the three groups [14,17,22,24]. Examination of fossil lineages, into which we can integrate the extant species, shows that there is a clear separation of the three groups, each one inclusive of a succession of valid species: the separation occurred, at least, since the Upper Miocene, but probably the Oligocene. It is the date of the appearance of the oldest attested *Testudo* s.s., *Testudo marmorum* Gaudry, 1862 (Greece). In Africa, *Testudo* s.s. is definitely known from the Pliocene (Morocco). However, *Testudo* ('s.l.') *semenensis* Bergounioux, 1955, from

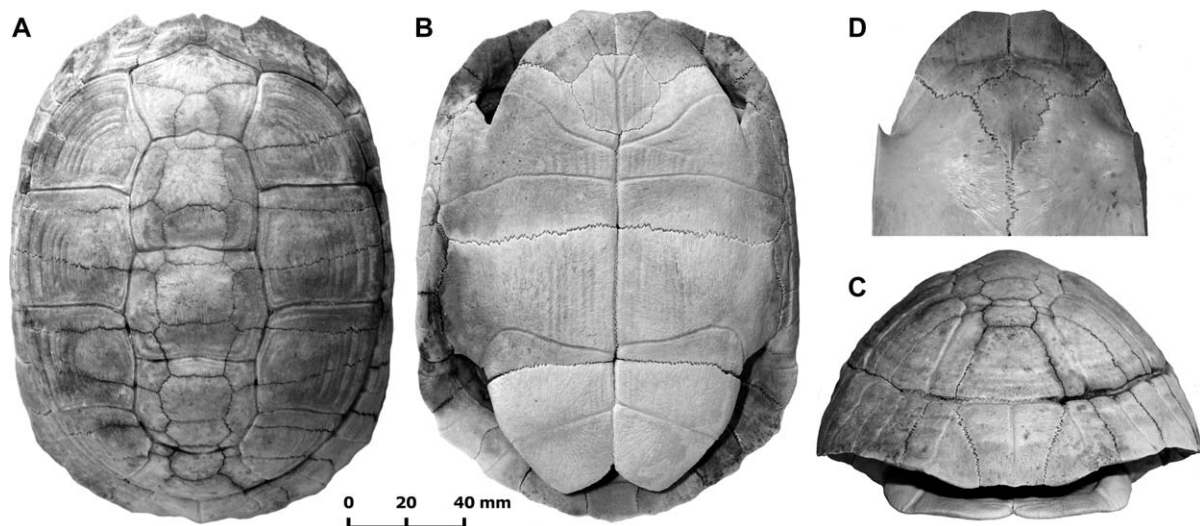


Fig. 1. *Eurotestudo hermanni* Gmelin, 1789, Collobrières, France. Carapace, views: A, dorsal, B, ventral, C, posterior. Plastron, anterior lobe, D, dorsal view.

Fig. 1. *Eurotestudo hermanni* Gmelin, 1789, Collobrières, France. Carapace, vues: A, dorsale, B, ventrale, C, postérieure. Lobe antérieur du plastron, D, vue dorsale.

the Upper Miocene (Tunisia), may be attributable to *Testudo* s.s [15,20]. *Agrionemys* is firstly known from the Upper Miocene of the Republic of Moldova, by *Testudo* *bessarabica* Riabinin 1915 [30] (*Prottestudo* Chkhikvadze, 1970) [6], and of Afghanistan ([17] and Rage & Lapparent de Broin, in prep.). *Agrionemys* might be related to *Testudo* *turgaica* Riabinin, 1926 [31], from the 'Middle' Miocene of Khazakstan as well as to other Asiatic or eastern European forms [8,34]. The stem lineage of *Eurotestudo* n.g. is identified in the 'Middle' Miocene with the appearance of *Paleotestudo canetotiana* (Lartet, 1851), France [5,16] and in the Upper Miocene with *Testudo* *antiqua* Bronn, 1831, Germany) [32]. Other older extinct western European species, such as *Testudo* *promarginata* Reinach, 1900, from the Lower Miocene (Germany, France) [5], may also be on the stem of *Eurotestudo* n.g. However, *T. promarginata* may predate the split between *Eurotestudo* n.g. and *Testudo* s.s. [20].

The diagnosis of the extant group *hermanni* has already been established on the basis of the morphological study of osteology [5,6,9,10,18,19,23,24] and external characters such as horny appendices, coloration and scales [1–4,24,26]. The present diagnosis of *Eurotestudo* n.g. is principally based on characters of the carapace, preserved in the fossils: plates and scute outlines as well as proportions, features which no doubt characterize the whole genus. Many specimens of the fossil species and extant populations of the lineages of *Testudo*, *Agrionemys* and *Eurotestudo* n.g. have been exam-

ined. The diagnosis of each lineage includes some unambiguous characters and various homoplastic characters: their appearance in the lineages is asynchronous and their variability has been established for each population.

2. Systematics

Order Chelonii Brongniart (Latreille), 1800
 Superfamily Testudinoidea Batsch, 1788
 Family Testudinidae Batsch, 1788
 Infrafamily Testudininei Batsch, 1788
Eurotestudo new genus

Etymology: from 'Europe', the continent of biogeographic origin, and '*Testudo*'

Type species: *Testudo hermanni* Gmelin, 1789, type locality: Collobrières, Var, France

2.1. Included species

Named valid species (sensu ICZN): The '*Eurotestudo*' *hermanni* group: extant *Eu. hermanni* (Fig. 1) and *boettgeri* from which '*T.*' *hercegovinensis* Werner, 1899 may be disassociated [28], and the fossil *Eu. pyrenaica* (Depéret & Donnezan, 1890), Pliocene of Perpignan (MN 15), *Eu. globosa* (Portis, 1890), Plio-Pleistocene boundary, Le Ville, Upper Valdarno, *Eu. lunellensis* (Almera & Bofill, 1903), 'Middle' Pleistocene of Caverna de Gràcia, and *Eu. szalai* Mlynarski, 1955, Pliocene of Weze (MN 15). The extant species plus *Eu. pyrenaica* and *Eu. lunellensis* are or can be

(respectively) well diagnosed. *Eu. globosa* (one male specimen in Le Ville, thick bones; referred fragments in other localities from Valdarno) may be a junior synonym of *Eu. hermanni*. *Eu. szalai* (some fragments) cannot be sufficiently diagnosed [1,4,5,10–12,21].

Material referred to the genus: all the specimens in the literature referred to *T. hermanni* and *Testudo* sp. from the Quaternary of Europe, which present the characters of *Eu. hermanni* exposed in the present diagnosis: in particular the populations of *T. hermanni* from the Quaternary of France, especially the populations from l'Escale (ca 0.6 Myr) and Lunel-Viel (ca 0.3 to 0.34 Myr), and '*Testudo* cf. *hermanni*' from Soave (Zoppega 2, Italy) (early Middle Pleistocene) [10,11, 33]. The unnamed Lunel-Viel and Soave populations certainly represent distinct diagnosable species.

The '*hermanni* lineage' initially includes *Paleotestudo canetotiana* [16] by the trend towards the fusion of the trochanters, more complete than in *Agrionemys* and *Testudo* s.s. [19], then '*T.* antiqua [32] by the common trend towards an external division of the supracaudal and fusion of the suprapyrgals and finally *Eurotestudo* n.g. [20] where these characters are the best realized.

2.2. Diagnosis

Eurotestudo n.g. is diagnosed by the obligatory combination of the following characters: (1) narrowed vertebral series, narrower than the costal series as a whole (in all populations; an apomorphic character); (2) fusion of the suprapyrgals into a trapezoid with a straight posterior border: the fusion varies from occasional in fossils (but often incompletely preserved) to most often present in extant populations (a rare homoplasy in *Testudo* s.s. and *Agrionemys*); (3) the quadrangular pygal becomes hexagonal with small latero-anterior sides (often present in all populations, a rare homoplasy in *Testudo* s.s. and *Agrionemys*), and which are sometimes covered by the 11th marginals; (4) tendency to having a divided supracaudal, externally and eventually internally; frequency of inner division of the supracaudal varies from rare to frequent depending on population (present in '*Ergilemys*', but presumably not by the same evolutionary process, see [20]); external division of the supracaudal occasional to constant, according to population, constant in *hermanni* and in the majority of cases in *boettgeri* (a rare homoplasy in *Testudo* s.s. and extant *Agrionemys* and in some other Testudininei such as *Pyxis*); (5) ventral surface of the gulars, making a posteriorly pointed triangle, frequently ventrally in relief relative to horizontal plan, often present in all

populations (a homoplasy in extant *Agrionemys*); there is often a medial anterior bend between the gulars (a homoplasy in *Testudo* s.s. and in extant *Agrionemys*) (Fig. 1).

Additional characters: external characters, not fossilized, possibly generic. Synapomorphies for the extant species (unique among the Testudinidae) are: (1) the small scales on the outer area of the front face of the forearm (in addition to the large and regular ones): irregular antero-distal area of small scales in *Eu. hermanni*, all smaller and very numerous in *Eu. boettgeri* [3]; (2) the fragmented, almost indistinct frontal scale; (3) the color pattern of the plastron with two parasagittal dark bands, each one whole or broken up [1,3,4].

2.3. Morphological comparisons

A cladistic analysis, previously performed and detailed elsewhere [20], includes, in the ingroup the species: *Testudo turgaica*, *Agrionemys bessarabica*, *A. horsfieldii*, *A. kazachstanica* Chkhikvadze, 1988; *T. marmorum*, *T. marginata* Schoepff, 1793, *T. weissingeri* Bour, 1995, *T. antakyensis* Perälä, 1996, *T. kenitrensis* Gmira 1993, *T. graeca* (s.l.) from the Maghreb, *T. promarginata*, *Paleotestudo canetotiana*, *T. antiqua* and the *hermanni* group (above mentioned valid species), and three outgroup taxa of terrestrial testudinids: *Manouria impressa* (Günther, 1882), *Indotestudo elongata* (Blyth, 1853) and '*Er.* bruneti Broin, 1977, a species attributed to the genus *Ergilemys* Chkhikvadze, 1972 [7] sensu [5], Oligocene, La Milloque, France. Many Miocene and Oligocene fossil species, all insufficiently known, although potentially belonging to the lineage of *Eurotestudo* n.g., were disregarded. Among them, some Oligo-Miocene fragmentary specimens from France, attributed to '*Ergilemys*' sp., have a hinge similar to that of *Testudo* s.s. only [5 (pl. 25, 28)], even in relatively young adults. The relationships of these specimens with '*Er.* bruneti' and the *Eurotestudo* n.g. lineage are unclear. All the above taxa are Testudininei by characters given in the analysis [20]. The characters of the clades are present in some other Testudininei.

Out of the 18 characters of the analysis, *Testudo* s.l. shares with *Indotestudo* and '*Er.* bruneti': (1) the coincidence of the costal-marginal scute sulci and the pleural-peripheral sutures and (2) the fusion of the two 12th marginals into a supracaudal. With '*Er.* bruneti', *Testudo* s.l. shares the shell form: more elevated than that found in *M. impressa*, with elevated peripherals and marginals, arched with domed lateral pleural slopes

and with two anterior and posterior slopes meeting at a domed more or less flattened part, and more or less strong protuberances below the vertebrals 2 or 3 or 4 and eventually the costals; basically quadrangular and moderately wide, not looking narrow or round; posterior border moderately postero-laterally expanded in dorsal view. In *Agrionemys*, the shell is rounded and shortened at the level of the bridge, with an elevated bridge and more convergent plastral lobes and a larger entoplastron. In the *T. marginata* group, the shell becomes elongated (much postero-laterally expanded at the peripheral border), differently from *I. elongata* (postero-medially expanded). In the *antiqua* group, the shell widens. In *Paleotestudo*, the posterior border is not at all expanded.

As a member of *Testudo* s.l., the *Eurotestudo* n.g. lineage shares with *Testudo* s.s. and *Agrionemys* particularly the following characters: (1) the posteriorly ascending dorsal epiplastral lip with a slightly convex surface: stopping its ascension abruptly (a) and, being more or less curved (b), located above the posterior surface of the epiplastron which is not thickened (c) – elements (a), (b), and (c) differentiate these chelonians from *Indotestudo* (Fig. 1D, figures in [5,9,20]) –; (2) the typically sinuous sulcus between the abdominal and femoral, with the latero-anterior sinuosity clearly extended on the hypoplastron and anterior to the inguinal notch (Fig. 1B); however, in *Testudo* s.s., the curve tends to be reduced, with the presence of the hypo-xiphial hinge, particularly in the *marginata* group; in *Agrionemys* the hypoplastral overlap by the femorals is apparently more extensive, partly because the hypoplastron is shortened; (3) the possible posterior reduction of the series of eight neurals (Fig. 1A) to 7 or 6; this character is very rare in *Eurotestudo* n.g., but it is the norm in extant *Testudo* species (in time after the fossil species *T. kenitrensis* and *T. marmorum* and some fossil *T. graeca* from Morocco), and in the extant *Agrionemys* species (evolving after the fossil species *bessarabica*); (4) the ‘*Testudo* s.l.’ type of suprapygal–pygal, as opposed to the ‘*geomydine*’ (in *Manouria impressa*) and ‘*Geochelone*’ (in *Indotestudo* and ‘*Er. bruneti*) types: both suprapygals constitute one trapezoid structure, with straight borders, in front of the pygal (Fig. 1C), that is completely elongated throughout its width and not only laterally as in the ‘*Geochelone*’ type (see [5,9,18] and other references included); consequently, the posterior border of the vertebral 5 is confluent with the limits of the suprapygal–pygal structure (complete coincidence of sutures and sulci); however, in extant *Agrionemys*, vertebral 5 is slightly shorter pos-

tero-medially so that the supracaudal slightly covers the suprapygal (particularly in *A. kazachstanica*) with a sinuosity [9] and the vertebral 5 may overlap the pygal, often in *Eurotestudo*, sometimes in *Testudo*; (5) the narrowing of the lateral scute border on the dorsal epiplastron.

In *Testudo* s.l., the suprapygals (two in general) are divided by a semicircular (primitively) or a semicircular–semitransversal, or a transverse line, according to the following evolutionary stages; the most derived stage is the fusion of the suprapygals into a trapezoid. The fusion of the suprapygals into a trapezoid with a posterior straight border is mostly known in *Eurotestudo* n.g., although it also occurs rarely in some species of *Testudo* and *Agrionemys*. The three genera evolved, in parallel, the following homoplastic characters (that are in general very frequently witnessed in Testudinini): (1) the partial to complete reduction of the dorsal cervical (constantly or occasionally present in a population); (2) a tendency for the pectorals to extend medioanteriorly toward the entoplastron and onto the entoplastron (without meeting each other anteromedially), more or less frequently according to population, and not only in *Agrionemys* and *Eurotestudo* n.g. (particularly in the *boettgeri*, Lunel-Viel and Soave populations), from which taxa this character is well known, but also in *T. graeca* [9].

With *Testudo*, *Eurotestudo* n.g. shares an epiplastral lip that curves onto the entoplastron, overhanging the dorsal surface. Below this, there is a depressed gular pocket. A tendency toward a gular pocket is obvious in *Eurotestudo* n.g.: a narrow and weak gular pocket is particularly found in the Lunel-Viel population, and one is often present in *P. canetotiana*. *P. canetotiana* (figures in [5,16]) is considered as belonging to the *Eurotestudo* n.g. lineage despite its similarity with *Testudo*. The differentiating conditions are the acquisition in *Testudo* of a characteristic hinge, in both sexes, between the hypo- and xiphial, with (a) a correlative elongation of the posterior lobe, (b) the fusion of the lateral extremities of the suture (at the hinge) and of the abdomino-femoral sulcus (except in juveniles and in the small-sized *T. kenitrensis*), and (c) the tendency to shorten the femorals on the hypoplastron (particularly in the *marginata* group). In *Testudo*, the gular pocket is constant, small to strong [6,9,23,24], except in *T. antakyensis* Perälä, 1996 (the lip is often not even curved; Fig. in [9] as *T. terrestris* Forsskål, 1775). In *Agrionemys* (figure in [9]) (unknown in *A. bessarabica*), the epiplastral lip is never curved up to entoplastron, as in fossils of the *Eurotestudo* n.g.

lineage ('*T.*' *antiqua*, *Eu. pyrenaica*, figures in [5,32]) and the epiplastral–entoplastral surface is rarely depressed into a gular pocket. On the other hand, the ventral surface of the gulars in relief can also be found in *Agrionemys*, but never in *Testudo*.

The process of modification of the suprapygal area, with the tendency to complete fusion of the plates, is most achieved in *Eurotestudo* n.g., making it unique among Palaearctic forms (present in some African small endemics [18]). Meanwhile, the process of fusion of the last neurals is more achieved in the two other genera, although homoplastically because the fusion progressively develops in each lineage separately. In the lineage of *Eurotestudo* n.g., there is no single species accumulating all the more derived states of the homoplasies. *P. canetotiana* has a higher tendency towards a gular pocket. The species have their particularities: '*T.*' *antiqua* has a wider shell [32]; '*Eu.*' *pyrenaica* has a triangular or trapezoid notch at the nuchal, not affecting the adjacent peripherals and the cervical is completely lacking, as in the Upper Miocene '*T.*' *amberiacensis* Depéret, 1894, France [5], which might belong to a *pyrenaica* group if it is confirmed that it belongs to *Eurotestudo*. The *Eu.* aff. *hermanni* populations from Lunel-Viel and Soave are more derived by the progression of the pectorals on the entoplastron. The Soave population and some elements from the Quaternary of the Iberian Peninsula (references in [11,19,20]) have the most developed epiplastral lip, thick and often very protruding, but lacking a gular pocket. The extant *Eu. hermanni* is most advanced by having a trapezoid suprapygal and the more consistently divided supracaudal (externally and internally), and perhaps also by featuring the very occasional presence of seven neurals (the series is not well enough known in other populations to make comparisons). *Eu. boettgeri* has the femorals much shortened.

Concerning fossil relatives of *Eurotestudo* n.g., *Paleotestudo canetotiana* is considered as belonging to the *Eurotestudo* lineage by the more advanced fusion of the femoral trochanters and its full aspect; some specimens have the gulars in relief ventrally and one has a hexagonal pygal. This is also congruent with its geographical context. As seen above, the species is also rather similar to *Testudo graeca* (s.l.) except for the absence of hinge and shorter posterior lobe. But it lacks the protuberances and the posteriorly expanded border of the shell. *P. canetotiana* is the first European form which presents the most derived evolutionary state of the anterior lobe shape: the trapezoid lobe with anteriorly prominent gulars, well laterally exposed, becomes widened at the anterior border and the gulars

do not participate in the lateral borders; presently the gulars occupy either only the complete anterior border of the lobe, or a narrow slice (protruding or not) in its medial part, the humeral lateral borders being rounded. This morphology is also present in *Testudo* s.s. (always) and in *A. kazachstanica* and some *A. horsfieldii*, but not in '*T.*' *turgaica* and *A. bessarabica*. However, in *Agrionemys*, the anterior lobe always has more converging lateral borders. '*T.*' *antiqua* belongs more confidently to the *Eurotestudo* n.g. lineage: tendency to feature a divided supracaudal, possibility for having fused suprapygals, general aspect of the shell which is of a quadrangular form, posteriorly expanded according to the norm in *Eurotestudo* n.g. contrarily to *Paleotestudo*. The epiplastral lip is wide and long, never curved up to the entoplastron and there is no gular pocket. The shell is particularly wide (width/length). Its femur is undescribed, and the possible fusion of the suprapygals needs to be confirmed. A revision of '*T.*' *antiqua* (as for some close fossil species) is necessary to reconsider its phylogenetic position with respect to its possible integration into the genus [20].

2.4. External characters indicating generic status

The extant species in the new genus *Eurotestudo* are unique among the Testudinidae by the following characters: (1) the scalation of the front face of the forearm includes a distal area of small and irregular (small scales in *Eu. hermanni*, very small and numerous in *Eu. boettgeri*), while there are only large and regular scales in other Testudinidae; (2) the frontal scale is fragmented, almost indistinct, while most tortoises have a large and well-delimited frontal, following two elongated prefrontals; (3) the color pattern of the plastron: from the basic pattern of postero-lateral dark spots, originating from the areolar zone (basically radiated), develops a system of parasagittal dark bands that is unknown among other chelonians. Another external character supports the separation of the new genus *Eurotestudo*: the thigh tubercle ('thigh-spur') may constitute a basic autapomorphy in the extant *Testudo* sp.; it is absent in *Agrionemys* and *Eurotestudo*. In return, the color pattern of the dorsal carapace of the '*Testudo*' type may constitute a basic synapomorphy linking *Eurotestudo*–*Testudo* s.s. Some characters (previously considered as synapomorphies) are actually weakly homoplastic:

– the caudal spur is moderate in *Agrionemys*, strong and lengthened in *Eurotestudo* and very small in *T. kleinmanni* plus *T. wernerii*. It is present and morpho-

logically variable in various lineages of terrestrial Testudinidae, but also in other chelonians (*Kinosternon*, the extinct *Meiolania*);

– the reduction of the fingers of the hand, considered as shared by *Agrionemys* and *Eurotestudo* n.g. is neither a synapomorphy nor a homoplasy: it is not the same character:

- four fingers in *Agrionemys*;
- five fingers, but nails 1 and/or 5 are often reduced, rarely absent in *Eu. hermanni* s.s. *Testudo* has primitively five fingers [1,3,4,9,23,24,27].

3. Discussion and conclusion

None of the approaches, either morphological [9,23,24] or molecular [14,22,etc.], provides a strong hypothesis of inter-relationships of the lineages or within species in the genera. The results differ according to the authors, the taxa included, the type and amount of genetic material, the number of specimens and the method employed. The *hermanni* group (including *Eu. hermanni* alone or with *Eu. boettgeri*) may be sister to *Agrionemys* [9,14] or else with *Indotestudo* or others [22]. Or it may be placed as the sister of a clade with *Agrionemys* and *Testudo* [24]. In recently constructed cladograms [20], the three genera are well separated after '*Er*'. *bruneti* in every hypothesis: '*T*'. *promarginata* is either the sister group of both *Testudo* s.s. and *Eurotestudo* or the sister taxon of the three genera in polytomy if the poorly preserved '*T*'. *turgaica* is excluded from the analysis. Even if the exact link-point between the three lineages is not definitely established, their separation and differentiation is well established. We can hypothesize that the shared origin of *Testudo* and *Eurotestudo* n.g. is more probable than that of *Eurotestudo* n.g. and *Agrionemys*, a previously proposed hypothesis [9]: according to the new analysis [20], similarities remaining between *Eu. hermanni* and extant *Agrionemys* spp. are mostly primitive. Beside the derived more curved epiplastral lip, shared by *Testudo* and *Eurotestudo* n.g, the derived color pattern of the dorsal carapace of the '*Testudo*' type, shared by extant species, is also significant. In any case, various homoplastic characters have evolved asynchronously in these three lineages. Although the relationships between *Eurotestudo* n.g., *Testudo*, and *Agrionemys* cannot be firmly established, these lineages are clearly and consistently separated according to all the approaches. Whatever their inter-relationships may be, the common origin of the three genera is in Asia before the Oligocene.

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