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A new species of *Neochelys* (Chelonii, Podocnemididae) from the Ypresian (Early Eocene) of the South of France*Une nouvelle espèce de Neochelys (Chelonii, Podocnemididae) de l'Yprésien (Éocène inférieur) du Sud de la France*Adán Pérez-García<sup>a,\*</sup>, France de Lapparent de Broin<sup>b</sup><sup>a</sup> Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, C/José Antonio Novais, 2, 28040 Ciudad Universitaria, Madrid, Spain<sup>b</sup> Muséum national d'Histoire naturelle, Département Histoire de la Terre, CR2P, USM 0203–CNRS, UMR 7207, Paléobiodiversité, CP 38, 8, rue Buffon, 75231 Paris cedex 05, France

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## ABSTRACT

The known European record of the Gondwanan group Podocnemididae begins in the Early Eocene. *Neochelys* underwent a rapid diversification and was an abundant and diverse representative of this group during the Eocene of Europe from the Early Ypresian to at least the Bartonian. However, several of its species are poorly known, and the phylogenetic relationships among them are poorly understood. A complete shell from the Ypresian of Hérault (southern France) is described here. It is assigned to a new species, *Neochelys liriae*. The availability of characters of *N. liriae* is tested by comparison with the other European species, which appear to be well differentiated, and particularly with the neighbouring French taxa *N. eocaenica* and *N. laurenti*, of which the latter has been little known to this point.

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## R É S U M É

Les premiers représentants européens du groupe gondwanien des Podocnemididae datent de l'Éocène inférieur. *Neochelys* s'est rapidement diversifié, formant un composant de cette famille abondant en individus et en espèces pendant l'Eocène européen, de l'Yprésien inférieur au Bartonien au moins. Toutefois, plusieurs de ses espèces sont peu connues, et les relations phylétiques interspécifiques non déterminées. Une carapace complète, provenant de l'Yprésien de l'Hérault (dans le Sud de la France), est décrite ici. Elle est attribuée à une nouvelle espèce, *Neochelys liriae*. La validité des caractères de *N. liriae* est testée par comparaison avec les autres espèces européennes, lesquelles apparaissent comme bien diversifiées, et particulièrement avec les espèces voisines françaises *N. eocaenica* et *N. laurenti*, cette dernière peu connue jusqu'à ce jour.

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## 1. Introduction

Pleurodiran turtles were abundant in the Late Cretaceous of Europe, represented by several taxa of Bothremydidae, a group that originated in Gondwana (Lapparent de Broin, 2001) and diachronically came to Europe. Almost all or all the described taxa can be referred to Bothremydini (Gaffney et al., 2006). However, the European Paleocene record of Pleurodira is very poor. Only a shell of Taphrosphyini (Bothremydidae) has been identified in the Montian of France (Broin, 1977). The English Lower Eocene *Palaeospis* Gray, 1870 has also been identified as a bothremydid (Lapparent de Broin, 2001). A high abundance and diversity characterizes another group of Pleurodira that also originated in Gondwana, the Podocnemididae Erymnochelyinae (sensu Lapparent de Broin, 2000), which is recorded in the Eocene of Europe. This group is represented by two forms. One of them, preliminarily attributed to *Erymnochelys* Baur, 1888 (Broin, 1977), is closely related to it (Lapparent de Broin in Merle, 2008). The other is *Neochelys*. This diverse freshwater genus is known in several countries of Europe, from the Early Ypresian to the Bartonian at least (Lapparent de Broin, 2003) (Table 1). The oldest materials come from the Earliest Ypresian (Sparnacian facies, Mammalian fauna MP7), where *N. arenarum* Broin, 1977, from Rians (Var, France), and indeterminate species from Dormaal (Flemish Brabant, Belgium) and Silveirinha (Figueira da Foz, Portugal) have been identified (Broin, 1977; Lapparent de Broin, 2003). *N. laurenti* (Tong, 1998) has been described from levels correlated with the MP8–9 zone at Saint-Papoul (Aude, southern France) (Lapparent de Broin, 2003; Laurent et al., 2010; Tong, 1998). *N. eocaenica* (De Stefano, 1902) has also been identified in southern France, in several locations of the Grès d'Aigne Formation (Aude-Hérault departments) (Broin, 1977), with a possible transitional Early-Middle Eocene mammal fauna (H.P. Labarrère, pers comm.). The Italian *N. capellinii* (Zigno, 1889) (Bolca, Verona) comes from the Early Lutetian. Schleich (1993) described *N. franzeni* from the Early Lutetian of Messel (MP11 of Hesse, Germany). The most recent record of defined species

of *Neochelys* comes from Spain, including *N. zamorensis* Jiménez Fuentes, 1992 (MP13–14 of Sanzoles, Zamora) and *N. salmanticensis* (Jiménez Fuentes, 1968) (probable MP16 of Teso de la Flecha, Salamanca) (Badiola et al., 2009; Cuesta Ruiz-Colmenares, 2003; Jiménez Fuentes, 1992), and from France, including the poorly known *N. mengaudi* (Bergounioux, 1935) (Late Bartonian, MP 16 of Castrais). More specimens attributed to *Neochelys*, usually not determined to a specific level, poorly described, or preliminarily related to some of the described species, have been identified in other French and Spanish localities up to the Priabonian (Broin, 1977; Jiménez Fuentes, 1992; Lapparent de Broin, 2003).

The phylogenetic relationships among the taxa of *Neochelys* are poorly understood. Several species are poorly known, having been identified by disjointed and generally fragmentary specimens (e.g. taxa from Dormaal and Silveirinha), and either the shells (e.g. *N. laurenti*) or the skulls (e.g. *N. salmanticensis* and probably *N. zamorensis*) have not yet been figured or described. Broin (1977) united the poorly preserved material from the Middle-Late Ypresian and Lutetian-Bartonian of the Paris Basin (France), Argenton-sur-Creuse (Indre, France) and southern France (Languedoc-Roussillon region) in a “*N. eocaenica* complex” around *N. eocaenica*, possibly also including *N. salmanticensis* and *N. capellinii*. However, the information available on the undefined part of the complex was very poor. The study of poorly described and hitherto unpublished articulated complete and partial shells from southern France (including a shell associated with a skull of *N. laurenti*) allows us to compare them to a new complete shell from the Grès d'Assignan Formation of Soleillades (Hérault, Minervois) studied here. It is also compared to the holotypes and other specimens of the European representatives of *Neochelys*.

The shell studied here was collected in Soleillades (Hérault, France), a hill situated at the foot of the Montagne Noire (Fig. 1). It comes from the Minervois part of the continental Molasse of the Carcassonne series, which includes the Calcaire de Ventenac Fm. (Early Ypresian),

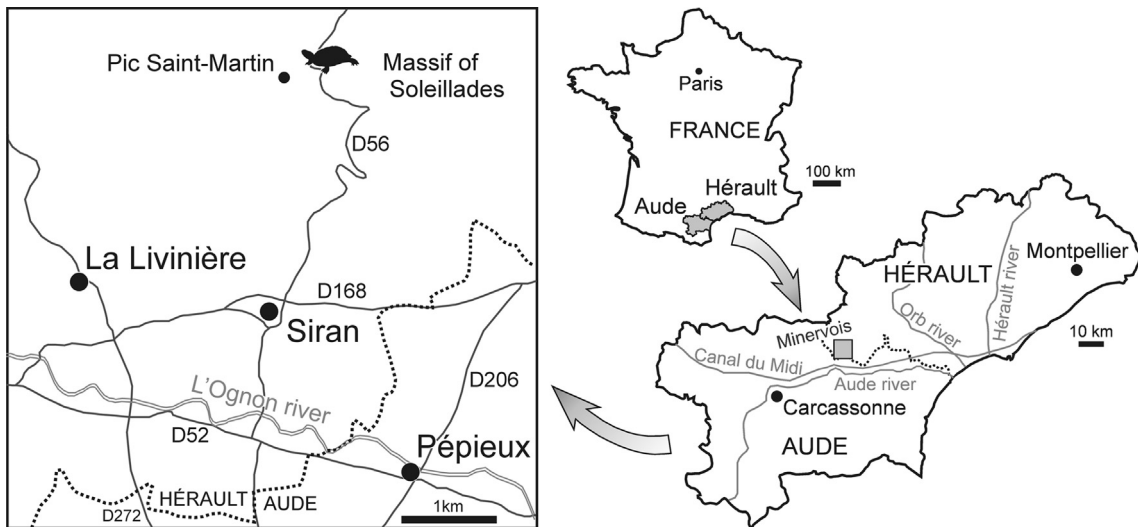
**Table 1**

Record of the up to now recognized species of the European genus *Neochelys*. In Minervois area (Fig. 1), *N. liriae* sp. nov.\* comes from the lower part of the Late Ypresian, from the Grès d'Assignan Fm., and *N. eocaenica*\*\* comes from the Late Ypresian or Early Lutetian from the Grès d'Aigne Fm. that is superposed to the Calcaire d'Agel Fm. (MP 10, with an indetermined species of *Neochelys*), itself superposed to the Grès d'Assignan (MP 8–9). *N. laurenti*\*\*\* comes from the upper part of the Early Ypresian, from Saint-Papoul, close to Carcassonne (MP 8–9).

**Tableau 1**

Espèces reconnues à ce jour du genre européen *Neochelys*. Dans le Minervois (Fig. 1), *N. liriae* sp. nov.\* provient de la partie inférieure de l'Yprésien supérieur, de la formation des grès d'Assignan, et *N. eocaenica*\*\* provient de l'Yprésien supérieur ou du Lutétien inférieur, de la formation des grès d'Aigne, laquelle est superposée au calcaire d'Agel (MP 10, avec un espèce indéterminée de *Neochelys*), formation elle-même superposée au grès d'Assignan (MP 8–9). *N. laurenti*\*\*\* provient de la partie supérieure de l'Yprésien inférieur de Saint-Papoul, des environs de Carcassonne (MP 8–9).

Eocene Stage	MP zone	Species	Type locality	Country
Priabonian	MP 17			
Bartonian	Ca. MP 15?–16	<i>N. salmanticensis</i>	Teso de la Flecha	Spain
Lutetian	MP 13–14	<i>N. zamorensis</i>	Sanzoles	Spain
	MP 12			
	MP 11	<i>N. franzeni</i>	Messel	Germany
Lutetian–Ypresian boundary	Ca. MP 10–11	<i>N. capellinii</i>	Purga di Bolca	Italy
		<i>N. eocaenica</i> **	Pépieux	France
Ypresian	MP 10			
	MP 8–9	<i>N. liriae</i> sp. nov.*	Soleillades	France
		<i>N. laurenti</i> ***	St. Papoul	France
	MP 7	<i>N. arenarum</i>	Rians	France



**Fig. 1.** Map of France showing the location of the Ypresian locality of Soleillades (Hérault) where the holotype of *Neochelys liriae* sp. nov. has been found.  
**Fig. 1.** Carte de la France montrant l'emplacement de la localité yprésienne de Soleillades (Hérault) où a été trouvé l'holotype de *Neochelys liriae* sp. nov.

the Grès d'Assignan Fm. (lower part of the Late Ypresian), the Calcaire d'Agel Fm. (Late Ypresian), and the Grès d'Aigne Fm. (Latest Ypresian–Early Lutetian) (Marandat, 1986). The new shell is the first known occurrence of a turtle in the Grès d'Assignan Fm. It comes from a layer of reddish-yellowish coarse-grained molasse–sandstone with fine continental marls intervals bearing abundant small bivalves and lignite fragments. Its attribution to *Neochelys* is justified here and its relationships with the other species of this genus are explained.

**Institutional Abbreviations:** MNHN.F., Paleontological Collection of the Muséum national d'Histoire naturelle, Paris, France. SAGA, Société Amicale des Géologues Amateurs du Muséum, Paris.

## 2. Systematic palaeontology

Order CHELONII Latreille, 1800  
 Infraorder PLEURODIRA Cope, 1864  
 Hyperfamily PELOMEDUSOIDES Cope, 1868  
 Superfamily PODOCNEMIDOIDEA Cope, 1868  
 Family PODOCNEMIDIDAE Cope, 1868  
 Subfamily ERYMNOCHELYINAE Broin, 1988  
 Genus *Neochelys* Bergounioux, 1954  
**Type species:** *Emys capellinii* Zigno, 1889  
*Neochelys liriae* sp. nov.  
 Figs. 2 and 3

**Holotype:** MNHN.F.EBA515, a complete and articulated shell (Figs. 2 and 3).

**Type locality and type horizon:** Soleillades, Siran, Hérault, Minervois, France (Fig. 1). Grès d'Assignan Formation, Early Eocene, lower part of the Late Ypresian.

**Etymology:** The specific name is in honor of M. Régis Liria, who discovered the holotype with M. Eric López and gifted to the MNHN.

**Diagnosis:** Member of *Neochelys* differing from all the known representatives of this genus by the subpentagonal morphology of its carapace, almost as wide as long, by the presence of clearly wider than long peripherals 1 and by the nuchal maximal width twice that of its anterior margin, the maximal width of this plate being about 20% greater than its length. In addition, an exclusive character combination characterizes it: broad and shallow nuchal notch, located on the anterior margin of the nuchal, peripherals 1 and medial region of the peripherals 2; seven neurals; marginals 1 markedly wider than long; marginals 1 overlapping less than one third of the latero-anterior nuchal margin; marginals 1 overlapping a quarter of the peripherals 1 width; lyre-shaped vertebral 1; vertebral 5 wider than the other vertebrals; anterior plastral lobe wider than the posterior one; subrounded anterior lobe, with rounded anterolateral angles; absence of gular protrusions; entoplastral length shorter than its distance up to the hyo-hyoplastral suture; entoplastral length longer than two times its distance up to the pectoro-abdominal sulcus; short dorsal epiplastral lip; rounded lateral margins of the posterior plastral lobe; anal notch with straight margins, three times wider than long, and moderate length; intergular wider than each gular; very narrow contact of the intergular with the pectorals; gulars in contact with the epi-entoplastral sutures or slightly overlapping the entoplastron. Holotype length about 25 cm.

## 3. Comparative description

The shell of the holotype of *Neochelys liriae* sp. nov. is smooth, only decorated with fine and short dichotomic sulci, some of them united in small polygons. All the plates are firmly sutured (Figs. 2 and 3).

The width of the carapace (244 mm) is slightly shorter than its length (262 mm) (Fig. 2). Its length is similar to that of some species of *Neochelys* (*N. arenarum*, *N. franzeni*), but others exceed 35 cm (*N. laurenti*, *N. eocaenica*, *N. capellinii*,

**Table 2**

Comparative shell characters of the nominated species up to now recognized as distinct in the genus *Neochelys*. Species (in horizontal): Ar, *N. arenarum*; La, *N. laurenti*; Li, *N. liriae* sp. nov.; Eo, *N. eocaenica*; Ca, *N. capellinii*; Fr, *N. franzeni*; Za, *N. zamorensis*; Sa, *N. salmanticensis*. Characters (in vertical): 1, carapace morphology: A, elliptical, longer than wide; B, subpentagonal, almost as wide as long. 2, length/width ratio of the peripherals 1: A, longer than wide or as long as wide; B, wider than long. 3, length/width ratio of the nuchal plate: A, about as wide as long or longer than wide; B, maximal width of the nuchal about 20% greater than its length. 4, nuchal maximal width in relation to that of its anterior margin: A, maximal width at least twice that of the anterior margin; B, maximal width less than twice that of the anterior margin. 5, number of neurals: A, six; B, seven. 6, Length/width ratio of the marginals 1: A, marginals 1 less than two times wider than long; B, marginals 1 more than two times wider than long. 7, overlap of the marginals 1 on the latero-anterior margin of the nuchal: A, marginals 1 overlapping more than one third of the latero-anterior margin; B, marginals 1 overlapping less than one third of the latero-anterior margin. 8, overlap of the marginals 1 on the peripherals 1: A, marginals 1 overlapping not more than a quarter of the peripherals 1 width; B, marginals 1 overlapping more than the 30% of the width of the peripherals 1. 9, morphology of the lateral margins of the vertebral 1: A, straight lateral margins, anteriorly diverging; B, lyre-shaped vertebral 1. 10, width of the vertebral 5 in relation to that of the other vertebrae: A, the vertebral 5 is not the widest; B, vertebral 5 wider than the other vertebrae. 11, morphology of the anterior plastral lobe: A, trapezoidal; B, subrounded. 12, ratio between the length of the entoplastron and its distance with the pectoro-abdominal sulcus: A, entoplastral length longer than two times that distance; B, entoplastral length less than two times that distance; 13, lateral margins of the posterior plastral lobe: A, rounded; B, straight. 14, configuration of the intergular-gular complex: A, intergular narrower than each gular; gulars slightly overlapping the entoplastron; relatively narrow to narrow intergular-pectorals contact or no intergular-pectorals contact due to a short medial contact of the humerals (less often); B, intergular narrower than each gular; gulars slightly overlapping the entoplastron and as long or nearly as long as the intergular; no intergular-pectorals contact and relatively long medial contact of the humerals; C, intergular wider than each gular; gulars in contact with the epi-entoplastral sutures (right side of the holotype) or slightly overlapping the entoplastron (left side); very narrow intergular-pectorals contact (no medial contact of the humerals); D, intergular narrower than each gular; gulars slightly overlapping the entoplastron; relatively wide intergular-pectorals contact (no medial contact of the humerals); E, intergular wider similar to that of the gulars; gulars not contacting the entoplastron; no intergular-pectorals contact and relatively long medial contact of the humerals; F, intergular wider than each of the gulars; gulars not overlapping the entoplastron; relatively wide intergular-pectorals contact (no medial contact of the humerals); G, intergular narrower than each gular; gulars slightly overlapping the entoplastron; relatively narrow to narrow intergular-pectorals contact: the intergular-gular complex of *N. zamorensis* (G) is similar to that of *N. arenarum* (A) but they differ by other features: in *N. arenarum*, the angle of the trapezoid anterior lobe is sharp at the external gularo-humeral sulcus limit; while in *N. zamorensis*, the gularo-humeral sulcus ends on the lateral border of the trapezoid anterior lobe, posteriorly to the angle, sharp (holotype) or rounded; H, intergular wider than each gular; gulars no contacting or in contact with the entoplastron; relatively narrow intergular-pectorals contact or rarely no contact with short medial contact of the humerals. 15, length of the dorsal shell: A, near 25 cm; B, greater than 35 cm. See more characters in Lapparent de Broin, 2003, Table 2.

**Tableau 2**

Comparaison des caractères de la carapace des espèces nommées et reconnues jusqu'à ce jour comme distinctes dans le genre *Neochelys*. Espèces (transversalement) : Ar, *N. arenarum*; La, *N. laurenti*; Li, *N. liriae* sp. nov.; Eo, *N. eocaenica*; Ca, *N. capellinii*; Fr, *N. franzeni*; Za, *N. zamorensis*; Sa, *N. salmanticensis*. Caractères (verticalement) : 1, morphologie de la dossière : A, elliptique, plus longue que large ; B, sub-pentagonale, presque aussi large que longue. 2, rapport longueur/largeur de chaque périphérale 1 : A, plus longue que large ou aussi longue que large ; B, plus large que longue. 3, rapport longueur/largeur de la plaque nucale : A, à peu près aussi large que longue ou plus longue que large ; B, largeur maximale de la nucale 20% plus grande que sa longueur. 4, largeur maximale de la nucale par rapport à son bord antérieur : A, au moins deux fois celle du bord antérieur ; B, moins de deux fois celle du bord antérieur. 5, nombre de neurales : A, six ; B, sept. 6, rapport longueur sur largeur des marginales 1 : A, marginales 1 moins de deux fois plus larges que longues ; B, marginales 1 plus de deux fois plus larges que longues. 7, recouvrement des bords latéro-antérieurs de la nucale par les marginales 1 : A, marginales 1 recouvrant plus d'un tiers des bords latéro-antérieurs ; B, marginales 1 recouvrant moins d'un tiers des bords latéro-antérieurs. 8, recouvrement des périphérales 1 par les marginales 1 : A, marginales 1 recouvrant moins d'un quart de la largeur des périphérales 1 ; B, marginales 1 recouvrant plus de 30% de la largeur des périphérales 1. 9, morphologie des bords latéraux de la vertébrale 1 : A, bords latéraux rectilignes divergeant antérieurement ; B, vertébrale 1 en forme de lyre. 10, largeur de la vertébrale 5 par rapport à celle des autres vertébrales : A, la vertébrale 5 n'est pas la plus large ; B, la vertébrale 5 est plus large que les autres vertébrales. 11, morphologie du lobe antérieur plastral : A, trapézoïdal ; B, sub-arrondi. 12, rapport entre la longueur de l'entoplastron et sa distance jusqu'au sillon pectoro-abdominal : A, longueur de l'entoplastron supérieure à deux fois cette distance ; B, longueur de l'entoplastron inférieure à deux fois cette distance ; 13, bords latéraux du lobe postérieur plastral : A, arrondis ; B, rectilignes. 14, configuration du complexe intergulaire-gulaire : A, intergulaire plus étroite que chaque gulaire ; gulaires chevauchant un peu l'entoplastron ; contact intergulaire-pectorales relativement étroit à étroit, ou pas de contact intergulaire-pectorales du fait d'un court contact médial des humérales (moins souvent) ; B, intergulaire plus étroite que chaque gulaire ; gulaires chevauchant un peu l'entoplastron et aussi longues à presque aussi longues que l'intergulaire ; pas de contact intergulaire-pectorales et relativement long contact médial des humérales ; C, intergulaire plus large que chaque gulaire ; gulaires atteignant la suture épi-entoplastrale (à droite) ou chevauchant un peu l'entoplastron (à gauche) ; contact intergulaire-pectorales très étroit (pas de contact médial des humérales) ; D, intergulaire plus étroite que chaque gulaire ; gulaires chevauchant un peu l'entoplastron ; contact intergulaire-pectorales relativement large (pas de contact médial des humérales) ; E, intergulaire aussi large que chaque gulaire ; gulaires ne contactant pas l'entoplastron ; pas de contact intergulaire-pectorales et relativement long contact médial des humérales) ; F, intergulaire plus large que chaque gulaire ; gulaires ne chevauchant pas l'entoplastron ; relativement large contact intergulaire-pectorales (pas de contact médial des humérales) ; G, intergulaire plus étroite que chaque gulaire ; gulaires chevauchant un peu l'entoplastron ; contact intergulaire-pectorales relativement étroit à étroit. Le complexe intergulaire-gulaire de *N. zamorensis* (G) est semblable à celui de *N. arenarum* (A), mais elles diffèrent par d'autres caractères : chez *N. arenarum*, le lobe antérieur trapézoïdal est marqué par un angle vif à la limite externe du sillon gularo-huméral, tandis que, chez *N. zamorensis*, le sillon gularo-huméral se termine sur le côté latéral du lobe antérieur trapézoïdal, postérieurement à l'angle vif (holotype) ou arrondi ; H, intergulaire plus large que chaque gulaire ; gulaires ne chevauchant pas ou chevauchant l'entoplastron ; contact intergulaire-pectorales relativement étroit, ou rarement pas de contact avec un court contact médial des humérales ; 15, longueur de la dossière : A, ca. 25 cm ; B, supérieure à 35 cm. Voir d'autres caractères in Lapparent de Broin, 2003, Tableau 2.

	Ar	La	Li	Eo	Ca	Fr	Za	Sa
1	A	A	B	A	A	A	A	A
2	A	A	B	A	A	A	A	A
3	A	A	B	A	A	A	A	A
4	A	A	A	A	B	A	B	A
5	A	B	B	B	B	B	B	B
6	A	B	B	B	B	A	A	A
7	A	A, B	B	B	B	A	A	A
8	A	B	A	A	B	A	B	B
9	A, B	B	A	B	A	A	A	A
10	A	A	B	B	A	A	A	A
11	A	B	B	B	B	B	A, B	B
12	A	A	A	B	A	B	B	B

Table 2 (Continued)

	Ar	La	Li	Eo	Ca	Fr	Za	Sa
13	A	A	A	A	A	A	B	A
14	A	B	C	D	E	F	G	H
15	A	B	A	B	B	A	A	B

*N. salmanticensis*) (Table 2, character 15). Its anterior edge has a wide and very shallow notch, situated on the anterior margin of the nuchal, peripherals 1 and the medial region of the peripherals 2. Its posterior region is moderately expanded, the pygal and the posterior peripherals being longer than wide. The subpentagonal morphology of the carapace (Table 2, character 1), being almost as wide as long, is not shared with any other species of *Neochelys*. The maximal width of the nuchal is about 20% greater than its

length (Table 2, character 3), which is also unique to this species. That width is twice that of the anterior margin as in the taxa from Silveirinha, *N. arenarum*, *N. laurenti*, *N. eocaenica*, *N. franzeni* and *N. salmanticensis*, but not in the taxa from Dormaal, *N. capellini* and *N. zamorensis* (Table 2, character 4). The latero-anterior margins of that plate are concave in the anterior region and convex in the posterior one. This specimen has seven neurals (Table 2, character 5), as in all the other species, except *N. arenarum*, with

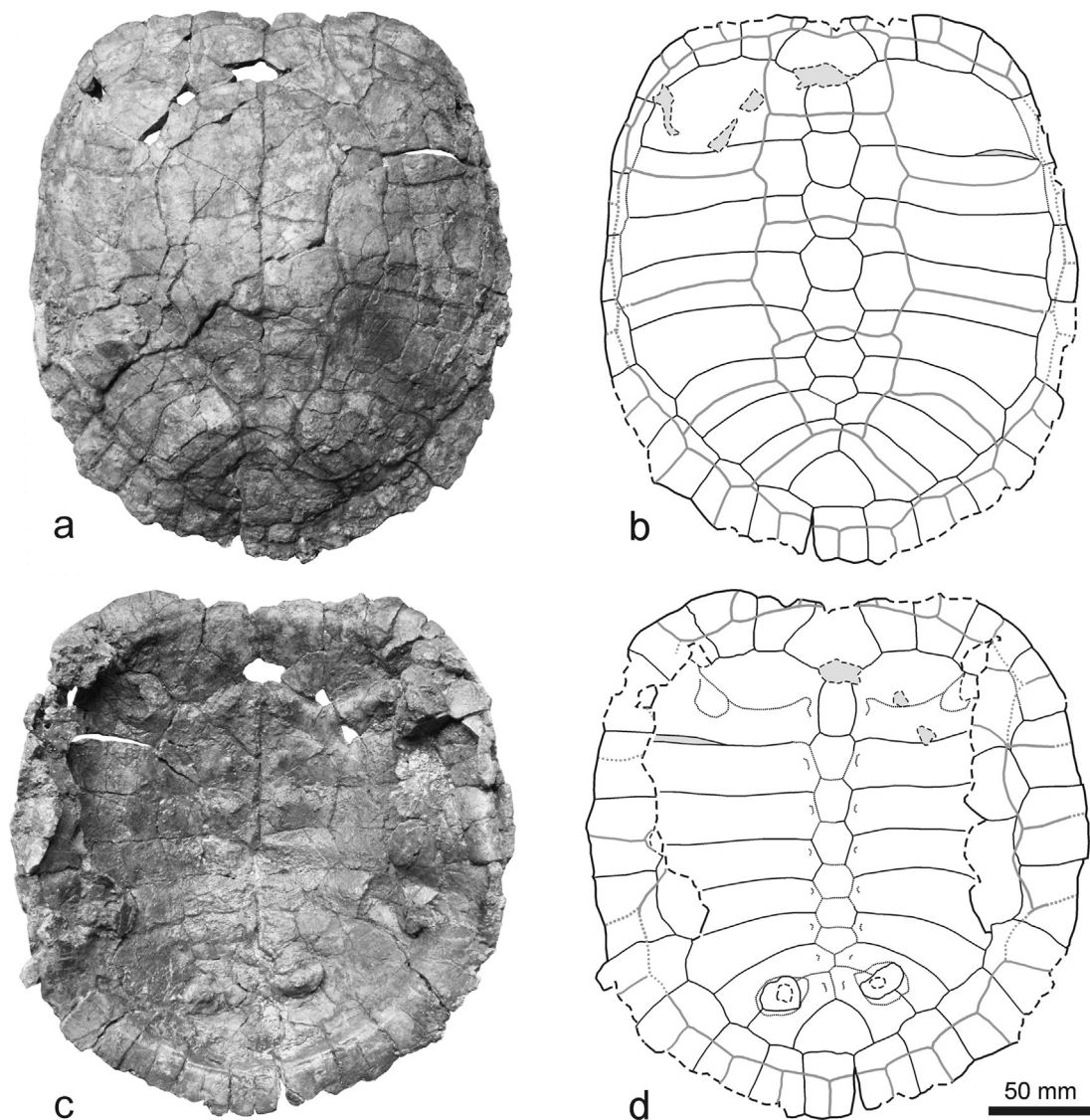
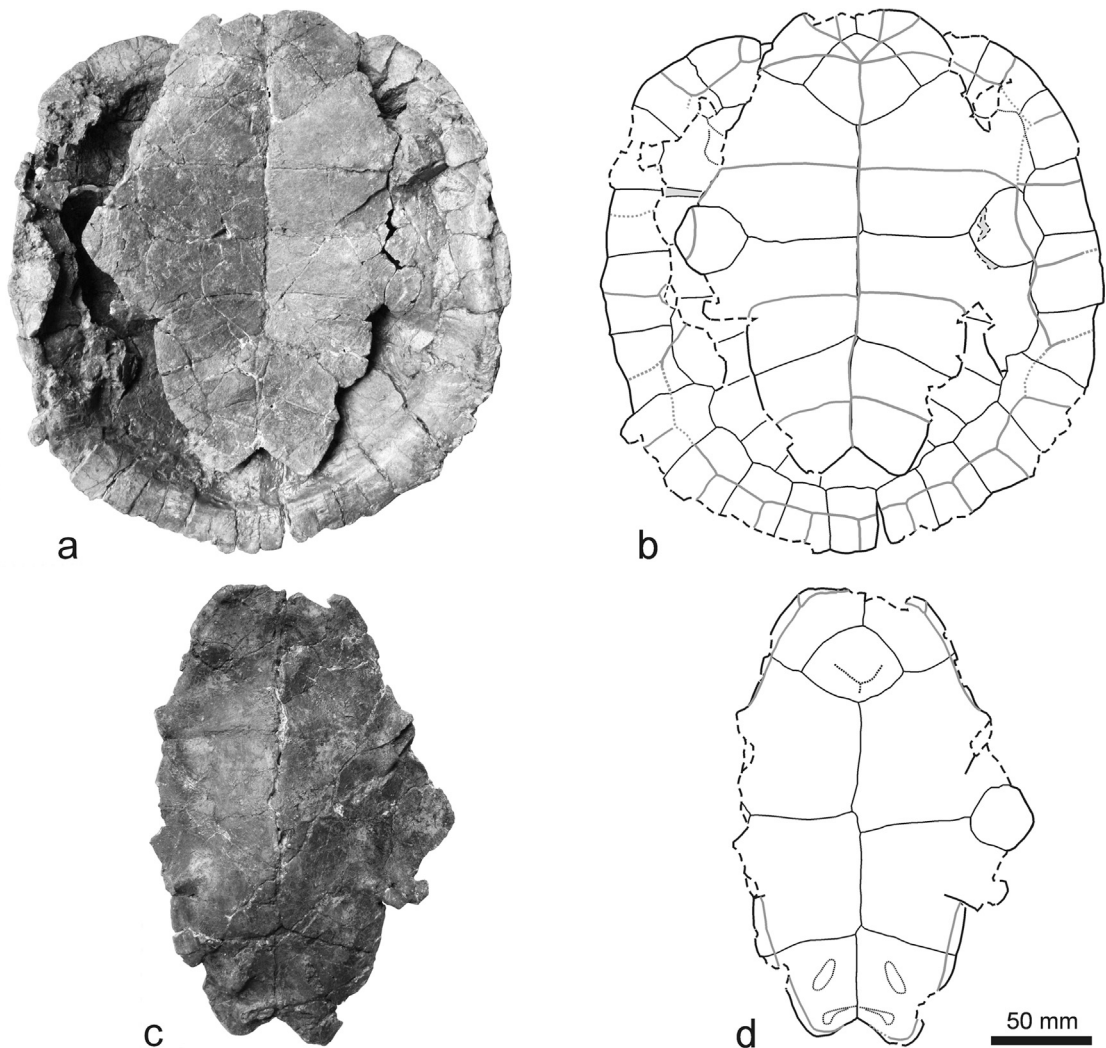


Fig. 2. Carapace of the holotype of *Neochelys liriae* sp. nov., MNHN.F. EVA515 from the Ypresian of Soleillades (France), in dorsal (a, b) and ventral (c, d) views.

Fig. 2. Carapace de l'holotype de *Neochelys liriae* sp. nov., MNHN.F.EVA515 de l'Yprésien de Soleillades (France), en vues dorsales (a, b) et ventrales (c, d).



**Fig. 3.** Shell of the holotype of *Neochelys liriae* sp. nov., MNHN.F.EVA515 from the Ypresian of Soleillades (France), in ventral views (a, b), and plastron in dorsal views (c, d).

**Fig. 3.** Carapace de l'holotype de *Neochelys liriae* sp. nov., MNHN.F.EVA515 de l'Yprésien de Soleillades (France), en vues ventrales (a, b), et plastron en vues dorsales (c, d).

six neurals, and some specimens of *N. eoacaenica*, with 6 to 8 neurals. The neural 1 is slightly longer than wide. The neurals 2 and 3 are as wide as long. The remaining neurals are wider than long, and this ratio increases from the 4th to the 7th. The neural 1 is rectangular, with convex lateral margins. The neurals 2 to 6 are hexagonal. The latero-anterior margins of the neurals 2 to 5 are shorter than the latero-posterior ones. Both margins have similar dimensions in the neural 6. The neural 7 is pentagonal, with the latero-posterior margins longer than the latero-anterior ones. The costals 7 and 8 have a sagittal contact. The maximal length of the costals 1 is nearly twice that of the costals 2. This specimen has a single suprapygial, wider than long. The peripherals 1 are clearly wider than long, and this character is unique to this species (Table 2, character 2). The posterior peripherals have a slight protruding angle at the distal limit between the marginals, not present in the pygal.

The axillary processes contact the distal half of the costals 1 and the posterior region of the peripherals 3. The inguinal processes contact the lateral region of the costals 5 and the antero-medial region of the peripherals 8. The most dorsal regions of the two ilia are preserved, sutured to the costals 7 and 8.

MNHN.F. EBA515 lacks a cervical scute. The vertebrales 1 and 5 and the pleurals widely overlap the nuchal, peripherals and pygal. The marginals 1, longer in the medial margin than in the lateral one, and with convex lateral margins, are more than two times wider than long, as in *N. eoacaenica*, *N. capellinii* and some *N. laurenti* (Table 2, character 6). This pair of scutes is short, overlapping least than a third of the length of the nuchal lateral edge, as in the taxon from Dormaal, *N. capellinii*, *N. eoacaenica* and some *N. laurenti* (Table 2, character 7). This overlap is longer in the other species, in which it may be close to

half of that margin length (*N. salmanticensis*, *Neochelys* from Silveirinha). These scutes overlap only one quarter of the width of the peripherals 1 but this overlap exceeds 30% of the peripherals 1 width in *N. laurenti*, *N. capellinii*, *N. zamorensis* and *N. salmanticensis* (Table 2, character 8). The width of the vertebrales increases from the 1st to the 3th. The 4th is the narrowest. The 5th is the widest as in *N. arenarum* and *N. eocaenica*, but the vertebrales 2 and 3 are the widest in *N. laurenti* (Table 2, character 10). The anterior margin of the vertebral 1 is medially concave and laterally convex. Its lateral margins are anteriorly concave and posteriorly convex. These margins are convex, or slightly in lyre in *N. arenarum*, but this morphology is well developed in *N. eocaenica* and, particularly, in *N. laurenti*. This contrasts with the almost straight and anteriorly diverging margins of *N. franzeni*, *N. capellinii*, *N. zamorensis* and *N. salmanticensis* (Table 2, character 9). The width of the anterior region of the vertebral 1, wider than the nuchal, is similar to the maximal width at the posterior half. The vertebrales 2 and 3 are hexagonal, with their anterior and posterior margins approximately similar in width. The 4th, also hexagonal, has the anterior margin more than 2.5 times wider than the posterior one. Its latero-anterior and latero-posterior margins are converging posteriorly. The vertebral 5 is more than three times wider posteriorly than anteriorly, overlapping the antero-medial region of the peripherals 10.

The plastron (233 mm) is about 10% shorter than the carapace (Fig. 3). The plastral lobes are relatively wide. The anterior (119 mm) is wider than the posterior (109 mm), as in *N. arenarum*, *N. laurenti*, *N. franzeni* and *N. salmanticensis*. The width of both lobes is similar in *N. capellinii* and *N. zamorensis*. There are specimens of *N. eocaenica* in which the posterior lobe is wider than the anterior one, but also others in which the anterior lobe is the widest. The anterior lobe (58 mm) is shorter than the posterior (85 mm), and both are shorter than the bridge (90 mm). This lobe is subrounded; its most anterior margin is transversely straight, as in *N. capellinii*, *N. laurenti*, *N. eocaenica*, *N. franzeni*, *N. salmanticensis* and in the taxon from Silveirinha, in contrast with the trapezoidal lobe of *N. arenarum* and *N. zamorensis* (Table 2, character 11). MNHN.F.EVA515 lacks a gular protrusion, as in all the known specimens of *N. eocaenica* and *N. franzeni*. A gular protrusion has been identified in the other species, and it generally varies from absent to slightly developed; but it is very pronounced in some specimens of *N. zamorensis* and some from Silveirinha and Dormaal.

The entoplastron is more than three times longer than the epiplastral symphysis. This plate is rhomboidal, wider than long, and large in relation to the width of the anterior lobe. The distance between the entoplastron and the hyo-hypoplastral suture is greater than its length. The length of the entoplastron is longer than twice the distance that separates it from the pectoro-abdominal sulcus (Table 2, character 12). The hypoplastra are longer than the hypoplastra. The size of the xiphoplastra is intermediate. The mesoplastra are about as wide as long. The lateral margins of the posterior lobe are more or less rounded, as in all the species of *Neochelys* except *N. zamorensis*, where they are clearly straight (Table 2, character 13). The anal

notch of MNHN.F.EVA515, nearly three times wider than long, has straight margins.

The pairs of scars of the pubes and ischia are visible. The second pair is subtriangular. The angle between the axis that is perpendicular to the axial plane and the ischiatic scars is less than 20°. The maximal size of the scars of both elements is similar. The scars of the pubes are oval. The angle between these scars and the axial plane is approximately 45°.

The anterior margin of the intergular is wider than that of each gular as in *N. franzeni*, *N. capellinii* and *N. salmanticensis*, but it also falls within the range of variability that is known in the material from Dormaal (specimens either with greater intergular width or with greater gular width). In *N. eocaenica*, the intergular is either as wide as the gulars or narrower. The intergular is narrower than the gulars in *N. laurenti*, *N. arenarum* and *N. zamorensis*. The intergular of MNHN.F.EVA515 overlaps the anterior third of the entoplastron. Its lateral margins are markedly divergent from its most posterior region to the contact with the gulars, and slightly divergent from that point to the anterior margin. The intergular-pectorals contact is very narrow, separating the humerals and differing, on one hand from *N. capellinii* and *N. laurenti*, with a relatively long medial contact of the humerals, and, on the other hand, from *N. franzeni*, with a wide intergular-pectorals contact and with a very wide intergular from the anterior margin to the contact with the pectorals. The intergular in *N. eocaenica* is narrower than in *N. franzeni*. The condition found in *N. liriae* sp. nov. falls within the known ranges of variability of *N. arenarum* and *N. zamorensis*, in which the intergular shortly separates or does not separate the humerals, and of *N. salmanticensis*, in which the humerals can contact medially or can be separated by an anteriorly wide but posteriorly narrowed intergular. As in *N. eocaenica*, the postero-medial end of the gulars of MNHN.F.EVA515 lies very close to the epi-entoplastral suture, the left gular slightly overlapping the entoplastron. Specimens of *N. franzeni* and *N. capellinii* in which the gulars do not contact the entoplastron, but also others where they contact its anterior margin, are known. The known variability of *N. salmanticensis* includes both cases but also the overlapping of the gulars on the entoplastron. The overlap is generally present in *N. arenarum*, and always present in the known material from Dormaal, *N. laurenti* and *N. zamorensis*, but can be very short in some *N. laurenti* (Table 2, character 14).

The scutes of *N. liriae* sp. nov. from the longest to the shortest in the sagittal axis, are: abdominals, femorals, pectorals, intergular, anals. The postero-lateral limits of the pectorals are in contact with the anterior margin of the mesoplastra. The marginal scutes overlap one third of the lateral width of these plates.

There is a weak dorsal epiplastral lip, accentuated at the gularo-humeral sulcus, and very short in the medial region of epiplastra. This lip, similar to that of *N. capellinii*, is deeper and longer in *N. arenarum* and *N. laurenti*. The area of the anal scutes overlapping the visceral region of the xiphoplastra is very narrow. However, that of the abdominal is markedly wider.

#### 4. Discussion and conclusions

The thickness of the plates, which are firmly sutured, shows that MNHN.F. EVA515 is an adult specimen. It is assigned to *Neochelys* because it shares with its representatives a unique combination of characters (see Broin, 1977; Lapparent de Broin, 2003, where these characters are compared with those present in other podocnemidids): shell decorated with fine and short dichotomic sulci; wide nuchal, much wider in the posterior margin than in the anterior one, with rounded posteriorly lateral borders; maximal length of the costals 1 almost twice that of the costals 2; sagittal contact of the posterior costals; presence of posterior peripherals points; axillary processes in contact with the distal half of the costals 1 and with the peripherals 3; inguinal processes in contact with the lateral region of the costals 5 and with the peripherals 8; iliac scars on costals 7 and 8; vertebrae 1 and 5, and pleurals, widely overlapping the nuchal, peripherals and pygal; vertebral 1 wider than the nuchal; marginals 1 shorter than half the length of the lateral nuchal margins; broad plastral lobes; anterior lobe shorter than the posterior; lobes shorter than the bridge; anterior lobe with a straight intergular–gular anterior border; broad and shallow to moderate anal notch; short epiplastral symphysis; large and rhomboidal entoplastron, posteriorly close to the axillary notch; intergular separating the gulars, and overlapping less than half the entoplastral length; humero–pectoral sulcus anterior to the epi–hyoplastral suture, except in the lateral region; postero–lateral boundary of the pectorals located near the anterior margin of the mesoplastra; abdomino–marginal sulcus longitudinally located on the mesoplastron; presence of a dorsal epiplastral lip, whose maximal thickness is situated in the gulo–humeral contact.

All the possible species of *Neochelys* to which the European specimens hitherto found belong are not yet defined, and the phylogenetic relationships among the defined taxa have not been established. Although the combination of some characters might help to identify taxa such as *N. arenarum* and those present in Dormaal and Silveirinha as more basal according to previous work on turtles in general and Pleurodira, in particular (Lapparent de Broin and Murelaga, 1999; Lapparent de Broin, 2003) (e.g. short pygal, relatively long marginals 1, short and straight anal notch, anterior margin of the intergular narrower than those of the gulars), a mosaic of primitive and derived characters is present in all of them.

The specimen studied here shows several autapomorphies and an exclusive character combination, allowing its attribution to a new species, *N. liriae* sp. nov. The characters of its shell allow us to identify it as a form morphologically related to but clearly different from both *N. laurenti* and *N. eocaenica*, taxa previously recognized in non-synchronous levels of the same Languedoc–Roussillon region (Table 1). These three species share a unique combination of characters, including: maximal width of the nuchal two or more times wider than of its anterior margin; seven neurals (variable in *N. eocaenica*); overlap of the marginals 1 on less than one third of the length of the nuchal lateral margin (variable in *N. laurenti*); marginals 1 at least two times wider than long (variable *N. laurenti*);

vertebral 1 in lyre; subrounded anterior plastral lobe; absence of gular protrusion (present, but poorly developed, in some *N. laurenti*); rounded lateral margins of the posterior lobe; length of the entoplastron shorter than its distance up to the hyo–hypoplastra suture. Although *N. liriae* sp. nov. shares only with *N. laurenti* the presence of an entoplastral length more than two times its distance up to the pectoro–abdominal sulcus, several characters shared with *N. eocaenica* but not with *N. laurenti* are recognized: overlapping of the marginals 1 on no more than one quarter of the peripherals 1 width; vertebral 5 wider than the other vertebrae; contact of the intergular with the pectorals.

In addition to *N. eocaenica* and *N. laurenti*, the *Neochelys* record of the Eocene of France also includes some indeterminate specimens, consisting in isolated plates or fragments of shells, sharing with *N. liriae* sp. nov. some character states not present in either of these two species (e.g. presence of an intergular wider than each of the gulars in the specimen from the “Lutetian of Languedoc” figured by Broin (1977) fig. 24). However, the presence of the autapomorphies or of the character combination of the new species is detected in none of them. Furthermore, each of the characters of the unique combinations given for *N. liriae* sp. nov., *N. eocaenica* and *N. laurenti* may also be individually shared by other species. A “*N. eocaenica* complex” sensu Broin (1977) that might include, besides *N. eocaenica* and conferred material (Broin, 1977), *N. liriae* sp. nov. and *N. laurenti* is not regarded here as a homogenous group.

This study sheds new light on the wide diversity of *Neochelys*. Future studies, incorporating not only shells but also cranial material (known in several localities, but generally unpublished) and some also poorly studied and unpublished material from the Bartonian–Priabonian levels of Spain and other French regions, are necessary. The characters that are also shared by some other species show the broad interrelationships within the genus *Neochelys*. Only a cladistic analysis with outgroups allowing a polarization of characters can establish the phylogenetic relationships among the representatives of *Neochelys*.

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