

## Anatomy and variability of *Cuvierichelys parisiensis*, a geoemydid turtle that crosses the Eocene-Oligocene boundary in Belgium

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### Abstract

Abundant material of turtles from the early Oligocene site of Boutersem-TGV (Boutersem, Belgium) is presented here. No information on the turtles found there was previously available. All the turtle specimens presented here are attributable to a single freshwater taxon that is identified as a member of Geoemydidae, *Cuvierichelys*. It is the first representative of the '*Palaeochelys* s. l.–*Mauremys*' group recognized in the Belgian Paleogene record. This material, which documents all the elements of both the carapace and the plastron of the taxon, cannot be attributed to the only species of the genus *Cuvierichelys* so far identified in the Oligocene, the Spanish form *Cuvierichelys iberica*. Rather, the taxon from Boutersem is recognized as *Cuvierichelys parisiensis*. Thus, both the paleobiogeographic and the biostratigraphic distributions of *Cuvierichelys parisiensis* are extended, its presence being confirmed for the first time outside the French Eocene record. The validity of some European forms is refuted, and several characters previously proposed as different between *Cuvierichelys iberica* and *Cuvierichelys parisiensis* are recognized as subjected to intraspecific variability.

**Keywords:** Freshwater turtle, *Cuvierichelys*, Paleogene, Western Europe

### Resumen

Abundante material de tortugas proveniente de una misma localidad, el yacimiento del Oligoceno inferior de Boutersem-TGV (Boutersem, Bélgica), es aquí presentado. Hasta ahora no existía ninguna información sobre las tortugas allí halladas. Todo el material de tortugas proveniente de ese yacimiento y presentado aquí es atribuible a un único taxón, correspondiente a una forma acuática. Se trata de un miembro de Geoemydidae, *Cuvierichelys*. Este hallazgo supone la primera identificación de un representante del grupo '*Palaeochelys* s. l.–*Mauremys*' en el registro del Paleógeno Belga. Sin embargo, este material, que permite identificar todos los elementos tanto del espaldar como del plastrón, no puede ser atribuido a la única especie del género *Cuvierichelys* hasta ahora identificada en el Oligoceno, la forma española *Cuvierichelys iberica*. El taxón de Boutersem es reconocido como *Cuvierichelys parisiensis*. Su identificación fuera del registro Eoceno francés permite ampliar tanto la distribución paleobiogeográfica como bioestratigráfica de esta especie. La validez de varias formas europeas es refutada y varios caracteres previamente reconocidos como diferentes entre *Cuvierichelys iberica* y *Cuvierichelys parisiensis* son justificados como sometidos a variabilidad intraespecífica.

**Palabras clave:** Tortuga acuática, *Cuvierichelys*, Paleógeno, Europa Occidental

## 1. Introduction

Testudinoidea is the most abundant and diverse group of turtles living today (van Dijk *et al.*, 2014). It includes the only currently living terrestrial turtles (the tortoises Testudinidae) as well as several lineages of freshwater turtles. Among them, Geoemydidae is particularly diverse, its representatives being

present on several continents. Both Testudinidae as Geoemydidae are recognized in Europe since the Eocene (Lapparent de Broin, 2001; Claude and Tong, 2004; Hervet, 2004a; Pérez-García and Vlachos, 2014). The record of Geoemydidae in the Paleogene of this continent is abundant. However, the recently proposed hypotheses about the diversity represented are markedly different from each other (see Hervet, 2004a

versus Claude and Tong, 2004). These differences are mainly generated by the relative scarce and fragmentary material found in many of the Paleogene localities where this group has been found. For that reason, these specimens generally provide very limited information on the intraspecific variability of the taxa represented.

Information on the members of Geoemydidae in the Belgian Paleogene record is very limited with only one member of Ptychogasterinae *Ptychogaster laurae* (Förster and Becker, 1888) mentioned in the early Oligocene of Hoogbutsel (Russell *et al.*, 1982). However, no representative of the '*Palaeochelys* s. l.–*Mauremys*' group sensu Hervet, 2003, very common in the European Paleogene record, has been, until now, identified in that country. The presence of this group in the Belgian Oligocene is reported here. The specimens studied here were collected by one of us (RS) in the locality of Boutersem-TGV (Boutersem, Belgium) (Fig. 1). The study of relatively abundant material from that location allows us to identify a species previously known only in the Eocene. This is the only turtle taxon from Boutersem identified by well-preserved specimens. The comparison between the specimens of the representative of the '*Palaeochelys* s. l.–*Mauremys*' group preserved in Boutersem provides new data on the intraspecific variability of this taxon. Some hypotheses that proposed the synonymy between various forms described in the European record are confirmed.

Institutional abbreviations: IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium. MGM, Museo Geominero, Instituto Geológico y Minero de España, Madrid, Spain.

## 2. Geographical and geological context

The site of Boutersem-TGV (Boutersem, Belgium) was a shallow outcrop at km 29,650 along the highway E40 (A3), ca. 30 km east of Brussels, temporarily exposed during the High Speed Train (TGV) railway construction in September 1999 (Fig. 1). The fossil bed occurred at the base of a fluvio-lacustrine complex, the Boutersem Member, which overlies the marine Neerrepn Sands. The latter belongs to the marine St. Huibrechts-Hern Formation located, at the base of the Rupelian (earliest Oligocene), dated at 33.9 Ma (Van Simaey and Vandenberghe, 2006; Vandenberghe *et al.*, 2012). Boutersem and its associated localities Hoogbutsel and Hoeleden are included in reference level MP 21 of the mammalian biochronological scale of the European Paleogene (see BiochroM'97, 1997; Smith, 2003), and are approximately 33.5 million years old.

The Boutersem Member consists of shell-beds, clayey sands, and shelly sands. It belongs to the Borgloon Formation, which is included in the Tongeren Group (Wouters and Vandenberghe, 1994; Mayr and Smith, 2001). Boutersem, along with associated localities at Hoogbutsel and Hoeleden, has been known since the early 1950's (Glibert and de Heinzelin

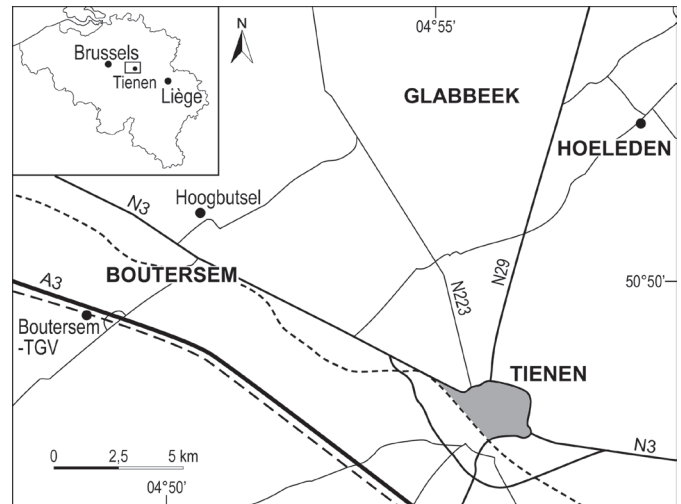


Fig. 1.- Geographic location of the locality of Boutersem-TGV (Boutersem, Belgium), that yielded the early Oligocene turtles studied here, identified as *Cuvierichelys parisiensis*. The location of the other synchronous localities of Hoogbutsel and Hoeleden are also indicated (black dots).

de Braucourt, 1952) and has produced a fairly extensive vertebrate faunal assemblage (see Smith, 2003 for an overview). The Boutersem sands contain molluscs (Marquet *et al.*, 2008) and also yielded a rich vertebrate fauna represented by amphibians (Folie *et al.*, 2010), lizards (Augé and Smith, 2009), birds (Mayr & Smith, 2001), and mammals (Smith, 2003, 2004 a,b; 2006 a,b; 2007; Smith and van den Hoek Ostende, 2006; Smith and Smith, 2012; Gunnell *et al.*, 2013). The mammal fauna is correlated with the reference level MP 21 defined on the fauna of Soumaillies (Aquitaine, France) (BiochroM'97, 1997). All the fossils are recorded from the oldest continental levels of the early Oligocene, near the 'Grande Coupure' (Stehlin, 1909).

## 3. Systematic paleontology

Testudines Batsch, 1788  
 Pan-Cryptodira Joyce, Parham and Gauthier, 2004  
 Cryptodira Cope, 1868  
 Testudinoidea Batsch, 1788  
 Geoemydidae Theobald, 1868  
 '*Palaeochelys* s. l.–*Mauremys*' group sensu Hervet, 2003  
*Cuvierichelys* Hervet, 2004a

*Cuvierichelys parisiensis* (Gray, 1831)  
 (Figs. 2-4)

*Material*:—34 specimens corresponding to disarticulated plates, and partial carapaces and plastra (Figs. 2-4).

*Locality and horizon*:—Boutersem-TGV site, Boutersem, Flemish Brabant, Belgium (Glibert and de Heinzelin de Braucourt, 1952; Smith, 2003). Boutersem Sand Member, reference level MP-21 (see BiochroM'97, 1997), Borgloon Formation, early Rupelian, early Oligocene.

*Description:*—Some specimens studied here correspond to adult individuals, showing well-ossified joints between the plates (Fig. 3N-P). However, most of them are identified as subadults. The contact between the peripherals and the costals of the subadults are not fully sutured, thus fontanelles between these plates remain open (Figs. 2A-D, 3Q-R). All the studied plates are relatively thin. No well-developed growth rings are identified in the carapace or in the plastron.

The nuchal plate is hexagonal, slightly wider than long (Fig. 2A-F). It lacks a marked medial thickening in the visceral surface. An almost absent to very shallow anterior notch is observed. The neural series is relatively wide. The taxon analyzed has eight (Fig. 3J-K) to nine (Fig. 2M-N) neurals. The first neural is rectangular, longer than wide (Fig. 2A-D). The other neurals are hexagonal, except the ninth, which is also rectangular and longer than wide (Fig. 2M-N). The second to fifth neurals are slightly longer than wide, and their latero-anterior margins are significantly longer than the latero-posterior ones. The sixth to eighth neurals are almost as wide as long, and their latero-anterior margins are almost as long as the latero-posterior ones (Figs. 2I-J, 2M-N, 3J-K). The carapace lacks lateral keels. However, a poorly-developed posterior medial keel is present in some specimens (Fig. 3L). A poorly-developed alternating pattern for the costals, composed by medially alternative long and short plates, versus laterally short and long ones, is identified (Fig. 2I-J, M-N). The proximal region of the dorsal ribs is relatively long (Figs. 2I, N). The distal region of the dorsal ribs is well-developed (Figs 2I-J, 3A-C), inserted into well-developed depressions present on the medial side of the peripherals (Fig. 3Ae, Ao, As, Aw'). This taxon has two suprapygal plates. The first one is markedly wider posteriorly than anteriorly (Fig. 3D-K). That plate can be almost as wide as long, or slightly wider than long. The second suprapygal is wider than the first one, being substantially wider than long (Fig. 3L-M). This plate is hexagonal. The pygal plate is rectangular, almost as long as wide (Fig. 3L-M, AV-AW). It has a small posterior notch. The plastral bridge is developed from the third to the seventh peripherals. The distal end of the bridge and posterior peripherals is dorsally directed.

The turtle from Boutersem has a cervical scute (Fig. 2-F). Dorsally, this scute is almost as wide as long in some specimens (Fig. 2A, E), but it is significantly longer than wide in others (Fig. 2C). Its dorsal length is less than half of the length of the nuchal, but greater than a third of the length of this plate (Fig. 2A, C, E). Ventrally, this scute is very short, especially in its medial region (Fig. 2B, D, F). The first vertebral scute is trapezoidal. It is wider anteriorly than posteriorly (Fig 2A, C, J). It is as wide as the nuchal in some specimens (Figs. 2A, 3R). However, it is wider than that plate in others (Fig. 3N). The first vertebral does not contact the second pair of marginals. However, it contacts the lateral edge of the first pair of marginals in some individuals (Fig. 2A), but not in others (Fig. 3N, R). The lateral margins of the first vertebral are substraight. The second to fourth vertebrae are hexagonal (Fig. 2C, J, M). The width of all of them is approximately

the same. The fourth vertebral is almost as wide as long (Fig. 2M). The fifth vertebral is trapezoidal, posteriorly wider than anteriorly (Fig. 3J, L). Posteriorly, it contacts the last two pairs of marginals. The sulci between the vertebrae are located on the first, third, fifth and last neurals (Figs. 2C, 2J, 2M, 3J). The medial region of these sulci shows an anterior directed convexity. The posterior margin of the fifth vertebral is located very close to the suture between the second suprapygal and the pygal, and it can be partially coincident with this suture (Fig. 3L). The marginal scutes overlap much of the dorsal and ventral surfaces of the peripheral plates, but are not in contact with the costal series. This taxon has twelve pairs of marginals, lacking dorsal or ventral merger between the scutes composing the last pair (Fig. 3L-M).

The plastral lobes are wide in relation to the total length of the plastron (Fig. 4). The anterior plastral lobe is subtrapezoidal, with rounded lateral margins (Fig. 4A-E, H-M). This taxon has small and subrounded gular protrusions (Fig. 4A-E, H-I). A moderately developed dorsal epiplastral lip is present. It is concave in anterior view (Fig. 4C). In all known specimens, this lip is longer in the antero-lateral region than in the medial area (Fig. 4B, D, H). However, the relationship between the length in both regions is not the same in all of them, because its posterior margin can be convex along its entire length (Fig. 4B), substraight along its entire length (Fig. 4D), or substraight along almost all its entire length except at its medial region, where it undergoes a marked change of curvature (Fig. 4H). Ventrally, the entoplastron is subrhombic, almost as wide as long (Fig. 4A, F, J). The total length of the hypoplastra is greater than that of the hypoplastra (Fig. 4A). However, the hypoplastra are longer in the axial plane. The axillary and the inguinal buttresses are well-developed, reaching the costal plates. The axillary buttresses reach between one third and half of the width of the first pair of costals (Fig. 2B, D, G). The inguinal buttresses contact the posterior margin of the fifth pair of costals, and the antero-lateral region of the sixth pair (Figs. 2I, 2L, 2N, 2P-Q, 2S-T, 3B-C). These buttresses reach between one third and half of the width of the fifth pair of costals. The lateral margins of the posterior plastral lobe are subrounded from the inguinal notches to their contact with the femoro-anal sulcus (Fig. 4N-Q). Posteriorly, they are substraight. The xiphiplastra are longer than wide (Fig. 4N-O) or as long as wide (Fig. 4P-Q). A well-developed anal notch is present. It is considerably wider than long. Its lateral margins vary from substraight (Fig. 4N-O) to subrounded (Fig. 4P-Q).

The taxon analyzed lacks intergular and inframarginal scutes. The gular scutes are triangular, almost as wide as long (Fig. 4A). The gulars of some specimens do not overlap the entoplastron (Fig. 4J). However, a short overlap is observed in other individuals (Fig. 4A, F, I). The humero-pectoral sulcus is close to the posterior margin of the entoplastron in some specimens (Fig. 4A). The pectorals are overlying the posterior region of this plate in others (Fig. 4J). The humero-pectoral sulcus is subperpendicular to the axial plane in some

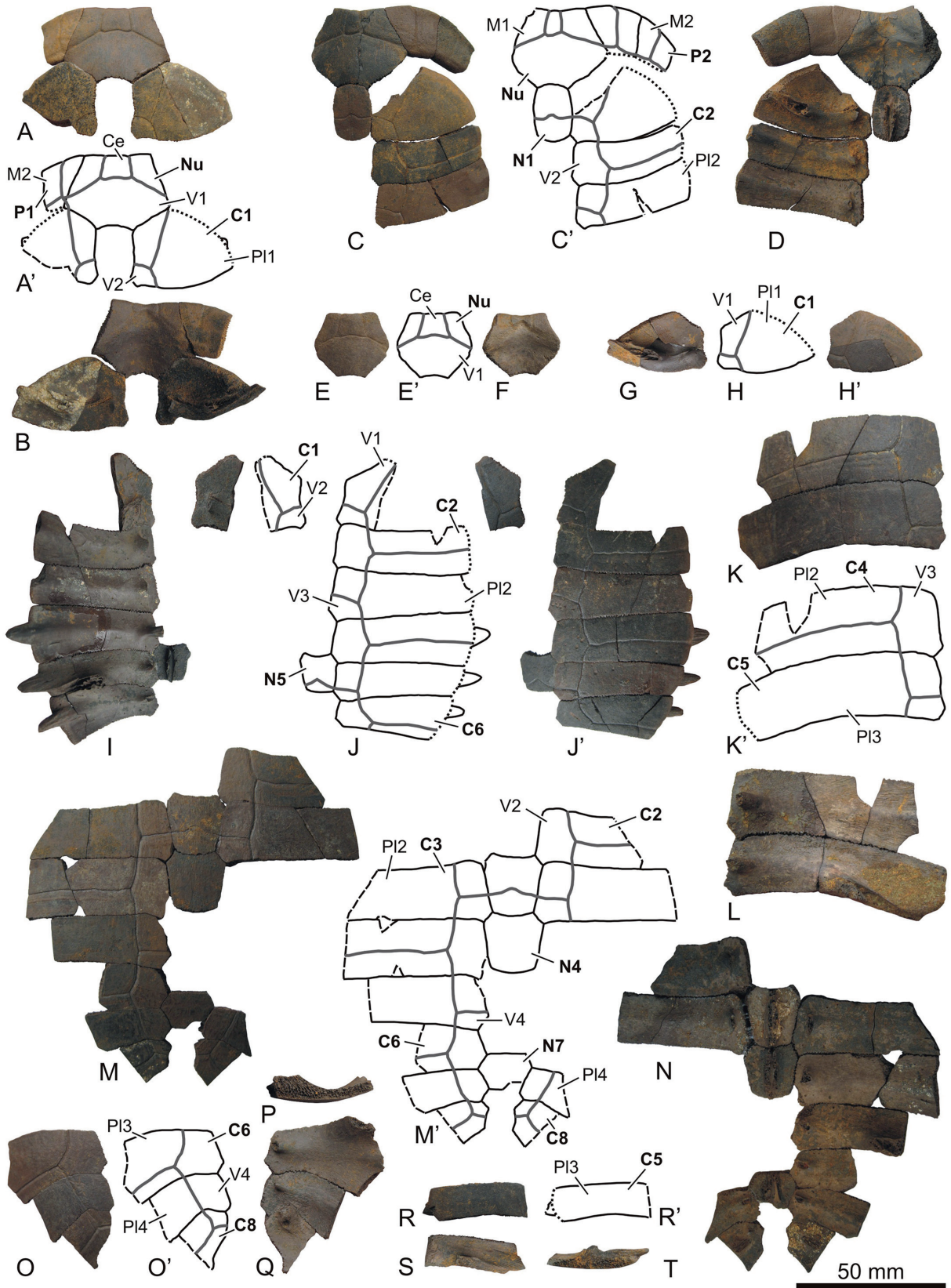


Fig. 2.- Specimens of *Cuvierichelys parisiensis*, from the early Oligocene of Boutersem (Belgium), corresponding to the carapace. A-B, IRSNB R305; C-D, IRSNB R306; E-F, IRSNB R307; G-H, IRSNB R308; I-J, IRSNB R309; K-L, IRSNB R310; M-N, IRSNB R311; O-Q, IRSNB R312; R-T, IRSNB R313. Abbreviations for the plates (in bold): C, costal; N, neural; Nu, nuchal; P, peripheral. Abbreviations for the scutes (in normal font): Ce, cervical; M, marginal; PI, pleural; V, vertebral. The solid lines represent the edges of the plates. The dashed lines indicate the broken margins. Those composed of a succession of points correspond to unsutured contacts. The scute margins are represented by thicker gray lines.

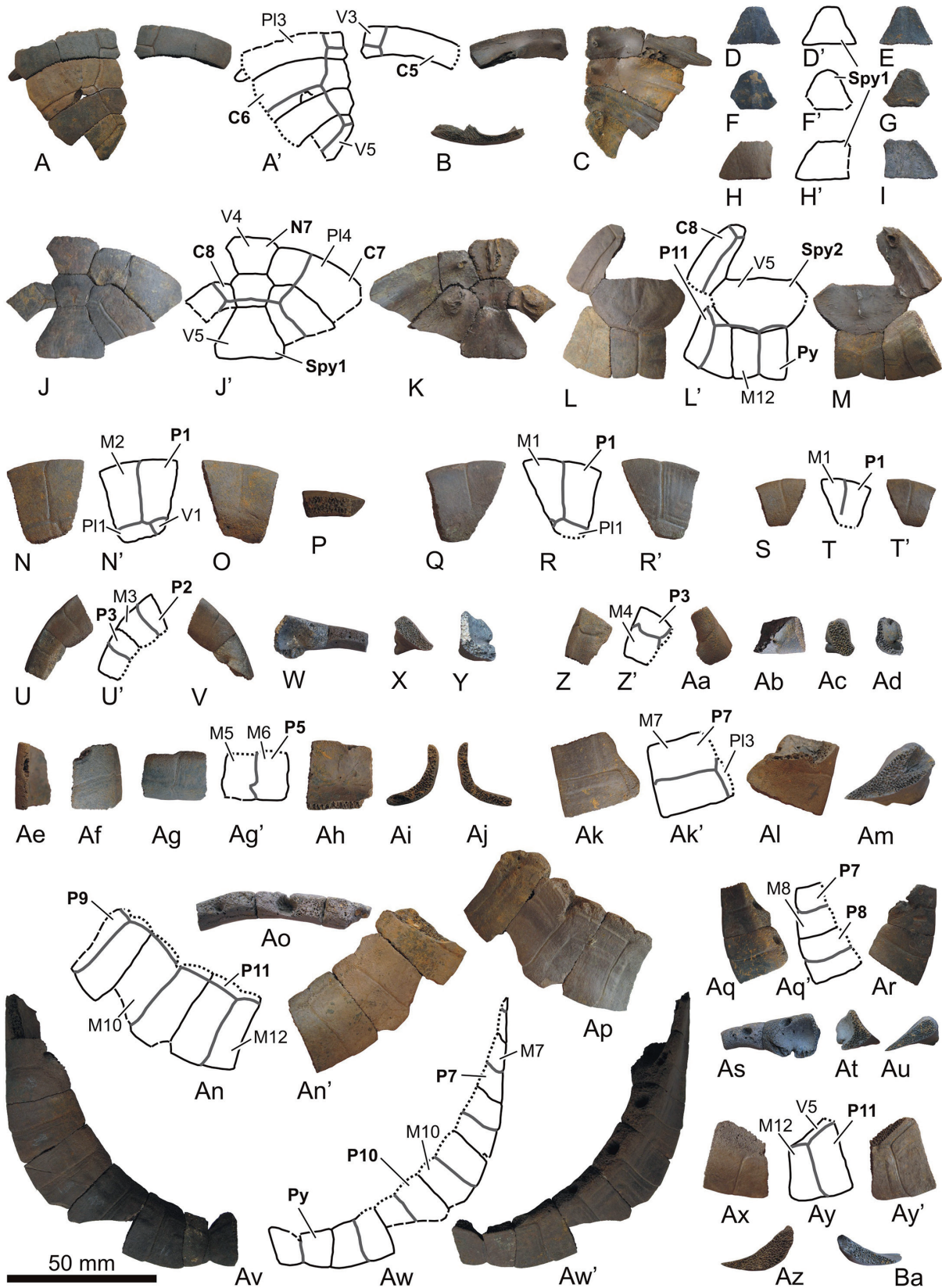


Fig. 3.- Specimens of *Cuvierichelys parisiensis*, from the early Oligocene of Boutersem (Belgium), corresponding to the carapace. A-C, IRSNB R314; D-E, IRSNB R315; F-G, IRSNB R316; H-I, IRSNB R317; J-K, IRSNB R318; L-M, IRSNB R319; N-P, IRSNB R320; Q-R, IRSNB R321; S-T, IRSNB R322; U-Y, IRSNB R323; Z-Ad, IRSNB R324; Ae-Aj, IRSNB R325; Ak-Am, IRSNB R326; An-Ap, IRSNB R327; Aq-Au, IRSNB R328; Av-Aw, IRSNB R329; Ax-Ba, IRSNB R330. Abbreviations for the plates (in bold): C, costal; N, neural; P, peripheral, Py, pygal; Spy, suprapygal. Abbreviations for the scutes (in normal font): M, marginal; Pl, pleural; V, vertebral. The solid lines represent the edges of the plates. The dashed lines indicate the broken margins. Those composed of a succession of points correspond to unsutured contacts. The scute margins are represented by thicker gray lines.

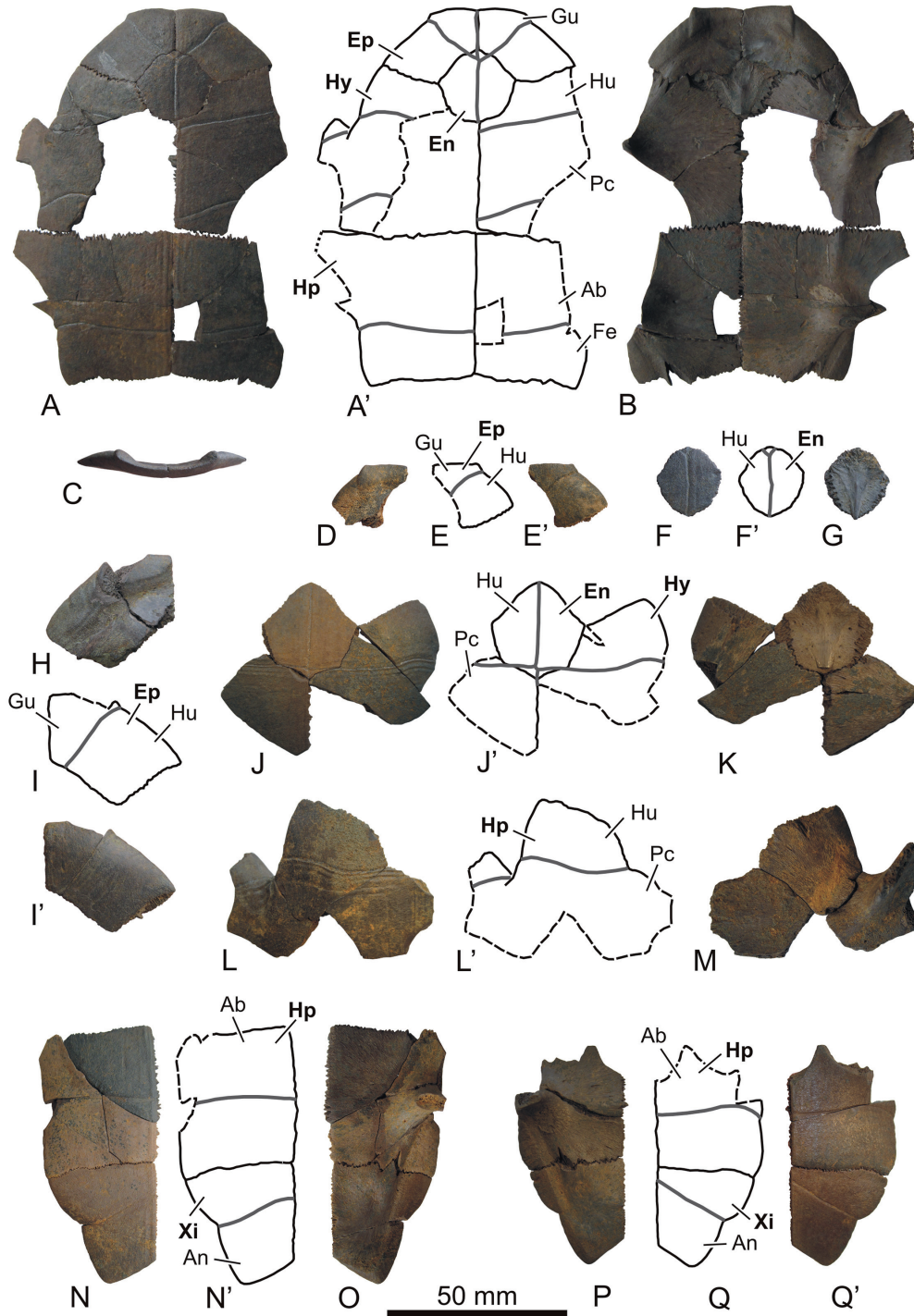


Fig. 4.- Specimens of *Cuvierichelys parisiensis*, from the early Oligocene of Boutersem (Belgium), corresponding to the plastron. A-C, IRSNB R331; D-E, IRSNB R332; F-G, IRSNB R333; H-I, IRSNB R334; J-K, IRSNB R335; L-M, IRSNB R336; N-O, IRSNB R337; P-Q, IRSNB R338. Abbreviations for the plates (in bold): En, entoplastron; Ep, epiplastron; Hp, hypoplastron; Hy, hyoplastron; Xi, xiphiplastron. Abbreviations for the scutes (in normal font): Ab, abdominal; An, anal; Fe, femoral; Gu, gular; Hu, humeral; Pc, pectoral. The solid lines represent the edges of the plates. The dashed lines indicate the broken margins. The scute margins are represented by thicker gray lines.

specimens, but it displays a poorly-developed medial concavity in others (Fig. 4A, J, L). The pectoral scutes are relatively long, the pectoro-abdominal sulcus being medially located close to the posterior region of the hyoplastra (Fig. 4A). Dorsally, the femoral scutes show a relatively wide overlap on

the lateral margin of hypoplastra and xiphiplastra (Fig. 4O-P). The medial length of the anal scutes is also subject to variability, the femoro-anal sulcus being located relatively close to the hypoplastra in some specimens (Fig. 4Q), but not in others (Fig. 4N).

## 4. Discussion

### 4.1. Identification of the Boutersem taxon as a member of the 'Palaeochelys s. l.–Mauremys' group and comparison with the European representatives

The characters available on all specimens from Boutersem presented here allow its allocation to a single taxon. This material documents all the elements of both the carapace and the plastron of the taxon represented in this early Oligocene locality. Furthermore, intraspecific variability can be recognized thanks to the presence of several specimens that preserve the same anatomical elements.

This material shows a combination of characters which allows its attribution to the 'Palaeochelys s. l.–Mauremys' group (Testudinoidea, Geoemydidae), but not to other members of Testudinoidea such as Testudinidae, Emydidae, Ptychogasterinae or Lindholmemydidae: relatively thin plates; absence of a marked medial thickening in the visceral surface of the nuchal; hexagonal second to eighth neurals; present but poorly-developed alternating pattern for the costals; unreduced length of the proximal region of the dorsal ribs; well-developed distal region of the dorsal ribs; trapezoidal first suprapygals, markedly wider posteriorly than anteriorly; first suprapygals narrower than the second one; relatively small pygal plate; first vertebral scute as wide or wider than the nuchal plate; no lyre-shaped lateral margins of the first vertebral, being substraight; moderately developed dorsal epiplastral lip; absence of 'ptychogasterid' spikes, corresponding to well-developed laterally thickening of a strong and long epiplastral dorsal lip along the entire length; well-developed axillary and inguinal buttresses, reaching the costal plates; deep anal notch; absence of intergular scutes; absence of inframarginal scutes (Claude and Tong, 2004; Hervet, 2004a, b; Pérez-García and Vlachos, 2014).

One of the best-represented members of this group in the European Paleogene record is *Palaeoemys* Schleich, 1994 (sensu Claude and Tong, 2004). This form is known in Great Britain, France and Germany, and is represented by several species. It is identified by abundant material, known from the early to the middle Eocene. The Belgian material analyzed here differs from the members of *Palaeoemys* in several characters, among others: the absence of lateral carapace keels (present in the juvenile specimens of forms such as *Palaeoemys hessiaca* Schleich, 1994, but both in the juvenile and the adult individuals of *Palaeoemys testudiniformis* (Owen, 1842)), as well as a well-developed medial keel; absence of a markedly wider than long pygal plate; absence of narrow vertebral scutes (i.e., first vertebral narrower than the nuchal plate in the representatives of this genus; and markedly longer than wide third vertebral, even being 1.5 times in some species); more developed anterolateral epiplastral lips than in *Palaeoemys*; proximity or contact of the humero-pectoral sulcus with the entoplastron, this sulcus being placed far behind the entoplastron in *Palaeoemys*; absence of the marked medial concavity identified the humero-pectoral and pectoro-

abdominal sulci of *Palaeoemys* (Claude and Tong, 2004; Hervet, 2004a).

The taxon from Boutersem differs from *Borkenia* Schleich, 1994 (a possible junior synonym of *Palaeoemys* sensu Claude and Tong, 2004), from the middle Eocene of Germany, because that form has a well-developed medial keel; its anterior plastral lobe is markedly trapezoidal; and the humero-pectoral sulcus is located at a posterior position (Claude and Tong, 2004; Hervet, 2004a).

Several species of the early Oligocene to the late Miocene of Europe have recently been proposed as possibly attributable to *Palaeochelys* Meyer, 1847 (see Claude and Tong, 2004). This hypothesis needs to be confirmed by a detailed study, and by the discovery of new material of several poorly-known species. These forms are known in the Oligocene of Italy, the Oligocene and Miocene of France, and the Miocene of Germany. The Boutersem taxon differs from the species recognized by Hervet (2004a) as attributable to *Palaeochelys* (i.e., *Palaeochelys busseensis* Meyer, 1847 and *Palaeochelys astrei* (Bergounioux, 1935)) by characters such as the absence of very wide first vertebral scute and pygal plate, relative to their lengths. In addition, it can also be recognized as different from the other forms reassigned by Claude and Tong (2004) to *Palaeochelys*. For example, a posterior narrowing of the second vertebral scute, posterior to the suture between the first two pairs of costals, characterized the species previously attributed by Hervet (2004a) to *Cucullemys* Hervet 2004a (represented by the type species, *Cucullemys crocheti* Hervet, 2004a) and *Bergouniouxchelys* Hervet 2004a (represented by the type species, *Bergouniouxchelys vallisnerii* (Bergounioux, 1954)). In addition, the morphology of the posterior region of the fifth vertebral scute of *Cucullemys crocheti*, with a well-developed convexity on the second suprapygals, is exclusive for this species (Hervet, 2004a).

The members of *Promalacoclemmys* Reinach, 1900, a genus known in the late Oligocene of Switzerland and the early Miocene of Germany, differ from the Boutersem taxon in several characters, among others: very wide vertebrals in relation to the pleurals, the width from the second to the fourth vertebrals considerably decreasing; first vertebral noticeably wider than the nuchal plate, having a long contact with the posterior margin of the second pair of marginals; relatively long visceral development of the cervical scute; well-developed gular protrusions (Hervet, 2004a).

*Palaeomauremys* Hervet 2004a is a genus represented by two possible species (sensu Hervet, 2004a), and identified in the late Oligocene of Germany and Switzerland. The absence of three discontinuous keels on the carapace, well-developed growth rings, and a well-developed posterior notch in the cervical scute confirms that the taxon from Boutersem does not belong to that form. In addition, characters such as the much shorter anal notch of the Belgian taxon than those of the members of *Mauremys* Gray, 1869, a genus well-represented from the French late Oligocene to the present (being represented in both Western Europe and the Near East), also excludes it from this genus.

All characters so far discussed are shared among the taxon from Boutersem and the representatives of two genera known in the European Paleogene record: *Landreatchelys* Hervet, 2004a (only known by its type species, *Landreatchelys oweni* (Lydekker, 1889)) and *Cuvierichelys* (represented by *Cuvierichelys parisiensis*, *Cuvierichelys iberica* (Bergounioux, 1958) and '*Cuvierichelys crassa*' (Owen and Bell, 1849), the validity of the latter species being doubtful sensu Hervet, 2004a).

#### 4.2. Generic allocation and implications

*Emys hordwellensis* Seeley, 1876 and *Ocadia oweni* Lydekker, 1889 are two taxa defined in the late Eocene of Hordwell (now Hordle Cliff, Hampshire, Great Britain). In 2004, Hervet conducted a systematic review of the known record of the '*Palaeochelys* sensu lato – *Mauremys*' group in Western Europe (Hervet, 2004a). *Emys hordwellensis* was considered by Hervet (2004a) as an invalid taxon, the material previously attributed to this form being reassigned to *Emys parisiensis* Gray, 1831, a taxon attributed to a new genus: *Cuvierichelys*. Therefore, the new combination *Cuvierichelys parisiensis* was proposed, the genus *Cuvierichelys* being identified from the late Eocene to the early Oligocene of Great Britain and France, as well as in the early Oligocene of Spain. *Ocadia oweni* was recognized by Hervet (2004a) as a valid species, but identified as the only known representative of the new genus *Landreatchelys*. Therefore, the combination *Landreatchelys oweni* was proposed, the genus *Landreatchelys* being exclusively known in the middle Eocene of France, and in the late Eocene of France and Great Britain. Claude and Tong (2004) noted that, since the only difference found by Hervet (2004a) between *Emys hordwellensis* and *Ocadia oweni* is the relative development of the epiplastron (i.e., a character recognized as variable for some species), the two forms may be considered synonymous. In that case, considering the synonymy proposed by Hervet (2004a) between *Emys hordwellensis* and *Emys parisiensis*, *Landreatchelys oweni* could be a junior synonym of *Cuvierichelys parisiensis*.

The diagnosis for both *Cuvierichelys* and *Landreatchelys* proposed by Hervet (2004a) indicated that both taxa lacked well-developed keels in the carapace, but that they could have a poorly-developed posterior medial keel; moderately wide first vertebral, as wide as or wider than the nuchal plate; substraight or slightly curved lateral margins of the first vertebral scute; subtrapezoidal anterior plastral lobe, with rounded lateral margins; gulars not overlying the anterior region of the entoplastron, or showing a short overlap. All these character states are also present in the Boutersem taxon. The diagnosis of *Landreatchelys* considered several characters that, even not having been included in the diagnosis of *Cuvierichelys* (see Hervet, 2004a), they are here recognized as shared with this taxon (or being part of its known range of variability), as well as with that from Boutersem: medium to large entoplastron; relatively short hyoplastra in the axial plane; narrow gulars relative to the width of the anterior lobe, being relatively

short; humero-pectoral sulcus close to the posterior margin of entoplastron, or pectorals scutes overlying the posterior region of this plate. Similarly, the diagnosis of *Cuvierichelys* considered several characters not included in the diagnosis of *Landreatchelys* but identified here as shared with this taxon, as well as with that from Boutersem: relatively long lateral region of the gular lips; relatively wide posterior lobe.

Hervet (2004a) reported that only scarce material of *Landreatchelys* was available. In fact, many characters of both its carapace and its plastron were not known. Therefore, this taxon was not incorporated in its phylogenetic hypothesis about the Western European representatives of the '*Palaeochelys* s. l.–*Mauremys*' group. In addition, Hervet (2004a) indicated that very limited information was available on the intraspecific variability of its only known representative, and also on the interspecific variability of taxa considered as potentially closely related to it. The abundant material from the early Oligocene of Boutersem allows us to recognize that all character states indicated by Hervet (2004a) as potentially different when *Cuvierichelys* and *Landreatchelys* were compared, can be recognized as part of the intraspecific variability of this Belgian taxon: absence of overlap, or more or less overlap of the posterior margin of the fifth vertebral scute on the pygal plate; relative length of the epiplastra; morphology and visceral development of the medial region of the gular lips. Therefore, the synonymy between *Landreatchelys* and *Cuvierichelys*, proposed by Claude and Tong (2004), is supported here. Indeed, this is consistent with the finding of material recognized as possibly attributable to *Cuvierichelys*, and specimens identified as possibly belonging to *Landreatchelys* in the same locality, reported by Hervet (2004a). Thus, the specimens analyzed here are attributed to *Cuvierichelys*, this genus being identified for the first time in the Belgian record.

#### 4.3. Specific attribution and implications

As indicated above, Hervet (2004a) stated that the record available demonstrated that *Cuvierichelys* was represented by two well-established species (*Cuvierichelys parisiensis* and *Cuvierichelys iberica*), and also by a possible third species, whose validity was doubtful ('*Cuvierichelys crassa*'). *Cuvierichelys parisiensis* is only known in the late Eocene (Priabonian) of France. '*Cuvierichelys crassa*' comes from synchronous levels, but from Great Britain. *Cuvierichelys iberica* is the youngest species, being recognized in the early Oligocene (MP23) of Spain.

Hervet (2004a) indicated that '*Cuvierichelys crassa*' was recognized by very little material, whose differences with *Cuvierichelys parisiensis* could possibly been justified by intraspecific variability (absence of medial keel in the material attributed to *Cuvierichelys parisiensis* but presence of very poorly developed keel in '*Cuvierichelys crassa*'), or by sexual dimorphism (xiphoplastra slightly wider in relation to its length in the case of the known material of '*Cuvierichelys crassa*' compared to that of *Cuvierichelys parisiensis*). The



identification of variability concerning both characters in the taxon from Boutersem, allows us to support this synonymy. In fact, the material hitherto known of both *Cuvierichelys parisiensis* and *Cuvierichelys iberica* is scarce. In this sense, the material of *Cuvierichelys parisiensis* currently available does not document all the elements of the carapace of this species. Therefore, very limited information on its intraspecific variability was known, although it was considered as potentially high (Hervet, 2004a). The identification of variability in the Boutersem material, together with the study of specimens of the type locality of *Cuvierichelys iberica* not studied by Hervet (2004a) (e.g., MGM 5N, MGM 51N, MGM 53N), allow us to refute the validity of several characters including in the differential diagnosis between *Cuvierichelys parisiensis* and *Cuvierichelys iberica*. Thus, the position of the humero-pectoral sulcus relative to the posterior margin of the entoplastron is here recognized as variable in *Cuvierichelys iberica*, as in the taxon from Boutersem. The presence of wider gulars in relation to the width of the anterior lobe in *Cuvierichelys parisiensis* than in *Cuvierichelys iberica* is refuted, being wide in the specimen MGM 51N, but narrow in MGM 53N. Due to the presence of variability in this character, the width of the dorsal gular lip, in relation to its length, is also variable. Therefore, different cannot be established between *Cuvierichelys iberica* and *Cuvierichelys parisiensis*. Characters, that could also be justified by individual variability are, among others: the width of the first vertebral scute in relation to that of the nuchal plate, morphology of posterior margin of the fifth vertebral scute and overlap on the posterior margin of the second suprapygal and anterior margin of the pygal, more rectilinear or more rounded morphology of the anterior plastral lobe. The taxon of Boutersem lacks the three keels that Hervet (2004a) considered as characteristic of *Cuvierichelys iberica*. However, it cannot be recognized as different from *Cuvierichelys parisiensis*, being attributed to this taxon. The presence of *Cuvierichelys parisiensis* is thus confirmed for the first time outside the French record, its stratigraphic distribution being expanded to the Oligocene.

## 5. Conclusions

The presence of a member of the '*Palaeochelys* s. l.–*Mauremys*' group (Testudinoidea, Geoemydidae) is recognized for the first time in the Belgian Paleogene record. Abundant material of both the carapace and the plastron, found at the early Oligocene (early Rupelian, MP-21) site of the Boutersem-TGV (Boutersem), is attributed to a single taxon. It is assigned to the poorly-known genus *Cuvierichelys*. The identification of intraspecific variability allows us to propose several synonyms, the validity of both *Landreatchelys* and '*Cuvierichelys crassa*' being refuted. Only one species of *Cuvierichelys* (i.e., the Spanish *Cuvierichelys iberica*) was identified in the Oligocene record. The taxon from Boutersem cannot be assigned to that species. Rather, it is identified as *Cuvierichelys parisiensis*, all the elements of its carapace being recognized for the first time.

Several characters previously considered as different between the two valid species of *Cuvierichelys*, *Cuvierichelys parisiensis* and *Cuvierichelys iberica*, are refuted here. The identification of *Cuvierichelys parisiensis* in Boutersem allows us to expand the paleobiogeographic distribution of this species. Its presence was only confirmed in the French record, but it is here also recognized in Belgium and in Great Britain. Moreover, its biostratigraphic range of distribution is also expanded, this species being identified, for the first time, in the Oligocene record. The synchrony between *Cuvierichelys iberica* and *Cuvierichelys parisiensis* is thus recognized.

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