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RESEARCH PAPER

New insights into the anatomy and systematic of '*Papoulemys*' *laurenti*, a representative of *Neochelys* (Chelonii, Podocnemididae) from the early Eocene of the south of France

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Abstract *Neochelys* is a European Eocene genus of turtles well represented by various species. It is one of the few members of Pleurodira identified during the Cenozoic of this continent. However, it has generally been recognized only by shells, and too few skulls are known to provide useful data for comparative diagnosis and relationships. The European Eocene '*Papoulemys*' had been proposed as a junior synonym of *Neochelys,* the species '*P.*' *laurenti* becoming *N. laurenti*, but this hypothesis was insufficiently justified. A second skull of this species, from its type locality (the French locality of Saint-Papoul), is analysed here together with several unpublished skulls of other *Neochelys* spp. from various countries and ages, providing new arguments to refute the validity of the characters used to diagnose '*Papoulemys*' as a genus distinct from *Neochelys*. They are exclusively cranial characters since only its holotype (a skull) was known. Several shells from the type locality, on which the reattribution to *N. laurenti* had been proposed (but only synthetically), are also studied in detail here, as well as other unpublished *Neochelys* spp. shells. We propose a new diagnosis for '*Papoulemys*' *laurenti*, reallocating the species to *Neochelys*. We also expand the available information on this genus and on several of its representatives.

Keywords Pleurodira · Podocnemididae · Erymnochelyinae · *Neochelys* · Early Eocene · Europe

Kurzfassung *Neochelys* war eine im Eozän Europas weit verbreitete und vielfältige Schildkrötengattung, wobei sie eines der wenigen Mitglieder der Pleurodira darstellt, die im Känozoikum dieses Kontinents identifiziert worden sind. Allerdings wurde sie im Allgemeinen anhand des Panzers erkannt, da ihre kraniale Information begrenzt ist. Einige Autoren legten '*Papoulemys*' aus dem europäischen Eozän als jüngeres Synonym von *Neochelys* nahe, so dass die Spezies '*P.*' *laurenti* zu *N. laurenti* wurde. Diese Hypothese wurde nur unzureichend begründet. Die Untersuchung eines zweiten Schädels in Hinblick auf die Zuordnung des Fundes sowie die Analyse weiterer nicht veröffentlichter Schädel anderer *Neochelys*-Arten aus unterschiedlichen Ländern und Zeitaltern bietet neue Argumente, die es ermöglichen die Gültigkeit der Figuren, die '*Papoulemys*' als von *Neochelys* verschiedene Gattung zu widerlegen. Diese entsprachen ausschließlich kranialen Figuren, da nur ihr Holotypus, ein Schädel, bekannt war. Mehrere Panzer dieser Fundzuordnung, in der die Wiederzuschreibung zu *N. laurenti* stattfand, allerdings nur auf eine eine synthetische Weise, werden hier ebenfalls im Detail untersucht, ebenso wie weitere unveröffentlichte Panzer von Neochelys-Arten. Dies ermöglicht es, die Gültigkeit der Art '*Papoulemys*' *laurenti* zu bestätigen, für die eine neue Diagnose vorgestellt wird. Die Neuzuordnung dieser Art zu *Neochelys* ist begründet, da sich Kenntnisse von dieser Gattung und mehreren ihrer Vertreter verbessert haben.

Schlüsselwörter Pleurodira · Podocnemididae · Erymnochelyinae · *Neochelys* · Unteres Eozän · Europa

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Introduction

Several representatives of the pleurodiran turtles Erymnochelyinae Broin (1988) (sensu Lapparent de Broin 2000), a clade of Podocnemididae originating in Gondwana, are recorded in the Eocene of Europe. Members of the genus *Neochelys* Bergounioux (1954), and taxa identified as closely related to *Erymnochelys* Baur (1888), are recognized in several European countries (de Broin 1977; Lapparent de Broin 2001; Righi and Delfino 2003; Merle 2008; Pérez-García and Lapparent de Broin 2013; Lapparent de Broin et al. 2014).

Cryptodiran turtles (representatives of Trionychia and Testudinoidea) have been identified in the French locality of Saint-Papoul (Aude department, Lauragais area, Languedoc-Roussillon region) in early Ypresian levels (de Broin 1977; Hervet 2003, 2004; Claude and Tong 2004; Laurent et al. 2010). In addition, another member of Podocnemididae, '*Papoulemys*' *laurenti* Tong 1998, identified as a representative of a new genus and species, was defined there. Only one specimen, a skull, was attributed to it by Tong (1998), who considered the taxon as more closely related to *Erymnochelys* than to *Neochelys*. However, new specimens from the type locality were attributed to the same species but identified in papers as representatives of *N. laurenti* (Lapparent de Broin 2001, 2003; Pérez-García and Lapparent de Broin 2013). These specimens (not figured or described) included a skull, associated with a shell, and other articulated shells, allowing Lapparent de Broin (2001) to consider the synonymy between *Papoulemys* Tong 1998 and *Neochelys* Bergounioux 1954. They were synthetically included, also identified as belonging to *N. laurenti*, in comparative studies of the *Neochelys* species (Lapparent de Broin 2003; Pérez-García and Lapparent de Broin 2013). The synonymy of the taxon '*Papoulemys*' with *Neochelys* and its individuality was not clearly supported by the revision of the Podocnemididae clade performed by Gaffney et al. (2011). Therefore, these authors considered '*Papoulemys*' either as closely related to *Neochelys* or as a possible member of this genus. However, the hypotheses proposed by Gaffney et al. (2011) were based only on skull characters, which were the only ones available for the *Papoulemys* holotype.

Now, though, several specimens comprising elements of both the cranial and postcranial skeleton from the '*Papoulemys*' type locality are described here and attributed to this insufficiently known taxon, identified here as *N. laurenti*.

Only one skull attributed to *Neochelys* has been previously figured and described in detail (de Broin 1977). It is a laterally bent and partly flattened skull of *N. arenarum* de Broin 1977, a taxon from early Ypresian levels of the Sables bleutés du Haut Var Formation, in the Var department (France). We describe a new *N. laurenti* skull and compare it with the holotype of '*Papoulemys*' *laurenti* and with other skulls of *N. arenarum* from its type locality presented by de Broin (1977) (but so far not studied in detail) to assess whether there is intraspecific variability in these two taxa. A study of these specimens, and the incorporation of information from cranial material of other European Eocene members of *Neochelys* (whose available information was very limited or non-existent) allow us to evaluate the validity of some of the character states previously considered as diagnostic at the generic or specific level.

The articulated and well-preserved shells corresponding to *N. laurenti*, briefly noted in the afore-mentioned analysis, are presented in detail with figures for the first time. This more comprehensive presentation allows us to compare it with the other known shells of *Neochelys* and to identify intraspecific variability.

Neochelys has been identified in several Eocene outcrops in the Languedoc-Roussillon region (France, in the Aude and Hérault departments) (Fig. 1), where it is also represented by two other species that could be closely related to *N. laurenti*. One of these species is *N. eocaenica* (De Stefano 1902) from the Grès d'Aigne Formation, late Ypresian–early Lutetian. The other is the recently described *N. liriae* Pérez-García and Lapparent de Broin 2013, from the Grès d'Assignan Formation, from early–middle Ypresian levels slightly younger than those of Saint-Papoul. Unpublished material that could belong to both species is presented here. This allows us to describe some character states and compare them to those present in *N. laurenti*.

Laurent et al. (2010) mentioned the presence at La Borie (Saint-Papoul) of an undefined new species of *Neochelys*, without figures or diagnosis but with a short description based on shell characters. '*Papoulemys*' *laurenti* and its published postulated synonymy with the genus *Neochelys* were not mentioned by these authors. La Borie is just a notable point in the same marl levels of the Saint-Papoul locality (the great quarry of the Tuileries du Lauragais), where the holotype of '*Papoulemys*' *laurenti* and the material of *Neochelys laurenti* described here have been found. The states of the characters provided by Laurent et al. (2010) for identification of the La Borie shells as belonging to a putative undefined new species are the same as those in *Neochelys laurenti*, the only member of *Neochelys* so far recognized in Saint-Papoul. Therefore, these specimens probably correspond to *N. laurenti*.

A cervical vertebra whose characters are consistent with the hitherto unpublished cervical vertebrae of *Neochelys* (e.g., *N. salmanticensis* (Jiménez Fuentes 1968) from the

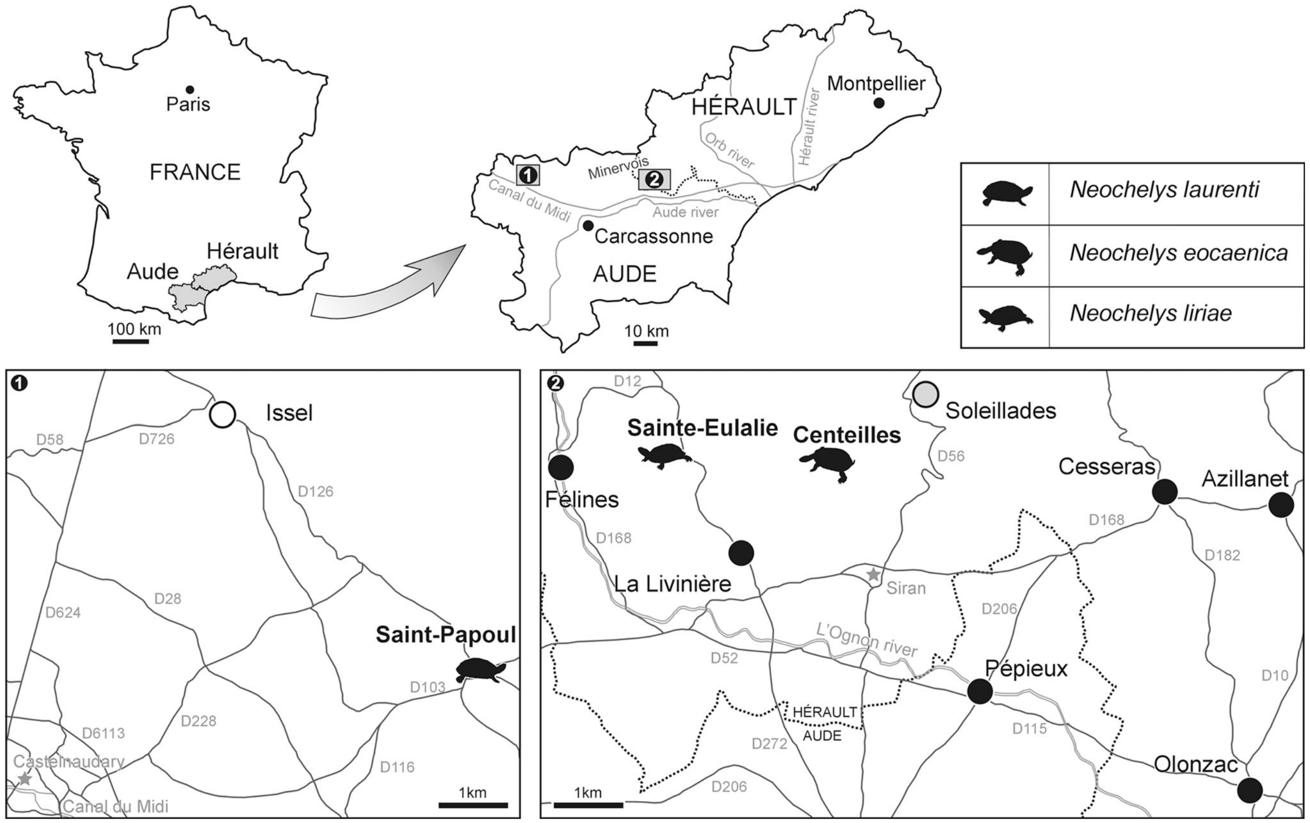

Fig. 1 Geographical location of the outcrops of Aude and Hérault (France) where the new specimens of *Neochelys* from the Languedoc-Roussillon region studied in this paper were found: *Neochelys laurenti* (Tong 1998), Clays of Saint-Papoul (upper part of the early Ypresian), Saint-Papoul (Aude); *Neochelys* cf. *liriae*, Grès d'Assignan Formation (lower part of the late Ypresian), Sainte-Eulalie (Hérault); *Neochelys eocaenica* De Stefano 1903, Grès d'Aigne Formation (late Ypresian–early Lutetian interval), Centeilles (Hérault). The *black circles* denote localities close to the sites where specimens assigned to *Neochelys eocaenica* have been found, in the Grès d'Aigne Formation. The *gray circle* denotes the type locality of *Neochelys liriae*, in the Grès d'Assignan Formation. The white circle denotes a locality close to the sites where material corresponding to an indeterminate species of *Neochelys* has been found, in the sandstone-molasse of Issel (late Ypresian–early Lutetian level of the Issel Series)

Eocene of Spain) is recognized in the type locality of '*P.*' *laurenti*.

We intend to definitively demonstrate the synonymy of *Papoulemys* with *Neochelys*, to propose a new diagnosis for the valid species *N. laurenti*, and to evaluate its specific relationships based on the study of several specimens corresponding to skulls and postcranial elements. A new diagnosis for the genus *Neochelys* is also proposed here.

Institutional abbreviations MCZ, Museum of Comparative Zoology, Harvard University, USA; MDE, Musée des Dinosaures, Espéraza, France; MNHN.F., Paleontology Collection, Muséum National d'Histoire Naturelle, Paris, France; MNHN.RA., Collection of Reptiles et Amphibiens, Muséum National d'Histoire Naturelle, Paris, France; MNHN.ZA.AC., Collection of Reptiles of Comparative Anatomy, Muséum National d'Histoire Naturelle, Paris, France; NHMUK, Natural History Museum, London, UK; SAGA, Société Amicale des Géologues Amateurs, Paris, France; MHNT, Musée d'Histoire Naturelle de Toulouse; SMF, Senckenberg Naturmuseum Frankfurt, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; STUS, Sala de las Tortugas de la Universidad de Salamanca, Salamanca, Spain; UD, Sciences de la Vie, de la Terre et de l'Environnement collections of the Université de Bourgogne, Dijon, France; ZSM, Zoologische Staatssammlung München, Germany.

Systematic paleontology

Chelonii Latreille 1800
Pleurodira Cope 1864
Pelomedusoides Cope 1868
Podocnemidoidea Cope 1868
Podocnemididae Cope 1868
Erymnochelyinae Broin 1988
Neochelys Bergounioux 1954

Type species: *Emys capellinii* Zigno 1889

Included species: *Neochelys capellinii* (Zigno 1889), *Neochelys nicolisii* (Zigno 1890), *Neochelys eocaenica* (De Stefano 1902), *Neochelys mengaudi* (Bergounioux 1935), *Neochelys salmanticensis* (Jiménez Fuentes 1968), *Neochelys arenarum* de Broin 1977, *Neochelys zamorensis* Jiménez Fuentes 1992, *Neochelys franzeni* Schleich 1993, *Neochelys laurenti* (Tong 1998), *Neochelys liriae* Pérez-García and Lapparent de Broin 2013.

Distribution: Eocene (from the early Ypresian to the late Bartonian) of Europe (known in Italy, France, Spain, Germany, Belgium, and Portugal) (see Lapparent de Broin 2003; Pérez-García and Lapparent de Broin 2013).

Emended diagnosis: *Neochelys* is a podocnemidid due to the presence of a cavum pterygoidei, and it is recognized as a member of the Erymnochelyinae due to the large anterior opening of the cavum pterygoidei, with its wide dorsal opening in the sulcus cavernosus, most of the base of the prootic having disappeared. The genus is characterized by a carapace length from circa 20–55 cm, known from the cranial and postcranial skeleton, sharing the following exclusive combination of characters: a relatively narrow skull, without a beak and with rounded lateral margins; a snout much shorter than the orbits, narrow and prominent, with anterior parallel edges; an orbit length circa 20 % that of the skull from the anterior edge to the parietal end; laterally facing orbits, higher than the suborbital space; moderate interorbital space, approximately as wide as the orbit length; absent interorbital groove; transverse to sinuous prefrontal-frontal contact, without a medial prominence; very short temporal emargination, with the maximum length in the lateral region; absence of a contact between the parietals and the jugals, and contact between the postorbitals and the quadratojugals; parietal-quadratojugal contact length longer than the total length of the postorbitals; rectangular to rounded cheek emargination, less than half the height of the meatus quadrati; moderate posterior expansion of the triturating surface and no accessory ridges; vomer absent; transverse processus trochlearis pterygoidei; shallow and narrow fossa precolumellaris; basioccipital partially integrated or not included in the occipital condyle; not very expanded horizontal occipital shelf; cordiform interparietal scute with two rounded protuberances on the anterior margin; lower jaw without a well-developed beak; short symphyseal triturating surface on a relatively long mandibular symphysis; rounded lingual symphyseal angle; moderately widened mandibular posterior triturating surface; chorda tympani enclosed in the middle of the anterior border of a well-developed processus retroarticularis; high nuchal length in relation to posterior width (around 70–95 %); maximal length of the costals 1, almost twice that of the costals 2; sagittal contact of the costals 7 and 8 and, in some cases, also costals 6; presence of posterior peripheral points; vertebral 1 wider than the nuchal; marginals 1 shorter than half the length of the antero-lateral nuchal margins; relatively wide plastron with moderately converging lateral margins of the lobes; subtrapezoidal anterior plastral lobe (with angular or rounded edges), lacking an anterior concavity; relatively short epiplastral symphysis; large entoplastron, posteriorly close to the axillary notch; intergular always separating the shorter gulars, and overlapping less than half the entoplastral length, joining or not the humero-pectoral sulcus that is anterior to the epi-hyoplastral suture (except in the most lateral region in most cases); postero-lateral boundary of the pectorals located near the anterior margin of the hexagonal to rounded mesoplastra; absence of a developed notch at the lateral extremity of the femoro-anal sulcus; very short dorsal expansion of the plastral scute borders.

Neochelys laurenti (Tong 1998)
(Figures. 2a, b, 3a, b, 4a, 5, 6, 7, 8, 9, 10 and 11)

Synonyms: *Papoulemys laurenti*, Tong (1998); *Neochelys laurenti* in Lapparent de Broin (2001), Lapparent de Broin (2003), Pérez-García and Lapparent de Broin (2013); *Papoulemys laurenti* in Gaffney et al. (2011).

Holotype: Skull MDE T12 (Figs. 2a, 3a)

Referred material: Several shells: MNHN.F.SPP 28; MNHN.F. cast 5818–5819 (original in Galoyer private collection); MNHN.F.SPP 30; and a skull: MNHN.F.SPP 29 (associated with shell MNHN.F.SPP 28) (Figs. 2b, 3b, 4a, 5, 6, 7, 8, 9, 10, 11). All of them from the type locality and horizon.

Type locality and horizon: Saint-Papoul, Aude, France (Fig. 1). Great Quarry of Tuileries et Briqueteries du Lauragais (TBL) Guiraud Frères, now part of the Terreal France group. Greyish to black marl passages within the clays of Saint-Papoul, early Eocene, upper part of the early Ypresian (MP 8–9).

Emended diagnosis: Member of *Neochelys* differing from all known representatives of this genus due to a unique arrangement of the intergular and gular scutes: the intergular scute is narrower than each of the gulars, all of them overlapping the anterior region of the entoplastron, the gulars being as long to nearly as long as the intergular, and lacking an intergular-pectoral contact, with the humerals having a relatively long medial contact, this length varying from almost the length of the intergular on the entoplastron to two times as long. It is also distinguished from the other *Neochelys* species by an exclusive character combination: large size (skull length about 80 mm, shell length about 350 mm) similar to that of *N. eocaenica* and *N. capellinii*; occipital condyle comprising

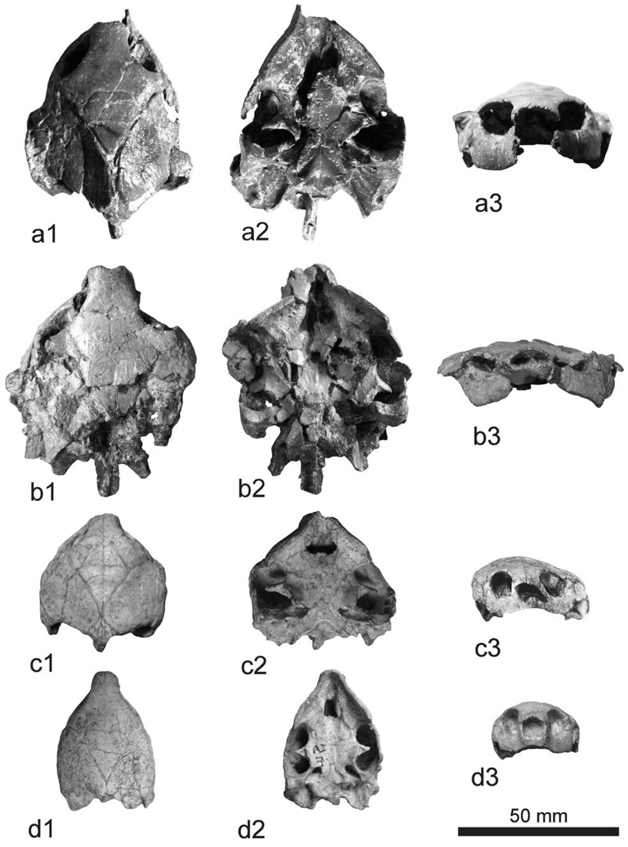

Fig. 2 Comparison of several French skulls of *Neochelys*. **a** MDE T12, holotype of '*Papoulemys*' *laurenti* Tong (1998), from the early Ypresian of Saint-Papoul (Aude). **b** MNHN.F.SPP 29, specimen of *Neochelys laurenti* studied in this paper, from the type locality. **c** MNHN.F.RI 6, skull of *Neochelys arenarum* de Broin (1977), from the early Ypresian of Rians (Var) (type locality). **d** MNHN.F.RI 7, another specimen of *Neochelys arenarum* from the type locality. All of them in dorsal (**1**), ventral (**2**), and anterior (**3**) views

mainly the exoccipitals instead of the condition in *N. arenarum*, where the basioccipital represents more than the lower half of the condyle; elliptical shell with rounded lateral margins, the anterior margin varying from straight to slightly notched, the notch being very shallow and exclusively located on the anterior margin of the nuchal plate and of the peripherals 1, as in *N. eocaenica*, *N. franzeni*, *N. capellinii*, *N. nicolisii*, and *N. salmanticensis*; seven neurals, as in all the species except in *N. arenarum* (six neurals); markedly longer than wide peripherals 1, differing from the condition in *N. liriae* (clearly wider than long peripherals 1); wider than long marginals 1, overlapping at least 30 % of the width of the peripherals 1, shared with *N. capellinii*, *N. nicolisii*, *N. salmanticensis*, and *N. zamorensis*; lyre-shaped vertebral 1, as in *N. eocaenica* and *N. liriae*; vertebrals 2 and 3 wider than the other vertebral scutes, shared with *N. franzeni*, *N. capellinii*, *N. nicolisii*, *N. zamorensis*, and *N. salmanticensis*; anterior plastral lobe wider than the posterior one, as in *N. arenarum*, *N. franzeni*, *N. salmanticensis*, and *N. liriae*; anterior plastral lobe with rounded edges, differing from the trapezoid condition present in *N. arenarum* and *N. zamorensis*; entoplastral length shorter than the distance that separates it from the hyo-hypoplastral suture, and longer than twice the distance that separates it from the pectoro-abdominal sulcus, a character combination shared with *N. arenarum* and *N. liriae*; rounded to almost straight lateral margins of the posterior plastral lobe as in all the species except *N. zamorensis,* where they are always straighter; anal notch with rounded or straight margins, between two and three times wider than long, shared with *N. eocaenica*, *N. franzeni*, *N. capellinii*, *N. nicolisii*, *N. zamorensis*, and *N. liriae*.

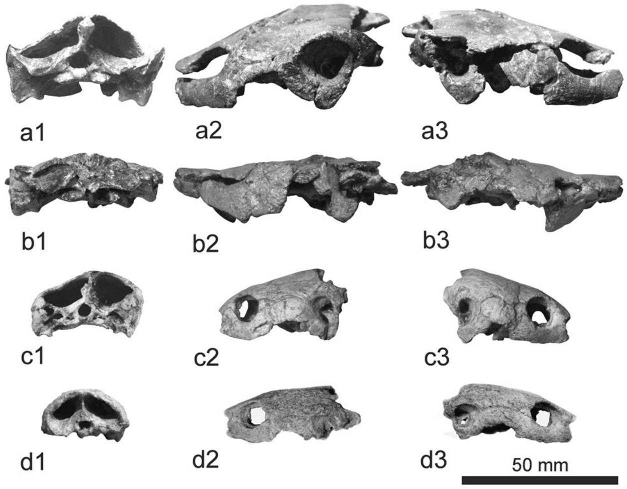

Fig. 3 Comparison of several French skulls of *Neochelys*. **a** MDE T12, holotype of '*Papoulemys*' *laurenti* Tong (1998), from the early Ypresian of Saint-Papoul (Aude). **b** MNHN.F.SPP 29, specimen of *Neochelys laurenti* studied in this paper, from the type locality. **c** MNHN.F.RI 6, *Neochelys arenarum* de Broin (1977), from the early Ypresian of Rians (Var) (type locality). **d** MNHN.F.RI 7, another specimen of *Neochelys arenarum* from the type locality. All of them in posterior (**1**), left lateral (**2**), and right lateral (**3**) views

cf. *Neochelys laurenti* (Tong 1998)
Figure 12

Material: A cervical vertebra (MNHN.F.SPP 31). All of them from the type locality and horizon.

Locality and horizon: From the type locality and horizon of *Neochelys laurenti*.

Description of the new *Neochelys* specimens from the type locality of '*Papoulemys*' *laurenti*

Skull

The second known skull of a podocnemidid from the type locality of '*P.*' *laurenti* (Saint-Papoul), briefly included in Lapparent de Broin (2003) as *Neochelys laurenti*, without a

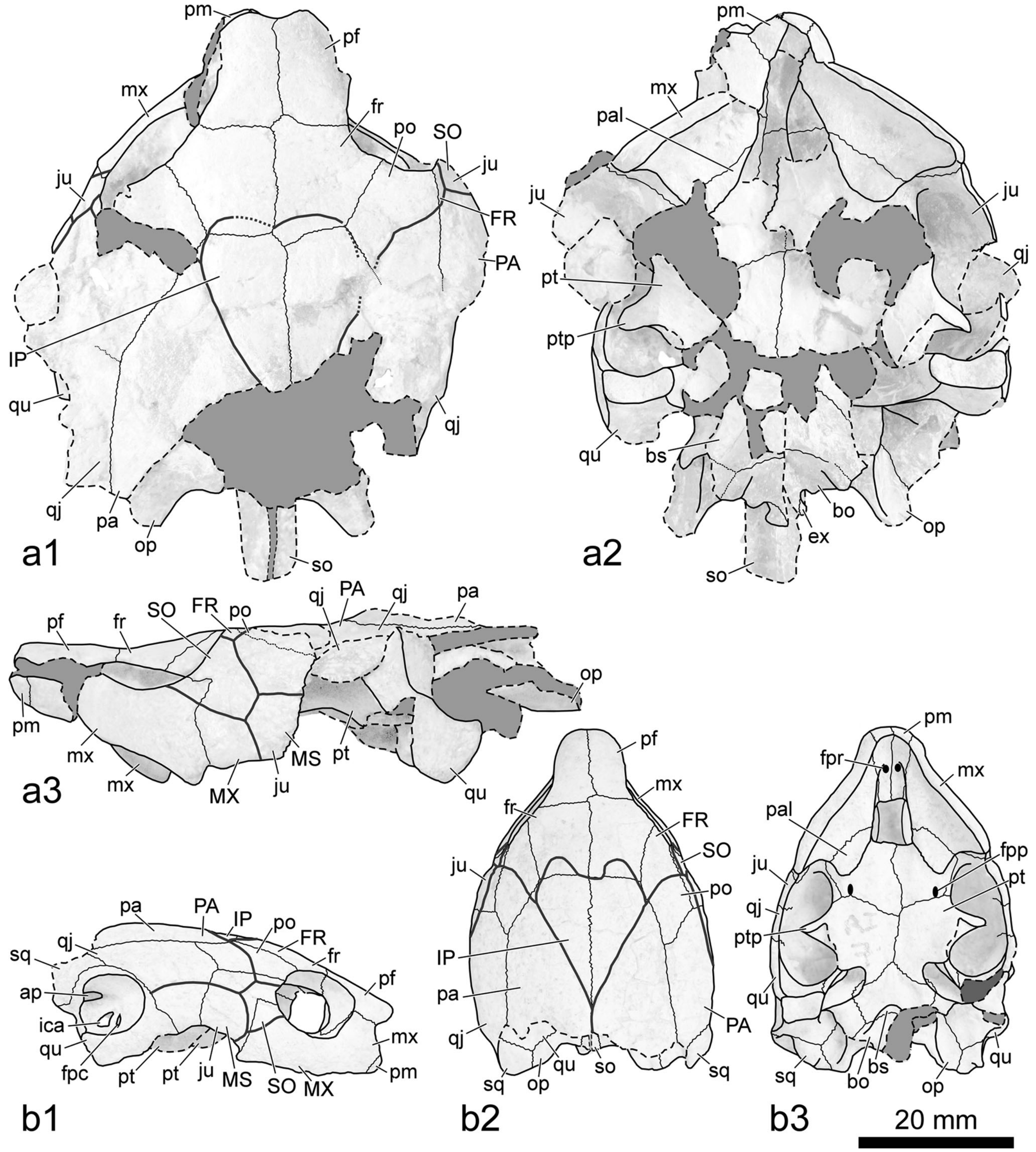

Fig. 4 Drawings showing the preserved elements in the two skulls of *Neochelys* presented for the first time in this paper. **a** MNHN.F.SPP 29, *Neochelys laurenti* (Tong 1998), from the early Ypresian of Saint-Papoul (Aude, France), in dorsal (**a1**), ventral (**a2**), and left lateral (**a3**) views. **b** MNHN.F.RI 7, *Neochelys arenarum* de Broin (1977), from the early Ypresian of Rians (Var, France), in right lateral (**b1**), dorsal (**b2**), and ventral (**b3**) views. *ap* antrum postoticum; *bo* basioccipital; *bs* basisphenoid; *ex* exoccipital; *fpc* fossa precolumellaris; *fpp* foramen palatinum posterius; *fpr* foramen praepalatinum; *fr* frontal; *FR* frontal scute; ica, incisura columellae auris; *IP* interparietal scute; *ju* jugal; *MS* masseterian scute; *mx* maxilla; *MX* maxillary scute; *op* opisthotic; *pa* parietal; *PA* parietal scute; *pal* palatine; *pf* prefrontal; pm premaxilla; *po* postorbital; *pt* pterygoid; *ptp* processus trochlearis pterygoidei; *qj* quadratojugal; *qu* quadrate; *SB* subocular scute; *so* supraoccipital; *sq* squamosal

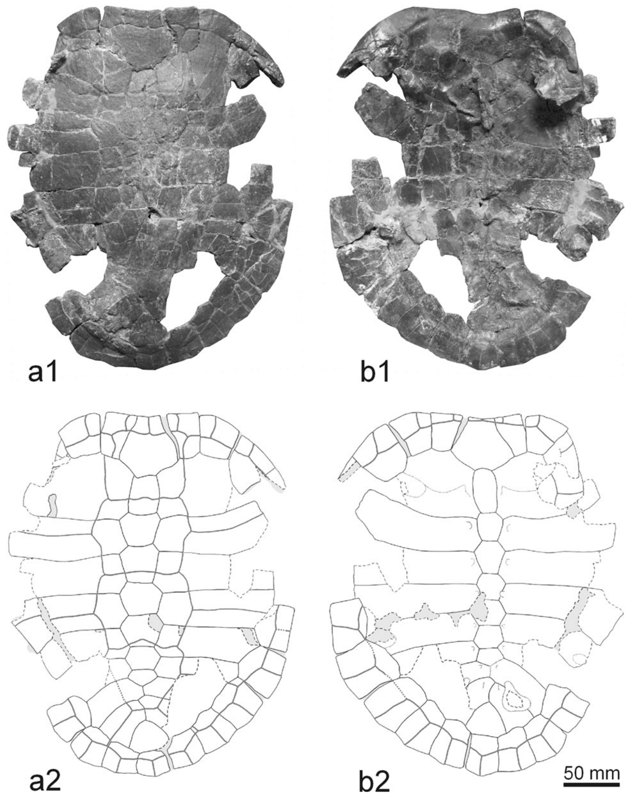

Fig. 5 Carapace of the specimen of *Neochelys laurenti* (Tong 1998) MNHN.F.SPP 30, from the early Ypresian of Saint-Papoul (Aude, France). **a** dorsal view; **b** ventral view

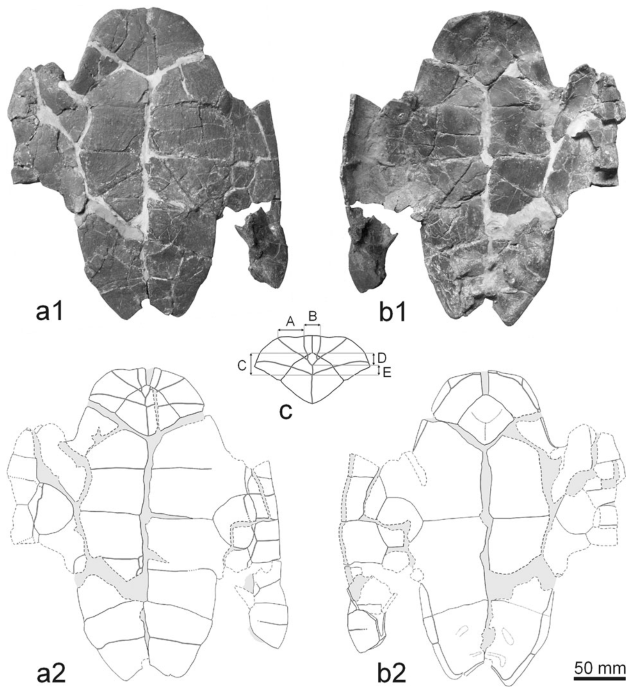

Fig. 6 Plastron of the specimen of *Neochelys laurenti* (Tong 1998) MNHN.F.SPP 30, from the early Ypresian of Saint-Papoul (Aude, France). **a** ventral view; **b** dorsal view; **c** reconstruction of the anterior lobe of the plastron of *N. laurenti* in which the relative dimensions between several of the elements composing the autapomorphic intergular-gular complex of characters of this species are indicated. *A* gular scute width; *B* intergular scute width; *C* entoplastron length covered by the intergular and humeral scutes; *D* intergular length on the entoplastron; *E* length of the medial contact of the humeral scutes

collection number, is analysed in this paper (Figs. 2b, 3b and 4a). It is identified as MNHN.F.SPP 29. This skull is dorso-ventrally flattened. Most of its bones are partially or completely preserved, although several are damaged, generally due to crushing.

There are no nasal bones. The prefrontals are longer than wide. Their medial length is similar to that of the frontals. At mid-length, the prefrontals constitute the narrowest region of the interorbital space. This region is relatively wide and flat. There is no interorbital groove. The sutures between the prefrontals and the frontals, and between the frontals and the parietals are subperpendicular to the axial plane. The frontals are in contact with the postorbitals latero-posteriorly. The prefrontals, frontals, and postorbitals delimit the dorsal margin of the orbits. The postorbitals are longer than wide, completely separating the jugals from the parietals. The parietals are long, forming much of the skull roof. They are in contact laterally with the postorbitals and quadratojugals. The contact of the parietals with the quadratojugals (better preserved on the left side) is long, indicating that, although not preserved, the temporal emargination was short. The posterior part of the skull roof is crushed and the well-developed crista supraoccipitalis appears just below this area. The jugals are in contact with the maxillae and the orbits anteriorly, the postorbitals dorsally, the quadratojugals posteriorly, and the palatines and pterygoids ventrally. The jugals and the maxillae delimit the anterior region of the cheek emargination; that slight emargination is longer than high. The ventral margin of the quadratojugals forms the posteriorly following portion of that emargination, preventing contact between the jugals and the quadrates. The premaxillae separate the maxillae, both in the anterior and palatal views. The specimen lacks a bony beak. The right maxilla is crushed on the right anterior part of the snout. However, it is apparent that the snout was protruding in relation to the widened posterior part of the maxillae, marked by an external concavity on the anterolateral face. This maxillary widening corresponds to that of the triturating surface area. In a palatal view, the missing posterior part of the premaxillae anteriorly limited the single choana, also bordered by the maxillae and palatines. This specimen lacks a vomer. The maxillae define the lower margin of the orbits. The maxillae and the palatines form a medial expansion of the posterior region of the triturating surface. The surface area corresponding to the maxillae is markedly larger than that corresponding to the

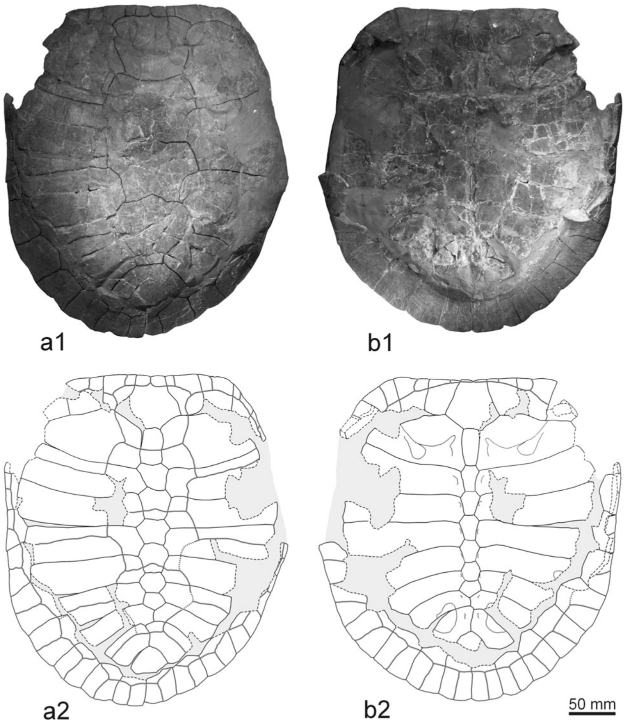

Fig. 7 Carapace of the specimen of *Neochelys laurenti* (Tong 1998) MNHN. F. casts 5818–5819 (Galoyer collection), from the early Ypresian of Saint-Papoul (Aude, France). **a** dorsal view; **b** ventral view

palatines, which constitute its posteromedial region. A median maxillary ridge is recognized. However, the triturating surface is smooth, lacking additional ridges. The processus trochlearis pterygoidei are well developed and transversely directed. Both pterygoids are in contact medially. The basisphenoid is wider than long. It forms a short, obtuse wedge that penetrates between the rear regions of both pterygoids. The contact between the basisphenoid and the basioccipital is convex. The horizontal occipital shelf is poorly developed. The occipital condyle is mainly composed of the exoccipitals, the basioccipital being restricted to a very small portion of its dorsal region. The mandibular condyles of the quadrates are located far below the occipital condyle. These elements are much shorter than wide. The paroccipital processes of the opisthotics, ventrally concave and medially bordered by a longitudinal curled edge, are well protruding posteriorly, being relatively wide at their (barely eroded) extremity.

The interparietal scute is longer than wide. This scute overlaps more than two-thirds of the length of the parietals. It forms an elongated heart, with two short anterior arcs covering the posterior part of the frontals, posterior to the frontal scutes. The boundary between the frontal and the parietal scutes obliquely crosses the postorbital bones. The ventralmost region of the frontal scutes is situated on the antero-dorsal area of the jugal bones. Two pairs of scutes that also overlap the maxillae, the subocular and the maxillary scutes, are also located on that pair of bones. In addition, the anterior regions of the masseterian and of the parietal scutes also overlap the jugals. The masseterian posterior region, usually situated on the ventral area of the quadratojugal and quadrate, and the tympanic scute on the meatus quadrati, are not preserved (see Siebenrock 1902).

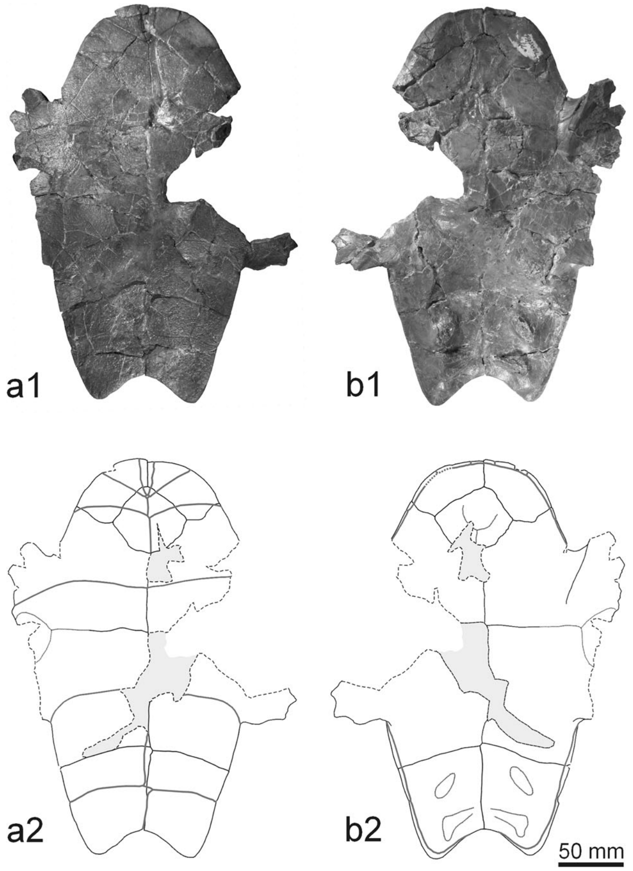

Fig. 8 Plastron of the specimen of *Neochelys laurenti* (Tong 1998) MNHN. F. casts 5818–5819 (Galoyer collection), from the early Ypresian of Saint-Papoul (Aude, France). **a** ventral view; **b** dorsal view

Shells

Several isolated plates from Saint-Papoul, corresponding to both the carapace and the plastron, were described without figures and attributed to an undetermined representative of Podocnemididae (Tong 1998), being considered as "rather different from what is known in *Neochelys* and *Erymnochelys.*" Lapparent de Broin (2001) indicated that several complete shells of *Neochelys* were found in the type locality of '*P.*' *laurenti*. In her comparative study of the Silveirinha material (early Eocene of Portugal), Lapparent de Broin (2003) noted some characters visible in the Saint-Papoul shells without including collection numbers, a detailed description, or drawings. In fact, one of these shells

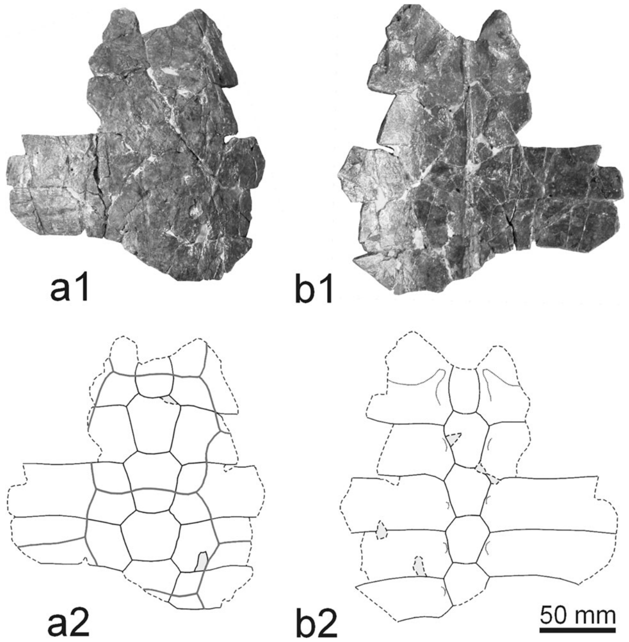

Fig. 9 Carapace of the specimen of *Neochelys laurenti* (Tong 1998) MNHN.F.SPP 28, from the early Ypresian of Saint-Papoul (Aude, France). **a** dorsal view; **b** ventral view

(specimen MNHN.F.SPP 28) was associated with skull MNHN.F.SPP 29. This Saint-Papoul material was also taken into consideration in Pérez-García and Lapparent de Broin (2013) for the study of *N. liriae*. This species is only known from the shell, so all the shell characters were taken into account, but only synthetically, as in Lapparent de Broin (2003). The detailed study of three of these Saint-Papoul shells (Figs. 5, 6, 7, 8, 9, 10 and 11) allows a description of their anatomy for the first time and the recognition of intraspecific variability in the taxon recognized as *Neochelys laurenti.*

Fine, short dichotomic sulci, some joined into small polygons, are identified in several areas of the shells assigned to *N. laurenti*. In addition, numerous shallow grooves corresponding to growth rings are seen in the carapaces. The preservation of some specimens also reveals microgranulation of the bone surface structure (Fig. 11).

The size of these three shells is close to 350 mm, and they are recognized as adult individuals, presenting firmly sutured plates. Two of them are nearly complete shells, whereas the third preserves the medial dorsal part of the carapace and most of the plastron.

Carapace: The general morphology of the two complete carapaces we attribute to *Neochelys laurenti* is elliptical, one being more quadrangular (Fig. 7) and the other more ovoid (Fig. 5). The anterior margin of the taxon varies from straight (Fig. 7) to slightly notched (Fig. 5), the notch being very shallow and located on the anterior margin of the nuchal plate and of the antero-medial margin of the peripherals 1. Its lateral margins are curved at the level of the peripherals 2. The posterior shell region is expanded, with the posterior peripherals longer than wide. These peripherals and the pygal have a slight protruding angle at the distal limit between the marginals. The nuchal plate is approximately as long as wide. However, the first pair of peripherals is noticeably longer than wide. The species has seven neurals. The first one is rectangular, longer than wide, with convex lateral margins. Neurals 2–6 are hexagonal, wider than long. The width/length ratio increases towards the posterior region of the neural series. The most anterior hexagonal neurals have shorter antero-lateral margins than the postero-lateral ones. The lengths of both margins are similar to each other in the posterior neurals. The most posterior neural is pentagonal, wider than long.

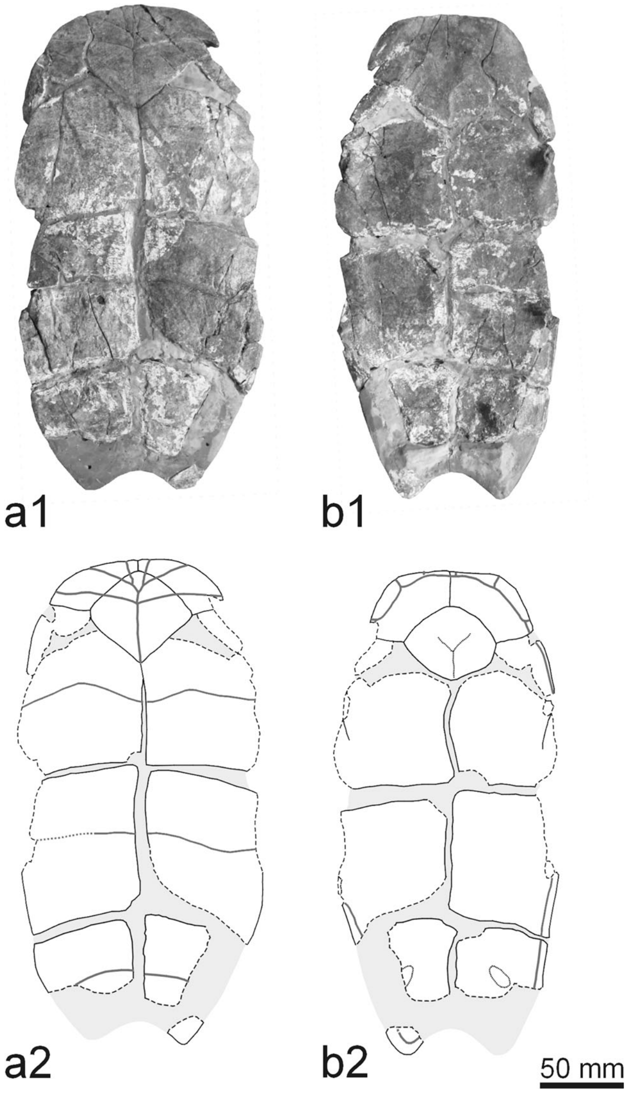

Fig. 10 Plastron of the specimen of *Neochelys laurenti* (Tong 1998) MNHN.F.SPP 28, from the early Ypresian of Saint-Papoul (Aude, France). **a** ventral view; **b** dorsal view

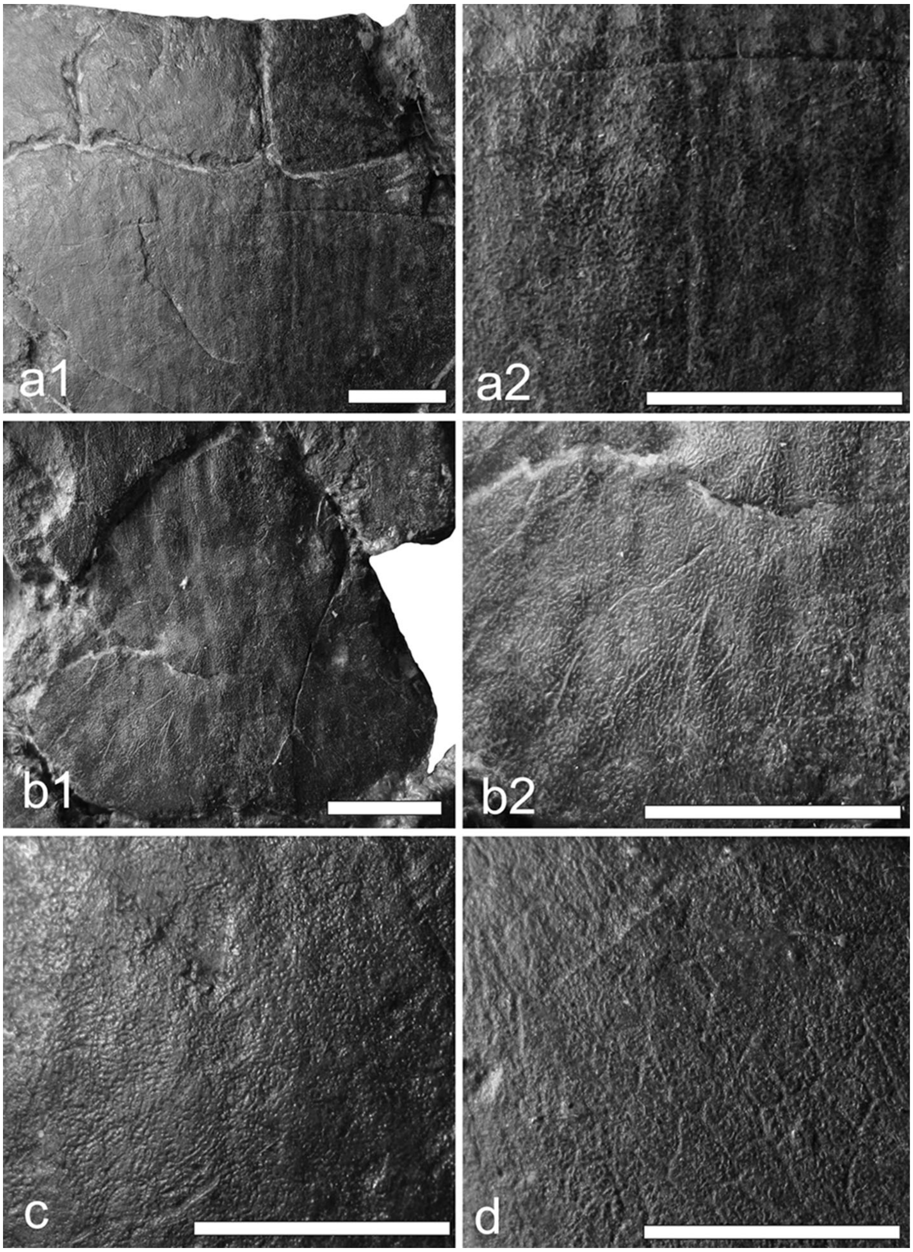

Fig. 11 Details of the outer surface of the shell of *Neochelys laurenti* (Tong 1998) MNHN.F.SPP 30, observed on the nuchal (**a**), suprapygal (**b**), lateral region of the third left costal (**c**), and lateral region of the right hypoplastron. Scale bars equal 10 mm

The last two pairs of costals are in contact sagittally. The length of the first pair of costals is slightly shorter than twice that of the second pair. The taxon has a single pentagonal suprapygal plate. Its width is similar or slightly greater than its length.

In the ventral view, the scar for the carapace suture with the axillary processes is present on the distal half of the costals 1. The anterior part of the processes are sutured with the anterior half of the peripherals 3. The inguinal processes are sutured with the lateral side of the costals 5 and the anteromedial area of the peripherals 8. The scars for the sutures of the ilia are located on costals 7 and 8 (Figs. 5b, 7b).

This species lacks a cervical scute. The vertebral 1 overlaps at least the posterior two-thirds of the nuchal plate, and the medial region of the first pair of peripherals. The pleural scutes generally overlap more than one-quarter of the width of the peripheral plates. The vertebral 5 overlaps the anterior third of the pygal plate and of the medial region of the last pair of peripherals. Marginals 1 are wider than long. However, the ratio between both dimensions varies among the analysed specimens. Therefore, the length of the latero-anterior margin of the nuchal plate covered by these scutes varies, but it is always less than half its length. The widest vertebral scutes are the second and the third ones, with a similar width.

Vertebral 1 is lyre-shaped and posteriorly variable in width (wider than the nuchal) (compare Figs. 5a and 7a). Vertebrals 2, 3, and 4 are hexagonal, the second one with the anterior and posterior margins being similar in width. Vertebral 4 has an anterior margin more than 2.5 times wider than the posterior one. Vertebral 5 is more than three times wider at its posterior border than at its anterior one. It overlaps the anterior-medial margin of the peripherals 10 (Fig. 5a2).

Plastron: The anterior plastral lobe is wider and shorter than the posterior one and both lobes are wider than long. The length of the bridge is greater than that of each of these lobes. The anterior lobe is subrounded, changing its curvature in the region covered by the gular scutes (extragulars sensu Hutchison and Bramble 1981), where it becomes transverse. The lateral margins of the posterior plastral lobe moderately converge towards the posterior region, being rounded in some specimens but substraight in others. The anal notch is relatively wide, between two and three times wider than long, and wider than each xiphiplastron at the femoro-anal sulcus. Its lateral margins may be straight or slightly rounded.

The maximal width of the intergular scute (gular sensu Hutchison and Bramble 1981) is at the anterior plastral margin. This width is less than that of each gular, and may even be less than half the width of these scutes. The intergular scute overlaps less than one-third of the length of the entoplastron. It is as long as the gulars in one specimen (Fig. 8a), but longer in the two others (Figs. 6a, 10a). This scute does not touch the pectorals due to the long medial contact of the humerals. The gular scutes posteriorly overlap the entoplastron. The humero-pectoral sulcus is significantly anterior to the epi-hyoplastral suture in two specimens (Fig. 10a), laterally crossing the suture in the third one (Fig. 8a). The order of the plastral scutes, from longer to shorter in the axial plane, is: abdominals, femorals, pectorals, anals or intergulars, and humerals. The intergular scute is barely longer than the anals in one specimen (Fig. 6a), but it is shorter in the other specimen in which the xiphiplastra are fully preserved (Fig. 8a). The pectoral scutes do not overlap the mesoplastra. The marginals overlap the lateral region of this pair of plates.

There is a relatively well developed dorsal epiplastral lip covered by the dorsal scute rim, being especially large near the gularo-humeral sulcus. This lip is very short and flat in the medial region of the epiplastra. The width of the femoral and anal scute rim covering the latero-visceral region of the xiphiplastra is narrower in one specimen (Fig. 8b) than in the other (Fig. 6b). In all these specimens, the width of the scutes covering the posteriormost tip of the xiphiplastra is greater and deeper than in other areas of the notch.

Cervical vertebra

A vertebra from Saint-Papoul (MNHN.F.SPP 31) is identified (Fig. 12). It is an almost complete cervical vertebra, only lacking the tip of the left transverse apophysis. It is elongated, longer than wide (20.5 mm long and 10 mm high; centrum 17 mm long). The centrum has formed articulations, corresponding to a procoelous vertebra. The cotyle (anterior end of the centrum) is triangular, barely wider than high and the posterior condyle is oval, moderately wider than high. A ventral tubercle is situated just behind the cotyle, forming the anterior and more developed part of the concave ventral crest, which is reduced in height up to the level of the condyle. Two separate ventral tuberosities lie just below and behind the posterior condyle. Both prezygapophyses are separate, facing mediodorsally. The neural arch extends posterodorsally, ending in a unique, high pedicel. It curves sharply and is divided into two parts that bear the (widely separated) postzygapophyses, each ventrally facing and covered by a tuberosity. The neural spine is reduced to a fine crest. The postzygapophyses are longer than the prezygapophyses. This vertebra has laterally well-developed transverse apophyses occurring as wings issuing from the boundary neural arch-

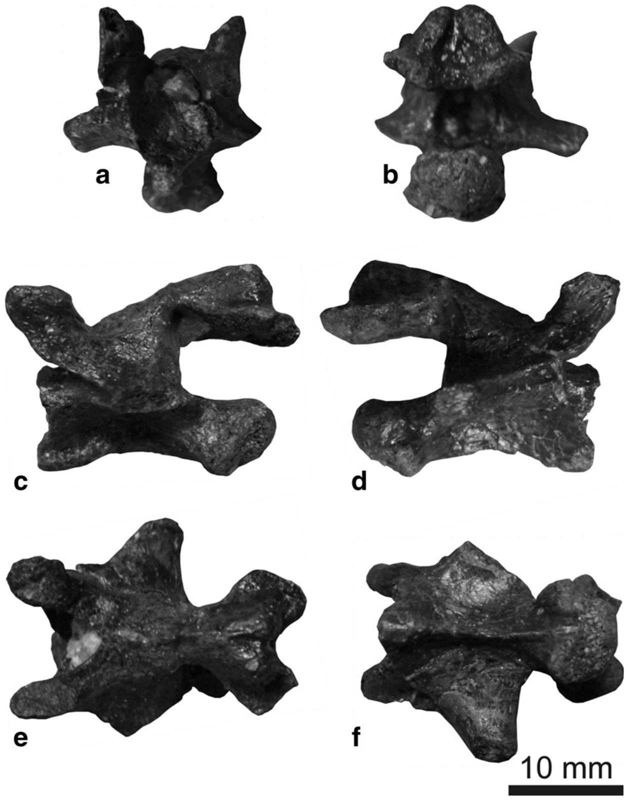

Fig. 12 MNHN.F.SPP 31, cervical vertebra of cf. *Neochelys laurenti*, from the early Ypresian of Saint-Papoul (Aude, France), in anterior (**a**), posterior (**b**), left lateral (**c**), right lateral (**d**), dorsal (**e**), and ventral (**f**) views

centrum, anteriorly beginning below the base of each prezygapophysis, and extending along the mid-length section of the centrum, and they are posteriorly directed with an oblique anterior border and a barely concave posterior border. The centrum is narrow behind the transverse apophyses, narrower than the cotyle and condyle. The ventral crest reduction, the relatively significant height and well-defined curvature of the neural arch pedicel, and the separated tubercles above the postzygapophyses indicate that it is possibly a 7th cervical vertebra.

Discussion

Comparison of *Neochelys* with the other known podocnemidids

Neochelys was defined by the species *N. capellinii*, only known from shells (Zigno 1889). de Broin (1977) defined *N. arenarum*, a species to which she could assign both postcranial material (especially shells and isolated plate and bone elements) and skulls. Therefore, in that paper, the cranial material of *Neochelys* was studied for the first time, and the known postcranial material of this genus was reviewed. Subsequently, cranial and postcranial material from other members of *Neochelys* was recognized, allowing a better understanding of this taxon (see Pérez-García and Lapparent de Broin 2013 and references therein). We show here that the new skull from Saint-Papoul, MNHN.F.SPP 29 (Figs. 2b, 3b, 4a), is in fact the only pleurodiran taxon so far recognized in that locality: '*Papoulemys*' *laurenti, Papoulemys* being a junior synonym of *Neochelys* (Lapparent de Broin, 2001, 2003; Pérez-García and Lapparent de Broin 2013). This new skull specimen is associated with a shell, MNHN.F.SPP 28 (Figs. 9, 10). The study of this shell, as well as that of other shells from the same locality, and corresponding to the same taxon, allows the reallocation of the species '*P.*' *laurenti* to the taxon *Neochelys*. A new diagnosis for *Neochelys* is proposed in this work. The information so far available on the European cranial material assigned to *Neochelys* was very limited. However, a review of the (generally poorly described) material, and the observation of undescribed specimens corresponding to several species from various countries and ages, allows us to refute the validity of the characters used to recognize '*Papoulemys*' as a genus different from *Neochelys*. The study of both cranial and postcranial material from Saint-Papoul leads us to conclude that all this material belongs to only one species: *Neochelys laurenti—Papoulemys* being recognized as a junior synonym of *Neochelys*. The availability of characters in *Neochelys* allows a confirmation of its assignment to Erymnochelyinae Broin 1988 (sensu Lapparent de Broin 2000), that is, to a member of the magnatribe Erymnochelydand in Gaffney et al. 2011 (but not including *Peltocephalus dumerilianus* and *Caninemys tridentata* Meylan et al. 2009, taxa that we allocate to the South American group of podocnemidid species), and not belonging to the tribe Stereogenyini sensu Gaffney et al. 2011 (see the papers of both authors). *Neochelys* is attributed to Erymnochelyinae based on several characters, among which the most relevant is the presence of an inner enlargement of the podocnemidid cavum pterygoidei, which has a large anterior opening in the sulcus cavernosus, with the disappearance of most of the base of the prootic. This character is present in all the species of this group with a sufficiently known skull, comprising *Neochelys arenarum* (e.g., MNHN.F.RI 4), *Erymnochelys madagascariensis* and the Stereogenyini *Mogharemys blanckenhorni*, *Cordichelys antiqua*, *Latentemys plowdeni*, *Brontochelys gaffneyi*, *Lemurchelys diasphax*, *Stereogenys cromeri*, and *Bairdemys* spp. The inner anterior enlargement also exists in *Peltocephalus dumerilianus* but without the considerable prootic inner erosion. All the characters included in the new diagnosis of *Neochelys* are compared here with those present in the other known members of Podocnemididae.

Skull: *Neochelys* differs from other podocnemidids in a conjunction of diagnostic characters (see diagnosis). The skull characters diagnostic of the genus *Neochelys* are known in species identified as belonging to the genus by their shell, in conformity with the type species *N. capellinii*. They are: *N. arenarum, N. franzeni, N. salmanticensis*, and *N. zamorensis* (the skulls of these last two species are unpublished but under study). The relatively narrow skull of *Neochelys* differs from that of taxa such as *Bairdemys venezuelensis* (Wood and Díaz de Gamero 1971) and *Caninemys tridentata*. The presence of anteriorly and posteriorly rounded lateral margins of the skull is shared with *Erymnochelys madagascariensis*, but not with '*Neochelys*' *fajumensis* (Andrews 1903) (sensu Gaffney et al. 2011) or with the representatives of *Podocnemis* Wagler 1830. The absence of a skull beak differs from the condition observed in *Peltocephalus dumerilianus* and *Erymnochelys madagascariensis*. Although the snout of *Neochelys* is prominent, as in several podocnemidids (e.g., *Erymnochelys madagascariensis*, *Peltocephalus dumerilianus*, *Stereogenys cromeri* Andrews 1901, *Dacquemys paleomorpha* Williams 1954, *Bairdemys sanchezi* Gaffney et al. 2008, and *Carbonemys cofrinii* Cadena et al. 2012), its narrow morphology and parallel edges is exclusive to *Neochelys*. The length of the orbits in *Neochelys* (circa 20 % of the total skull length) is greater than that present in some podocnemidids such as *Erymnochelys madagascariensis*, *Peltocephalus dumerilianus*, *Podocnemis bassleri* Williams 1956, *Caninemys tridentata*, *Bairdemys sanchezi*, and *Bairdemys venezuelensis*. The height of the orbits in

Neochelys, higher than the suborbital space, differs from the condition in *Peltocephalus dumerilianus*, the representatives of *Bairdemys* Gaffney and Wood 2002, *Podocnemis bassleri* and, especially, *Caninemys tridentata*. *Neochelys* orbits are located more laterally than in most known Podocnemididae members (e.g., *Erymnochelys madagascariensis* and '*Neochelys*' *fajumensis*), this condition being similar to that of *Latentemys plowdeni* Gaffney et al. 2011 and *Carbonemys cofrinii*, but less lateral than in *Dacquemys paleomorpha*. The *Neochelys* interorbital space is relatively wider than that of most South American podocnemidids (excluding *Peltocephalus dumerilianus*, *Caninemys tridentata*, and *Carbonemys cofrinii*), but it is narrower than that of the African '*Neochelys*' *fajumensis*, *Dacquemys paleomorpha*, *Stereogenys cromeri*, and *Erymnochelys madagascariensis*. A well-developed apomorphic interorbital groove, such as that found in *Podocnemis* or such as that (poorly and differently developed) in some '*Neochelys*' *fajumensis* specimens, is absent in *Neochelys*. The prefrontal-frontal contact of *Neochelys* is transverse to sinuous, lacking the medial prominence present in '*Neochelys*' *fajumensis*. The very short temporal emargination of *Neochelys* differs from that of the other podocnemidids except *Dacquemys paleomorpha*, a taxon with an exceptional squamosal-parietal posterior prolongation of the skull roof. The maximal length of the temporal emargination of *Neochelys* is located in its lateral region, as in *Erymnochelys madagascariensis*, but not in '*Neochelys*' *fajumensis* or in the South American podocnemidids, except *Peltocephalus dumerilianus*. The primitive absence of contact between the parietals and the jugals, resulting in contact between the postorbitals and the quadratojugals, is shared with the other podocnemidids, except *Podocnemis* (with an apomorphic condition corresponding to the parietal-jugal contact). *Neochelys* shares with taxa such as *Podocnemis* and *Peltocephalus dumerilianus* the presence of a parietal-quadratojugal length longer than the total length of the postorbitals. However, the length of the postorbitals is considerably greater than that of the parietal-quadratojugal suture in the South American Cretaceous and Paleocene podocnemidids (i.e., *Lapparentemys vilavilensis* (Broin 1971), *Peiropemys mezzalirai* Gaffney et al. 2011, *Bauruemys elegans* (Suárez 1969)), and slightly greater than the suture in the case of '*Neochelys*' *fajumensis*. That character is recognized as subject to interspecific variability in *Bairdemys*, the postorbitals being longer than the parietal-quadratojugal suture in the case of *Bairdemys venezuelensis*, but shorter in *Bairdemys hartsteini* Gaffney and Wood 2002. The horizontal plate along the ventral edge of the crista supraoccipitalis of *Neochelys* is very poorly developed. A more developed plate is present in taxa such as *Peltocephalus dumerilianus*, *Erymnochelys madagascariensis*, and '*Neochelys*' *fajumensis*. Further development of this structure is experienced by *Bairdemys venezuelensis*. The cheek emargination of *Neochelys* is lower than that of *Podocnemis*, *Peiropemys mezzalirai*, *Bauruemys elegans*, and *Lapparentemys vilavilensis*, but higher than that of *Erymnochelys madagascariensis* and *Peltocephalus dumerilianus*. Its rectangular to rounded morphology differs from that in *Erymnochelys madagascariensis* and in *Peltocephalus dumerilianus*, taxa in which it has been secondarily filled, forming a small, angular notch. *Neochelys* lacks the well-developed middle-posterior expansion of the triturating surface (serving as a secondary palate) present in members of the subtribe Stereogenyina Gaffney et al. 2011: *Cordichelys antiqua* (Andrews 1903), *Latentemys plowdeni*, *Shweboemys pilgrimi* Swinton 1939, *Brontochelys gaffneyi* (Wood 1970), *Lemurchelus diasphax* Gaffney et al. 2011, *Stereogenys cromeri*, the representatives of *Bairdemys* and, with more moderate development, in '*Shweboemys*' *pisdurensis* (Jain 1977). Furthermore, *Neochelys* lacks the accessory ridges in the triturating surface present in the members of *Podocnemis*, *Dacquemys paleomorpha*, *Mogharemys blanckenhorni* (Dacqué 1912), *Peltocephalus dumerilianus* and (poorly developed) in *Erymnochelys madagascariensis* and '*Neochelys*' *fajumensis*. The derived absence of a vomer differs from the condition observed in some species of *Podocnemis* and in some taxa from the Cretaceous and Paleocene of South America (e.g., *Lapparentemys vilavilensis*, *Peiropemys mezzalirai*, and *Bauruemys elegans*), as well as in *Caninemys tridentata*. The presence of a shallow fossa precolumellaris is shared by *Neochelys* and *Erymnochelys madagascariensis*. However, this fossa is narrow in *Neochelys*, as in *Peltocephalus dumerilianus* where it is also longer. A medial concavity (an inflexion between two arcs of a circle) on the anterior margin of the interparietal scute of *Neochelys* is shared with *Dacquemys paleomorpha* and *Bauruemys elegans*, contrasting with the convexity in taxa such as '*Neochelys*' *fajumensis*, *Peiropemys mezzalirai*, and *Mogharemys blanckenhorni*. The poorly expanded horizontal occipital shelf of *Neochelys* is similar to that observed in *Erymnochelys madagascariensis*, in contrast to its absence in *Peltocephalus dumerilianus* or its great development in many other pocnemidids such as all the extant species of *Podocnemis*.

Lower jaw: The lower jaw of *Neochelys* is known in *N. arenarum*, *N. salmanticensis*, and *N. zamorensis* and partially in *N. franzeni* (the lower jaw of *N. salmanticensis* and *N. zamorensis* being unpublished, but under study). The lack of a well-developed beak in the lower jaw of *Neochelys* differs from the condition in *Peltocephalus dumerilianus* and *Erymnochelys madagascariensis* and, probably (based on a premaxillary depression), in *Dacquemys paleomorpha*. The mandibular symphysis of *Neochelys* is shorter than that of *Peltocephalus dumerilianus*, being similar in length to that of *Erymnochelys madagascariensis*. Its symphyseal triturating surface is shorter than that of *Peltocephalus dumerilianus* and *Erymnochelys madagascariensis*, being similar to that of *Lapparentemys vilavilensis* and *Bauruemys elegans*. Its posterior triturating surface is wider than in *Bauruemys elegans*, being similar to that of *Lapparentemys vilavilensis*. The lingual symphyseal angle is rounded, as in *Lapparentemys vilavilensis* and *Bauruemys elegans*. The chorda tympani of *Neochelys* is enclosed in the middle of the antero-dorsal border of a well-developed processus retroarticularis, as in *Peltocephalus dumerilianus* and *Erymnochelys madagascariensis*, this foramen being very lateral in *Bauruemys elegans* (almost medially open in some specimens), and open in *Podocnemis* and in *Lapparentemys vilavilensis*.

Carapace: Shells are compared with those of pleurodiran genera such as some primitive Late Jurassic and Cretaceous ones and all podocnemidids (Lapparent de Broin 2001; Lapparent de Broin et al. 2004; Gaffney et al. 2006, 2011), with a choice of characters of representative taxa. The known range of sizes for the shells of *Neochelys* (see the list of species known by the shell, and the table of characters in Pérez-García and Lapparent de Broin 2013) is similar to that of other genera represented by various species, such as the extant *Podocnemis*, with some species less than 350 mm in maximum length (e.g., *Podocnemis erythrocephala* (Spix 1824) and *P. sextuberculata* Cornalia 1849), but also with much larger species, as is the case of *P. expansa* (Schweigger 1812), which can exceed 850 mm. The total length/posterior width ratio of the nuchal plate of *Neochelys* (0.7–0.95) is moderately larger than in *Bairdemys healeyorum* Weems and Knight 2013, *Cordichelys antiqua*, and *Brasilemys josai* Lapparent de Broin 2000 (circa 0.65), and larger than in more primitive taxa such as *Platychelys oberndorferi* Wagner 1853 (a pleurodiran turtle prior to the derivation of Pelomedusoides and chelids), *Yaminuechelys gasparinii* de la Fuente et al. 2001 (a primitive chelid), and aff. *Platycheloides nyasae* Haughton 1928 from Gadoufaoua (0.33–0.5) (a primitive Pelomedusoides). The maximal length of the costals 1 of *Neochelys*, almost twice that of the costals 2, differs from the condition of short costals 1 observed in the Stereogenyina *Stereogenys libyca* Andrews 1903, *Stereogenys cromeri*, *Cordichelys antiqua*, and *Bairdemys healeyorum*, but also in the primitive aff. *Platycheloides nyasae* and *Teneremys lapparenti* (Broin 1980). The absence of a medial keel differentiates *Neochelys* (except in *N. franzeni*) from representatives of *Podocnemis* such as *P. vogli* Müller 1935, *P. cayennensis* (Schweigger 1812) (i.e., *P. unifilis* Troschel 1848), *P. sextuberculata*, and *P. negrii* Carvalho et al. 2002, as well as *Kenyemys williamsi* Wood 1983. *Platychelys oberndorferi* has three well-developed and strongly tuberculated keels, while a single more or less developed and slightly tuberculated keel is present in *Teneremys lapparenti* and in *Pelusios* (Pelomedusidae); aff. *Platycheloides nyasae* lacks keels. *Podocnemis sextuberculata* and *Stereogenys libyca* differ from *Neochelys* because the medial contact of the costal series exclusively occurs between the plates of the last pair. Although *Neochelys* shares with *Erymnochelys madagascariensis* the presence of posterior peripheral points, they are not developed in *Kenyemys williamsi* or *Turkanemys pattersoni* Wood (2003). The axillary processes of the shells of *Neochelys laurenti* and those of *Neochelys eocaenica* are in contact with the distal half of the costals 1 and with the anterior half of the peripherals 3. These processes reach the boundary between the peripherals 2 and 3 in *Neochelys arenarum*. The condition observed in other Podocnemididae members falls within this range of variability. However, these processes are in contact with the posterior region of the peripherals 3 in *Teneremys lapparenti*. The inguinal processes of all these taxa are in contact with the lateral region of the costals 5 and with the peripherals 8.

The presence of a vertebral 1 wider than the nuchal differs from the condition observed in *Kenyemys williamsi*, *Stereogenys libyca*, and *Bairdemys healeyorum*. The presence of marginals 1 shorter than half of the length of the lateral nuchal margins, observed in *Neochelys*, is shared with some podocnemidids such as '*Podocnemis*' *argentinensis* Cattoi and Freiburg (1958), *Erymnochelys madagascariensis*, '*Podocnemis*' *aegyptiaca* Andrews (1900), *Peltocephalus dumerilianus*, *Cordichelys antiqua*, '*Neochelys*' *fayumensis*, '*Stereogenys*' *podocnemoides* (Reinach 1903), and *Stereogenys libyca*, as well as with some more primitive forms (e.g., *Brasilemys josai*, *Teneremys lapparenti*, aff. *Platycheloides nyasae*). This condition differs from that present in taxa such as the members of *Bairdemys*, *Lapparentemys vilavilensis*, *Cerrejonemys wayuunaiki* Cadena et al. (2010), and also in *Yaminuechelys gasparinii* (a primitive chelid with a short, wide nuchal and cervical, representative of the primary condition). This condition is variable in *Platychelys oberndorferi*. The visceral region of the marginals 2 and 3 of *Neochelys* is longer than in *Stereogenys cromeri*, but similar to that in most podocnemidids.

Plastron: The lateral margins of the plastral lobes of *Neochelys* are much less convergent than in primitive taxa such as *Platychelys oberndorferi* and *Teneremys lapparenti*, and also than in *Cordichelys antiqua*, the members of *Bairdemys* and *Albertwoodemys testudinum* Gaffney et al. (2011). The anterior plastral lobe of *Neochelys* is subtrapezoidal (with angular or rounded edges) as in *Stereogenys cromeri* and *Stereogenys libyca*, but without an anterior concavity. *Neochelys* differs from forms with a shorter and very broad base of the anterior lobe, such as *Cordichelys antiqua*, members of *Bairdemys*, and *Albertwoodemys testudinum*. The anterior lobe of *Neochelys* is shorter than the posterior, both lobes being shorter than the bridge, unlike the condition observed in primitive taxa, with a short bridge (e.g., *Platychelys oberndorferi*, *Teneremys lapparenti*).

Neochelys has a relatively short epiplastral symphysis, unlike the long symphysis of *Stereogenys libyca* and *Stereogenys cromeri*, and the moderately long symphysis of '*Stereogenys*' *podocnemoides*. However, it is longer than that of *Cordichelys antiqua* and *Bairdemys healeyorum*. *Neochelys* is characterized by a large entoplastron posteriorly close to the axillary notch, unlike those of *Podocnemis*, *Peltocephalus*, and some taxa from the late Cretaceous of South America such as *Bauruemys elegans*, '*Podocnemis*' *brasiliensis* Staesche (1937), and *Roxochelys wanderleyi* Price (1953). The posterior plastral lobe in *Neochelys* lacks the well-developed notches in the area of contact with the femoro-anal sulcus observed in *Stereogenys libyca* and in some species of *Podocnemis* such as *P. expansa* and *P. pritchardi* Wood (1997). The anal notch of *Neochelys* is wide, unlike that of *Stereogenys libyca*, but it is not deep in contrast to that of *Albertwoodemys testudinum*. The iliac scars of *Neochelys* overlap the costals 7 and 8, but are not in contact with the suprapygal plate as in most other podocnemidids, differing from the primitive condition seen in *Platychelys oberndorferi*, where not only do these scars overlap the pygal plate, but also the peripherals 11.

The intergular of *Neochelys* is longer than the gulars or sometimes as long, unlike in *Erymnochelys madagascariensis*, 'aff. *Erymnochelys*' *eremberti* (see in Merle 2008), '*Neochelys*' *fajumensis*, '*Podocnemis*' *aegyptiaca*, *Kenyemys williamsi*, and *Turkanemys pattersoni*; in all these taxa, the gulars are in contact with the midline, posteriorly to the short intergular, characterizing the *Erymnochelys* group (Broin 1988; Lapparent de Broin 2000). The presence of an intergular always separating the gulars is shared with primitive taxa (such as *Platychelys*, aff. *Platycheloides nyasae*, *Teneremys lapparenti*), fossil and extant chelids and pelomedusids, and all the other podocnemidids. The presence of an intergular overlapping less than half of the entoplastral length is shared with forms such as '*Podocnemis*' *argentinensis*, '*Stereogenys*' *podocnemoides*, the representatives of *Bairdemys*, '*Podocnemis*' *bramlyi* Fourteau (1920), *Cordichelys antiqua*, all the extant species of *Podocnemis* except *P. sextuberculata*, *Peltocephalus dumerilianus*, *Roxochelys wanderleyi*, *Bauruemys elegans*, '*Podocnemis*' *brasiliensis* Staesche (1937), *Portezueloemys patagonica* de la Fuente (2003), and *Lapparentemys vilavilensis*. The arrangement of the humero-pectoral sulcus of *Neochelys*, usually considerably anterior to the epi-hyoplastral suture (except often in the lateral extremity), is shared with taxa such as '*Stereogenys*' *podocnemoides*, *Stereogenys libyca*, *S. cromeri*, the species of *Bairdemys*, *Albertwoodemys testudinum*, '*Podocnemis*' *bramlyi*, *Cordichelys antiqua*, *Kenyemys williamsi*, *Erymnochelys madagascariensis*, '*Neochelys*' *fajumensis*, '*Podocnemis*' *aegyptiaca*, and 'aff. *Erymnochelys*' *eremberti*. Although that sulcus is also anterior to the epi-hyoplastral suture on the epiplastral medial part in adults of *Lapparentemys vilavilensis*, the lateral distance between the sulcus and suture is greater than that observed in the former taxa and the sulcus is distinctly sinuous. That sulcus is approximately on the epi-hyoplastral suture in several members of *Podocnemis* (*P. expansa*, *P. vogli*, *P. cayennensis*, *P. lewyana*). It is markedly posterior to the suture in some podocnemidids (e.g., *Peltocephalus dumerilianus*, '*Podocnemis*' *brasiliensis*, *Roxochelys wanderleyi*), and posterior to the entoplastron in more primitive taxa (e.g., *Platychelys*, aff. *Platycheloides nyasae* and *Teneremys lapparenti*) and pelomedusids. The occurrence of the postero-lateral boundary of the pectorals near the anterior margin of the mesoplastra, observed in *Neochelys*, differs from the condition in primitive taxa (e.g., *Teneremys lapparenti*) and in *Peltocephalus dumerilianus*, taxa that have a long overlap of the pectoral scutes on the mesoplastra. It also differs from the condition that characterizes some taxa such as *Albertwoodemys testudinum*, the representatives of *Bairdemys*, and *Stereogenys libyca*, in which the distance between the pectoral scutes and the mesoplastra is relatively large. The very short dorsal epiplastral lip relative to the epiplastral symphysis of *Neochelys* contrasts with the long lip present in '*Stereogenys*' *podocnemoides*, *Stereogenys libyca*, *S. cromeri*, '*Neochelys*' *fajumensis* and, especially, *Albertwoodemys testudinum*.

Taxonomic implications of the specimens from the early Eocene of Saint-Papoul

Comparison of the skull of Neochelys laurenti *with those of other members of* Neochelys: Skull MNHN.F.SPP 29 (Figs. 2b, 3b, 4a) shares with the '*Papoulemys*' *laurenti* holotype most of the characters used by Tong (1998) in the diagnosis of the *Papoulemys* genus (dorsolaterally directed orbits, relatively wide and flat interorbital space, smooth triturating surface without additional ridges, and weak temporal emargination), in particular those that differentiate '*Papoulemys*' and *Neochelys* according to Tong (1998) (occipital condyle comprised mainly of the exoccipitals; and the presence of a large, longer than high cheek emargination, preventing contact between the jugal and the quadrate). However, some differences are observed in other characters of that diagnosis (see below).

As indicated, the European Eocene record includes several species of *Neochelys*. However, the information provided by the cranial material is very limited. *N. arenarum* (early Ypresian, MP7, of Rians, Var, France) is the only species in which the skull has been described in detail. de Broin (1977) attributed four unprepared skulls and a complete prepared one to that species. The latter, MNHN.F.RI 6, was thoroughly figured (de Broin 1977: Figs. 13–17, Pl. II Figs. 1, 2). Schleich (1993) defined *N. franzeni*, to which were attributed two skeletons with the skull, from the early Lutetian (MP11) of Messel (Hessen, Germany) (SMF ME1091 and SMF ME 715). However, the information provided on their postmortem flattened skulls was, on the whole, limited to their width and length dimensions and to the dorsal shape of the skull, with the morphology of the interparietal scute. We also identify a third specimen of *N. franzeni*, from the type locality, the unpublished skeleton SMF ME1267, also preserving a flattened skull and compatible with the two type specimens. In an informative guide, Jiménez Fuentes et al. (1988) illustrated a lateral view of a *Neochelys* sp. skull from Coreses (Eocene of Zamora, Spain). Jiménez Fuentes et al. (1988) did not provide any information on that specimen, which is currently under study. Many unpublished skulls that may correspond to several *Neochelys* species (now under study) have been found in several Spanish localities, both in Zamora and in Salamanca. A basisphenoid of *Neochelys* sp. from the Portuguese locality of Silveirinha (early Ypresian, MP7, Figueira da Foz, Portugal), found with some carapace remains, has been described and discussed by Lapparent de Broin (2003).

The only skull of *N. arenarum* so far figured was laterally bent and partly flattened (Figs. 2c, 3c). However, the other skulls of this taxon from the type locality were subsequently more or less completely prepared, enabling observation of the cavum pterygoideum inner entrance, justifying the classification of the genus in the Erymnochelyinae (Lapparent de Broin 2000: 70). A complete and undistorted skull of *N. arenarum* (from its type locality and corresponding to one of those cited by de Broin 1977) has been prepared and is analysed here (Figs. 2d, 3d, and 4b). This specimen allows a better understanding of the morphology of this taxon's skull and of its elements. The identification of more than one skull of both '*P.*' *laurenti* and *N. arenarum* reveals intraspecific variability in some characters.

In the absence of comparable skulls belonging to different species of *Neochelys*, it was not possible to decide if the character states recognized by de Broin (1977) in *N. arenarum* were unique for that species or shared by all the representatives of *Neochelys*. Therefore, de Broin (1977) did not include any cranial characters in the diagnosis of this genus and species, and Tong (1998) defined '*Papoulemys*' exclusively based on the skull.

All the characters shared by the '*Papoulemys*' holotype and the skull of Saint-Papoul MNHN.F.SPP 29, and present in the diagnosis proposed by Tong (1998), are also found in some or all the known skulls of *Neochelys*.

The occipital condyle of the skull of *N. arenarum* analysed here (MNHN.F.RI 7) is broken, so the percentage of this element formed by the basioccipital is not known. The condition observed in the two specimens of '*P.*' *laurenti*, in which the occipital condyle is formed mainly by the exoccipitals, differs from that in the only known skull of *N. arenarum* preserving this region. The basioccipital of that skull represents more than the lower half of the condyle (see Fig. 17 in de Broin 1977). Tong (1998) considered '*P.*' *laurenti* as a form more closely related to *Erymnochelys* than to *Neochelys*, essentially on the basis of this feature. The observation of the occipital condyle of several unpublished (but now under study) skulls of *Neochelys* (some associated to *Neochelys* shells) from various Spanish localities confirms that both conditions are present in the genus *Neochelys*. A condition similar to that observed in *N. arenarum* is recognized in skull STUS 8636, from Valdegallina (Zamora, Spain), a locality where (in a preliminary way) the presence of a taxon potentially corresponding to *N. zamorensis* Jiménez Fuentes 1992 (or to a closely related form) has been recognized (Jiménez Fuentes 1993, 2003). The condition in the skull of skeleton STUS 12152, from the type locality of *N. salmanticensis* (Jiménez Fuentes 1968) (Teso de la Flecha, Salamanca), is similar to that recognized in the Saint-Papoul specimens. Several skulls of the same species will need to be studied to determine whether this character varies intraspecifically in representatives of the genus *Neochelys*. In fact, a high variability is known in some extant representatives of Podocnemididae, as in the case of the Erymnochelyinae member *Erymnochelys madagascariensis* (Grandidier 1867). The basioccipital of the *Erymnochelys madagascariensis* specimen MNHN.ZA.AC.1932-578 forms a wedge that prevents medial contact of the exoccipitals in a dorsal view, whereas the exoccipitals of MNHN.ZA.AC.1946–1971 and NHMUK 79.10.29.2 (de Broin 1977, pl. 3) are in contact medially along much of the dorsal surface of the occipital condyle. Some variability is also observed in *Peltocephalus dumerilianus* (Schweigger 1812), with specimens in which the basioccipital forms a very small part of the posterior region of the occipital condyle (e.g., MNHN.ZA.AC.609 and MNHN.ZR deposit, Lescure coll. specimen), and others in which it constitutes almost the entire lower third of the condyle (e.g., ZSM 16-0, cotype of *Emys macrocephala* Spix 1824; the specimen of the MCZ, H. coll., figured by de Broin 1977, pl. 4).

Due to deformation, the cheek emargination of the right side of the *N. arenarum* skull figured by de Broin (1977) seemed to be smaller and have a larger height/length ratio than that of the holotype of '*P.*' *laurenti*. However, its left side (Fig. 3c2) reveals that, as in the new specimen of *N. arenarum* and in other specimens described by de Broin (1977) but not figured (MNHN.F.RI 4, MNHN.F.RI 5), the morphology of this slight emargination is similar to that of '*P.*' *laurenti* and the other *Neochelys* representatives (Fig. 3).

The Saint-Papoul specimens share with other known representatives of *Neochelys* other characters of the diagnosis of '*P.*' *laurenti* proposed by Tong (1998): dorsolaterally directed orbits (as indicated above, more laterally than dorsally), a flat interorbital space, a smooth triturating surface without additional ridges, and weak temporal emargination. Information on the Saint-Papoul and Rians skulls presented here and observation of other European *Neochelys* skulls confirm the consideration of several character states proposed by Gaffney et al. (2011) as being shared by '*Papoulemys*' and *Neochelys* (some of these characters also being present in other Pleurodiran genera): an absent interorbital groove (primitively for the family), long parietal-quadratojugal contact (primitively), a relatively large postorbital (primitively), medial expansion of the triturating surface (derived), a median maxillary ridge (derived), absent vomer (derived), shallow fossa precolumellaris (rather primitive), a closed foramen jugulare posterius (derived), and an absent horizontal occipital shelf (primitive). Other characters are also considered here (see the diagnosis of *Neochelys* and comparisons of this genus with other podocnemidids).

Tong (1998) included two other characters in the diagnosis of '*Papoulemys*,' identified by her as being different from those in *Neochelys*: the long triangular skull shape in dorsal view and the presence of short prefontals that do not completely cover the apertura narium externa dorsally. Although Tong (1998) indicated that the holotype of '*Papoulemys*' is longer and narrower than that of the *N. arenarum* specimen figured by de Broin (1977), the skull of *N. arenarum* MNHN.F.RI 7 has a higher length/width ratio than in both specimens (Figs. 2d, 3d, 4b). The deformation affected the two skulls from Saint-Papoul differently, such that differences are observed not only in their length/width ratios, but also in the width of the interorbital space. The skulls of *N. franzeni* figured by Schleich (1993) (SMF ME1091 and ME 715, Plates 1 and 2) are also flattened, their width/length ratio being greater than the originals. Comparison between skulls from localities where several specimens are identified (e.g., Rians, Valdegallina) reveals that, in addition to the morphological differences arising from the deformation, there is intraspecific variability due both to ontogenetic development and, possibly, to individual variability. This deformation and variability accounts for the fact that, although MNHN.F.RI 6 differs from the holotype of '*P.*' *laurenti* in that the length of the palate from the snout to the palatine/pterygoid suture is shorter than the width of the palate at this suture, the condition in the skull from Rians MNHN.F.RI 7 is the same as that of the holotype of '*P.*' *laurenti*. A study of several specimens from the same locality (i.e., Saint-Papoul, Rians and, especially, Valdegallina) reveals that the prefrontal, the length of which in relation to the frontals is variable (longer in the skulls of '*P.*' *laurenti* and *N. arenarum* presented here than in the previously figured specimens of both taxa), may or may not completely cover the apertura narium externa dorsally.

Apart from several of the characters mentioned by Tong (1998) as being shared by '*Papoulemys*' and *Neochelys*, Gaffney et al. (2011) included in their emended diagnosis of '*Papoulemys*' two characters that they considered different from those in *Neochelys*. The first character was discussed above—the condylus occipitalis consisting mostly of exoccipitals. The other character is a larger quadratojugal exposure on the cheek. Probably due to deformation, this exposure is smaller in the lateral view of the *N. arenarum* specimen figured by de Broin (1977) than on the left side (Fig. 3c2). Moreover, this length is subject to intraspecific variability (e.g., Valdegallina specimens), the skull length in *N. arenarum* MNHN.F.RI 7 being similar to that of the holotype of '*P.*' *laurenti*.

The holotype of '*P.*' *laurenti* does not preserve the premaxillae and skull MNHN.F.SPP 29 (Saint-Papoul) confirms that this taxon lacked a bony beak. This condition is shared with the other representatives of *Neochelys*, but not with other members of Erymnochelyinae such as the extant *Erymnochelys madagascariensis* that Tong (1998) more closely approximated with '*Papoulemys*'.

Therefore, discoveries of new specimens from Saint-Papoul and from other European locations provide data to refute all the characters that supported '*P.*' *laurenti* as a species not assignable to the genus *Neochelys*. On the other hand, it is true that *Neochelys* shares some characters with *Erymnochelys* (see comparisons between *Neochelys* and the other podocnemidids) due to their probable close phylogenetic relationship.

The length of specimen MNHN.F.SPP 29 and of the holotype of '*P.*' *laurenti* is close to 80 mm in both specimens, significantly longer than that of *N. arenarum*. Other characters differentiating the skulls of the two species will probably be evidenced by revision of all the *Neochelys* species, including several species with hitherto unknown or poorly known skulls (in preparation). On the other hand, the available information on the shell characters is enough to show here several specific differences.

Gaffney et al. (2011) included both *Neochelys* (at the generic level) and '*Papoulemys*' in their phylogenetic analysis. *Neochelys* was coded not only considering *Neochelys arenarum*, but also the African '*Podocnemis*' *fajumensis* Andrews 1903, attributed by these authors to *Neochelys* (i.e., *Neochelys fajumensis*). Attributing this species to *Neochelys* is clearly refuted here by comparison of this taxon with other podocnemidids. A new diagnosis for *Neochelys* is proposed here, separating and disregarding the elements characteristic of '*N.*' *fajumensis*, a taxon that needs a new generic definition after a comparative revision. In the data matrix proposed by Gaffney et al. (2011), *Neochelys* and '*Papoulemys*' only differ in the coding of two skull characters. The first character is the absence of an interorbital groove in '*Papoulemys*' (character 3, state 0), in contrast to its presence in some *Neochelys* representatives (states 0 and 1) (due to its presence in '*Neochelys' fajumensis*). After refutation of '*N.*' *fajumensis* as a member of *Neochelys* (see above) and noting that the possible weak groove in a wide interorbital space of '*N.*' *fajumensis* is different in shape from the well delimited groove in the narrow interorbital space of *Podocnemis*, the new encoding for that character in *Neochelys* is the same as in '*Papoulemys*.' The other character is the occipital condyle (character 41), coded as 0 in *Neochelys* (composed of basioccipitals plus exoccipitals), but as 1 (exoccipitals only) in '*Papoulemys*.' However, as indicated above, the condition in '*Papoulemys*' is also shared with some members of *Neochelys*. Gaffney et al. (2011) did not code any character of the '*Papoulemys*' shell due to the absence of a recognized shell for that taxon. Encoding of the characters of the shells of *Neochelys laurenti* in the data matrix proposed by Gaffney et al. (2011) would not differ in any character from that encoded by the same authors for the *Neochelys* genus. On the other hand, although included as a diagnostic feature in the definition of '*N. fajumensis*,' these authors did not include in the character list of their analysis an important shell character of the holotype and material assigned to '*Podocnemis*' *fajumensis*, already given by Andrews (1903, 1906): the contact of the gulars behind the short intergular, a character shared by all the taxa in the *Erymnochelys* group (see above) and not shared by *Neochelys*. Therefore, the hypothesis on the phylogenetic position of *Neochelys* obtained by Gaffney et al. (2011) is based upon an uncomplete character list. Consequently, the phylogenetic relationships among the *Neochelys* members, and also among the representatives of Erymnochelyinae, requires further detailed study, with the revision of all the taxa in Gaffney et al.'s (2011) list, and principally with the integration of many shell characters. It is noticeable that Gaffney et al. (2011) concluded by stating, "It is possible that a revision of *Neochelys* using the now available skull material (then including their '*N*'. *fajumensis* skulls) would place *laurenti* (i.e., *Papoulemys*) in that genus." However, although the revision of the genus *Neochelys* performed here does indeed show '*Papoulemys*' *laurenti* to be a member of *Neochelys*, '*N.*' *fajumensis* is not, based on both the skull and the shell.

Comparisons of the shell of Neochelys laurenti *with those of other members of* Neochelys *recognized in the Languedoc-Roussillon region*: As indicated, the Saint-Papoul shells analysed here (Figs. 5, 6, 7, 8, 9, 10 and 11) share with the *Neochelys* representatives a unique combination of characters and another character combination that allows us to diagnose the species *Neochelys laurenti* (see the generic diagnosis and the specific diagnosis in the systematic paleontology section).

The presence of *Neochelys* has previously been recognized in several outcrops of the Languedoc-Roussillon region (see de Broin 1977; Pérez-García and Lapparent de Broin 2013; Fig. 1). The first *Neochelys* taxon described there was *N. eocaenica*, defined in the late Ypresian–early Lutetian interval of the Grès d'Aigne Formation, in the Minervois area. Its presence has been recognized in the sandstone-molasse of this formation and in the "Marnes à tortues et limnées" levels of the same Grès d'Aigne Formation, in the countryside around the villages of Azillanet, Cesseras, Félines, La Livinière, Olonzac (Hérault), and Pépieux (Aude) (Bergounioux 1935, 1936; de Broin 1977; De Stefano 1902, 1906), including specifically indeterminable fragments. Several French Eocene specifically undetermined specimens from other Eocene areas (Argenton-sur-Creuse, Indre department, Lutetian; Parisian Basin, Ypresian; and from more or less undetermined points ranging from the early Ypresian to Bartonian of Languedoc) were grouped under the term '*N. eocaenica* complex' (de Broin 1977). Among those, specifically undetermined members of *Neochelys* were identified (de Broin 1977) in the sandstone-molasse of Issel (Aude), of the late Ypresian–early Lutetian levels of the Issel Series (Lauragais), a locality geographically close to Saint-Papoul and considered as closer or similar in age to the Grès d'Aigne Formation, based on the mammalian evolution (H.-P.Labarrère pers. comm.). The recently described *N. liriae* comes from an outcrop of the Grès d'Assignan Formation (lower part of the late Ypresian), in the Soleillades locality (Hérault), also belonging to the Minervois area (Pérez-García and Lapparent de Broin 2013). Another unpublished shell that probably belongs to the same species of *Neochelys* is identified in the same layer of the Grès d'Assignan Formation, in the locality of Sainte-Eulalie (Hérault) (Danilo et al. 2013) (Fig. 13a). All these specimens have been recognized only by postcranial materials, generally complete and fragmentary shells. The Saint-Papoul specimens are the oldest *Neochelys* material hitherto recognized in the Languedoc-Roussillon region (upper part of the early Ypresian). They are younger than *N. arenarum*. Moreover, Saint-Papoul is the only locality in that area where cranial remains have been identified. Based on the shell morphology as well as by the geographical location, *N. laurenti* seems relatively closer to the slightly younger *N. eocaenica.*

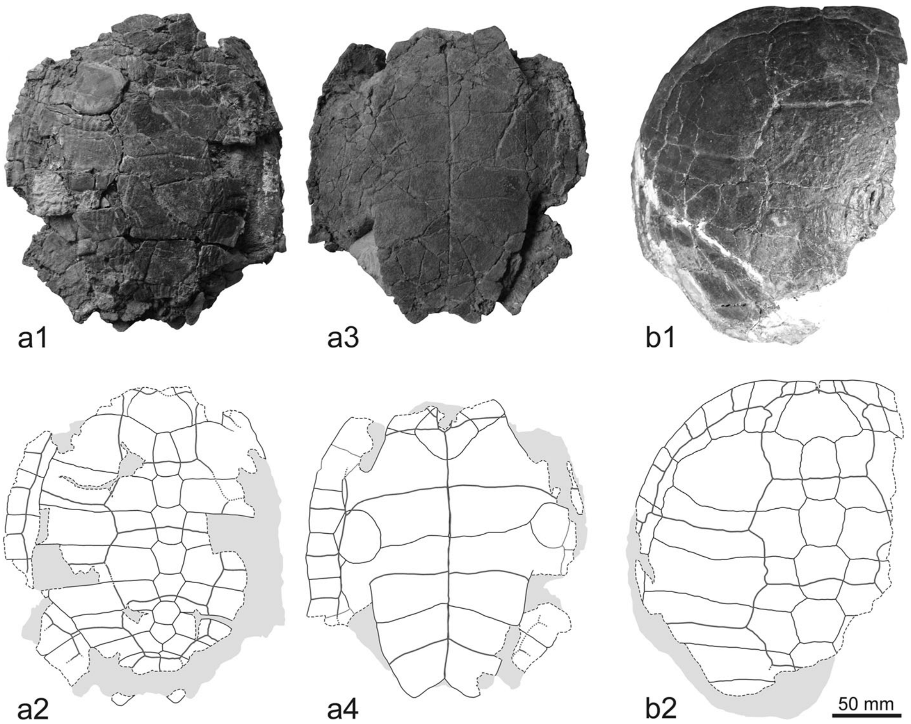

Fig. 13 Shells of two representatives of *Neochelys* not assignable to *Neochelys laurenti*, also from the Languedoc-Roussillon region. **a** MNHN.F.EBA 514, shell of *Neochelys* cf. *liriae* Pérez-García and Lapparent de Broin (2013), in dorsal and ventral views. Grès d'Assignan Formation, Sainte-Eulalie (Hérault, France). **b** MNHN.F.EBA 516, anterior region of a carapace of *Neochelys eocaenica* De Stefano 1903, in dorsal view. Grès d'Aigne Formation, Centeilles (Hérault, France)

The anterior region of the carapace of *N. eocaenica* was hitherto poorly known. It had only been partially figured by a specimen from the MHNT collection (Fig. 20 in de Broin 1977). The medioposterior portion of the carapace of this species is known from other published specimens, most also preserving the partial plastron (e.g., MNHN.F.OLZ 2, holotype of *N. eocaenica*; MNHN.F. OLZ 1, holotype of '*Ocadia bassani*' de Stefano 1906, UD 91-5059 holotype of '*Polysternum cassani*' Bergounioux 1936) (de Broin 1977). A new specimen attributed to this taxon, from the same level of the Grès d'Aigne Formation and from a vineyard close to the village of Centeilles (Hérault), is presented in Fig. 13b (MNHN.F.EBA 516). It is a partial carapace and allows us to better characterize the carapace of *N. eocaenica* and to compare it with that of *N. laurenti*. It shares exclusively with the species of *Neochelys* in the Languedoc-Roussillon region (*N. eocaenica*, *N. laurenti*, and *N. liriae*) the following character combination: lateral margins of the vertebral 1 lyre-shaped (more developed than in the previously known carapace of *N. eocaenica*), marginals 1 overlapping less than one-third of the length of the latero-anterior margin of the nuchal (the overlap may be longer in some specimens of *N. laurenti*), and marginals 1 at least two times wider than long (this ratio is lower in some *N. laurenti* specimens). This specimen shares with the known material of *N. eocaenica* s.s. (see de Broin 1977) and with *N. liriae* the overlapping of the marginals 1 on not more than one-quarter of the width of the peripherals 1. MNHN.F.EBA 516 shares with the known material of *N. eocaenica* and with some specimens of *N. laurenti* the presence of a shallow nuchal notch, located on the anterior margin of the nuchal and the peripherals 1; and its size, which is significantly higher than those of the French *N. liriae* and *N. arenarum* and of the German *N. franzeni*. The morphology of the anterior region of the shell of MNHN.F.EBA 516 is much more rounded than that of *N. laurenti* and *N. liriae*. Furthermore, it lacks the subparallel lateral margins present in the carapace of this latter taxon. Due to its preservation, most of these character states are not known in the specimen of *Neochelys* sp. from Sainte-Eulalie (Fig. 13a). However, the available combination of characters in the Sainte-Eulalie specimen is compatible with that of the holotype and only known specimen of *N. liriae*, from the same formation and a nearby locality.

In addition to the features shared between the anterior region of the shell of specimen MNHN.F.EBA 516 and the other specimens of *N. eocaenica*, *N. laurenti*, and the holotype of *N. liriae*, the information available on other anatomical elements of the Saint-Papoul specimens allows us to add other characters to the unique combination of characters of the taxa from the Languedoc-Roussillon region: the presence of seven neurals (this number may be higher in some specimens of *N. eocaenica* from the type formation); a subrounded anterior plastral lobe; the absence of a gular protrusion (present, but poorly developed, in some specimens of *N. laurenti*); rounded lateral margins of the posterior plastral lobe; and the entoplaston length being shorter than the distance that separates it from the hyo-hypoplastral suture.

An intergular scute narrower than the gulars (observed in all the *N. laurenti* specimens) is shared with some plastra of *N. eocaenica*. However, the intergular is as wide as the gulars in other specimens of *N. eocaenica*. The intergular is wider than each gular in *N. liriae*.

An entoplastral length longer than two times the distance that separates it from the pectoro-abdominal sulcus, observed in the specimens of *N. laurenti*, is shared with *N. liriae*, but not with *N. eocaenica*.

N. laurenti differs from both *N. eocaenica* and *N. liriae* in several characters: the overlap of the marginals 1 on the peripherals 1 exceeds 30 % of its width, as occurs, for example, in *N. capellinii*, *N. nicolisii*, *N. zamorensis*, and *N. salmanticensis* (this overlap occurs on one-quarter or less of the width of the peripherals 1 in *N. eocaenica* and *N. liriae*); vertebrals 2 and 3 are the widest of the vertebral series (vertebral 5 is the widest in *N. eocaenica* and *N. liriae*); the absence of contact of the intergular scute with the pectorals, with the humerals having a relatively long medial contact, as in *N. capellinii* (in which the gulars are small and narrower than the intergular); the postero-medial borders of the gulars overlap the entoplastron, as in the material from Dormaal, *N. zamorensis*, and most of the known specimens of *N. arenarum* (in which the intergular is narrower than the gulars).

Unique to *N. laurenti* is the combination of an intergular narrower than each of the gulars, both scute categories overlapping the entoplastron, the gulars being as long to nearly as long as the intergular, and the lack of an intergular-pectoral contact (Fig. 13c) (the humerals having a relatively long medial contact).

The study of the shells here attributed to *N. laurenti* confirms the validity of this species, heretofore only diagnosed by the skull.

Analysis of the cervical vertebra from Saint-Papoul: The described characters in the cervical vertebra MNHN.F.SPP 31 are compatible with those of the pleurodiran turtles (Broin 1991; Broin and de la Fuente 1993; Hirayama 1992, de Lapparent de Broin and Murelaga 1999; Lapparent de Broin et al. 2004, 2007; Williams 1950; Wood 2003), and are compatible with those of the Podocnemididae representatives based on the procoely and respective proportions and shape as a whole. No cervical vertebra of *Neochelys* has been described so far. The preliminary observation of unpublished material of *N. salmanticensis* from its type locality (i.e., skeleton STUS 12152, under study) shows its morphology to be similar to that of the Saint-Papoul specimen. The vertebra does not have the apomorphic saddle-shaped centra known in South American podocnemidid taxa such as *Bauruemys, Lapparentemys, Stupendemys* (see Lapparent de Broin et al. 1993), *Podocnemis* spp., and the extant *Peltocephalus.* The vertebra is relatively high with posteroventrally joined tubercles as in *Erymnochelys madagascariensis*, but a posterior condyle narrower for its height (all condyles typically widened and low in *Erymnochelys*). Although the cervical vertebra MNHN.F.SPP 31 is compatible in morphology and relative size with unpublished *Neochelys* vertebrae, we opt to allocate it to cf. *Neochelys laurenti* due to the scarcity of vertebral material from Saint-Papoul and the absence of descriptions of *Neochelys* cervical vertebrae.

Conclusions

The hitherto described, figured, and specifically determined skull of Pleurodira from the French locality of Saint-Papoul, the oldest so far reported in the Languedoc-Roussillon region, was preliminarily attributed to a new genus, '*Papoulemys*' Tong 1988, not identified in any other locality. The study herein of another skull from Saint-Papoul and of other *Neochelys* skulls from several regions allows us to consider the genus '*Papoulemys*' as a junior synonym of *Neochelys* Bergounioux 1954. The description and study of several shells corresponding to the same taxa as a '*Papoulemys*' *laurenti* skull allows the species to be diagnosed as being different from the other ones described. Therefore, the validity and individuality of the species '*Papoulemys*' *laurenti* is confirmed, but it is definitely reassigned to the genus *Neochelys.*

Reallocation of the hitherto insufficiently known '*Papoulemys*' to *Neochelys*, and the study of *Neochelys* skulls and shells from various European regions and various Eocene levels, expand the known diversity of this taxon, improve our knowledge of it and of several of its representatives, and reveal intraspecific variability in several of them.

A new diagnosis for *Neochelys* is given here. *Neochelys* is recognized as a taxon exclusively distributed in the Eocene of Europe, not present in Egypt, as previously hypothetized (Gaffney 2011). Its availability of characters allows its identification as an Erymnochelyinae Broin 1988 (sensu Lapparent de Broin 2000), and as an Erymnochelydand (sensu *nobis*) not belonging to Stereogenyini (sensu Gaffney et al., 2011). However, the phylogenetic relationships among *Neochelys* and the other members of these clades, as well as between the *Neochelys* representatives, are poorly understood. The review of several poorly known members of these lineages (e.g., '*Neochelys*' *fajumensis*, 'aff. *Erymnochelys*' *eremberti*), the description of several new forms under study, the detailed analysis of several members of *Neochelys* whose available information is limited, the proposal of new characters, and the revision of previously used characters are necessary to propose a well-justified hypothesis about the phylogenetic relationships among these taxa.

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