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Neochelys sp. (Chelonii, Erymnochelyinae), from Silveirinha, early Eocene, Portugal

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Abstract

Key-words: *Neochelys*; Portugal; Basal Eocene; comparisons; paleogeographical questions.

Constituted of isolated fragments with a smooth decoration, the turtle material from Silveirinha is examined in order to define its sure belonging to *Neochelys*, by comparison with other smooth turtles which may be present during the Palaeogene of Europe (freshwater Testudinidae, Erymnochelyinae, Bothremydidae). The elements are compared with the already known *Neochelys* species of the Eocene European localities. Questions are made about the possible geographical migrations of turtles between South and North during the early Eocene of western Europe. The phyletic relationships cannot be established but the species, seeming new and one of the more primitive as a whole (after the preserved elements), is the older from the Iberian Peninsula.

Résumé

Mots-clés: *Neochelys*; Portugal; Eocène basal; comparaisons; questions paléobiogéographiques.

Le matériel de tortue de Silveirinha, composé de pièces isolées à décoration lisse, est examiné afin de définir son appartenance effective à *Neochelys*, par comparaison avec les autres tortues lisses connues à l'Eocène d'Europe (Testudinidae d'eau douce, Erymnochelyinae, Bothremydidae). Les éléments sont comparés avec les espèces déjà connues du genre dans les localités éocènes d'Europe. Des considérations sont faites sur les possibles migrations des tortues à l'Eocène d'Europe entre le Sud et le Nord. Les relations phylétiques avec les autres espèces ne sont pas possibles à effectuer mais l'espèce, qui semble nouvelle et dans l'ensemble plutôt primitive d'après ce qui est préservé, est en tout cas la plus ancienne de la péninsule ibérique à ce jour.

Introduction

The first determination of a turtle from Silveirinha was given by Broin as *Neochelys* cf. *arenarum* Broin, *in* Telles Antunes & Russell 1981. It was based on the observation of a peripheral bone. In the Eocene continental localities of western Europe, *Neochelys*, up to day exclusively European, is generally associated with cryptodire turtles. Firstly, with freshwater forms: the ornamented Trionychidae and *Allaeochelys*, a carettochelyine, and smooth Testudinidae. Terrestrial Testudinidae are represented from the Cuisian (Broin, 1977). However, the more abundant material from Silveirinha 2, newly found by Prof. Dr. M. T. Antunes who kindly commited it to my care, only includes *Neochelys*. The material is constituted of isolated plates, most of which are small and not situated fragments, which might be confused with freshwater Testudinidae. None consistent enough in size can be attributed to another taxon than *Neochelys*, at least because of the texture and decoration when the anatomical characters are not preserved. Within the Pelomedusoides, as the *Erymnochelys* line and the Bothremydidae (see the Annexe) are represented during the Palaeogene of Europe besides *Neochelys*, the fragments from Silveirinha have been compared with their representatives. Podocnemididae are freshwater turtles, while the Bothremydidae are either freshwater or littoral forms. Outside of France, the *Erymnochelys* line is present in Africa and Madagascar (references *in* Lapparent de Broin, 2000a, *Erymnochelys* group) while Bothremydidae are more ubiquist (Americas, western Europe, Africa, Indian continent).

The genus *Neochelys* Bergounioux, 1954, has been recognized as a pleurodire (Broin, 1977) and included in the Pelomedusidae Cope, 1868. At that time, the Bothremydidae Baur, 1891, were also included in the Pelomedusidae. The restauration of this family was just considered (Broin, 1977; Gaffney & Zangerl, 1968) and was done *in* Broin (1988a), separating the monophyletic groups of the wide family Pelomedusidae: erection of the hyperfamily Pelomedusoides, including the Pelomedusidae reserved to a early derived line of forms, fossil and extant (including *Pelomedusa* and *Pelusios*), the Bothremydidae and the Podocnemididae (with Podocnemidinae and Erymnochelyinae and their plesion aff. *Teneremys* now named *Brasilemys* Lapparent de Broin, 2000b). Informations on South American Podocnemidinae are given *in* Broin (1991), completed by other works (see references *in* Carvalho *et al.,* 2002). Information and references on the systematics of Pelomedusoides, as it is here practized (particularly for the bothremydid groups), are then given *in* Antunes & Broin (1988), Lapparent de Broin & Murelaga (1999), Lapparent de Broin & Werner (1996). New bothremydids are described *in* Gaffney, Campos *et al.* (2001), Gaffney, Chatterjee *et al.* (2001), Gaffney, Moody *et al.* (2001c), Singh *et al.* (1998), with another and insufficient grouping of the genera, because not taking into account important characters, in particular those of the carapace, which are here essential. *Neochelys* is known in Europe (see the Annexe) during the Eocene (questionably during the Oligocene). The distribution of the Pelomedusoides in Africa and in Europe is given *in* Lapparent de Broin (2000a, 2001), and the characters at the nodes in the Pelomedusoides group are given *in* Lapparent de Broin (2000b). The latter particularly underlines the problems still existing about the interrelationships of the erymnochelyine genera, including *Neochelys*. The identification of the species of the genus *Neochelys* with a diagnosis clearly separating them and considering the apomorphic characters has not yet been done since Broin (1977), in spite of the discovery of new species (Schleich, 1993; Tong, 1998). The present study gives the opportunity to look for the principal discriminant specific characters within the genus, resumed in the Tabs. 1 and 2. A mosaic of primitive and derived characters, or unpolarized characters, appears for each named species as well as for the Silveirinha species. In spite of the lack of determinant specimens at the specific level in the material from Silveirinha and the insufficient degree of study of the material of the European *Neochelys* species, in particular in Spain, it is possible to hypothetize the presence of a new species at Silveirinha, which cannot be named and precised in its relationships with the other species.

Systematics

Subclass	PARAREPTILIA Olson, 1947
Ordo	CHELONII Brongniart, 1800 (Latreille, 1800)
Infraordo	PLEURODIRA Cope, 1864
Hyperfamily	Pelomedusoides Cope, 1868
Superfamily	Podocnemidoidea Cope, 1868
Family	Podocnemididae Cope, 1868
Subfamily	Erymnochelyinae Broin, 1988a
Genus	*Neochelys* Bergounioux, 1954

Neochelys sp.
(fig. 1-16)

Synonymy. *N.* cf. *arenarum* Broin; Antunes & Russell, 1981: 174.

Horizon and locality: Early Eocene, MN 7. Silveirinha, Portugal.

Material: Coll. UNL. Silveirinha 1: one peripheral (Antunes & Russell, 1981). Silveirinha 2: around 153 fragments. 130 are not situated on the skeleton (no more than ca 0,5 to 3 centimeters) from the carapace (peripheral, pleural, plastral fragments). 23 are situated bones, UNL n° 1 to 23, including figured specimens, pl. I: Skull: one basisphenoid (21, fig. 1). Carapace: Dorsal carapace: a partial nuchal (23, fig. 8). Partial peripherals: right peripheral 1 (4, fig. 10), left peripheral 1 (3, fig. 9), an anterior peripheral fragment (16), bridge peripherals including a partial left peripheral 7, (7, fig. 13; 18, 19), posterior right peripherals 9 (15), 10 (2, fig. 14), 9? (17), not situated (14). One pygal (1, fig. 15). Proximal extremity of two pleurals 3 or 5 (5, fig. 11; 6, fig. 12). Distal extremity of a pleural 3, 5 or 7 (20). Fragment of a left pleural 8 (8, fig. 16). Plastron: Partial left epiplastron (9, fig. 2). One left mesoplastron (13, fig. 3). A medial part of hyo- or hypoplastron (11, fig. 5). A left partial xiphiplastron (21, fig. 4). A partial right, xiphiplastron (10, fig. 6). An extremity of left xiphiplastron (12, fig. 7). Girdle: a proximal part of a right ischium (22).

Description and comparison (Figs. 1-16): the specimens belong to several individuals, mostly adult because of the well grown plates which were firmly sutured or because the depth of the plate fragments. The size of the adult figured specimens varies from 10-11 cm carapace long (pleural 8, fig. 16) to ca 23 cm (peripheral 10, fig. 14). The preserved skull fragment might belong to a longer carapace, ca 28 cm long. The plates are "smooth", only decorated with fine and short dichotomic or linear sulci, some of them united in small polygones (fig. 3). This is frequent in freshwater forms, as well cryptodire (for example Chelydridae) as pleurodire but not in the Eocene freshwater Testudinidae. The scute sulci are often sinuous somehow as in some freshwater Testudinidae but more finely. Some peripherals present a slight protruding angle at the external limit of the marginals: these peripherals points are present in a variable number of the peripherals and more or less strong in *Neochelys* (Tab. 2). They represent a primitive

Podocnemidid character, generally well preserved and sometimes much secondarily accentuated in the genus. The character is not present in the freshwater Palaeogene Testudinidae. It occurs much later (from Oligocene) in some *Ptychogaster* and in some terrestrial Testudinidae, in particular of the "European *Ergilemys*"- *Testudo* group.

There are growth annuli visible on some dorsal plates such as the peripheral 1 (fig. 9), a character of continental smooth forms of turtles, also as well pleurodire as cryptodire, frequent in *Neochelys*. The vertebrals 1 and 5 and the costals widely overlap the peripherals and pygal (mainly anteriorly and posteriorly), a character early acquired by Pelomedusoides (see Broin, 1980): the costal overlap is also present (variably) in the freshwater Testudinidae but with different relations between the plates and scutes.

The carapace of *Neochelys* shares characters with the Erymnochelyinae, particularly those from the Palaeogene of the Fayum: *"Stereogenys"* podocnemidoides, *S. cromeri* and *S. libyca*, *"Podocnemis" - Dacquemys fajumensis*, *Shweboemys antiqua* (less) and other taxa from Egypt and Africa [see the Fayum forms *in* Andrews (1906), Dacqué (1912), Reinach (1903) and references *in* Lapparent de Broin (2000b)]. It is also comparable with that of the Podocnemidinae and Bothremydidae. The characters shared with *Neochelys* are never present all together in one of these taxa.

Skull

The basisphenoid (fig. 1) belonged to a skull ca 5,3 long maximum. The medial full length is 1,15 cm and the ventral visible length was 0,8-0,1 cm, the anterior part being hidden by the pterygoids junction below the basisphenoid. It may represent a ca 28 cm carapace long (maximum) by comparison with *Podocnemis vogli*. It is podocnemidid because of its triangular sub-pentagonal ventral shape (fig. 1a) and because it presents medial borders of podocnemidid fossae. These borders are laterally situated, above the sutures of the free pterygoid wings (lateroanteriorly situated and covering the fossae in Podocnemididae) and, lateroposteriorly, the suture with the quadrate. On these borders, each fossa bears the sulcus leading the cerebral inner carotids to the sella turcica. The basisphenoid notch of entrance in the sella turcica, i.e. the basal preserved part of the foramen anterior canalis carotici interni, is relatively anterior on each border, lateral to the back of the sella turcica. The entrance was done just by a foramen, not by a canal through the basisphenoid. The sella turcica is preserved by its posterior part. It makes a weak fossa which is not posterodorsally covered by an anterior horizontal protrusion of the dorsum sellae. Its low posterior border is shortly vertical, slightly oblique towards the back. This is a derived condition by comparison with the other turtles (cryptodiran and pleurodiran), by convergence close to the condition of the cryptodiran *Chelydra*. This condition is that of *Neochelys arenarum* (not known in other species of the genus) and that of the Erymnochelyinae where the inner cavity of the skull is known: *Erymnochelys madagascariensis*, *Shweboemys* cf. *antiqua*, *S. gaffneyi*, and the erymnochelyine skull from Moghara, Egypt (Williams, 1954). There are some variations in the degree of verticality or posteriorly oblique direction (*S. gaffneyi*, more derived) of the back border of the sella. The position of the foramina with respect to the back of the sella turcica is more (*Erymnochelys*, *S.* cf. *antiqua*) or less anterior to that of *Neochelys*. In Podocnemididae, the foramen of entrance in the sella turcica may be elongated in a short canal beginning in the "enlarged carotid canal" of the podocnemidid fossa posteriorly to the back of the sella turcica and leading to it, but not in *Neochelys*. The foramina of the Silveirinha specimen and *N. arenarum* are not approximated and their diameter is relatively moderate (primitive conditions) as in the observed Erymnochelyinae. In the Podocnemidinae and the Bothremydidae (when known: *Bothremys* sp. *in* Gaffney, 1977; the Oman skull *in* Roger *et al.*, 1994; *Rosasia*, *in* Antunes & Broin, 1988; *Solhafah* Lapparent de Broin & Werner, 1998), primitively as in the observed Pelomedusidae and Chelidae (some, and see Gaffney, 1979), the cavity of the sella turcica is deep and the dorsum sellae anteriorly horizontally protruded (sometimes deeper and more protruded in several taxa, by secondary evolution). In *Bauruemys elegans* Martín Suarez, 1969 (late Cretaceous from Brazil), aff. *Roxochelys vilavilensis* Broin, 1971, and the extant *Podocnemis cayennensis*, *P. expansa*, *P. vogli*, *P. lewyana* and *Peltocephalus dumerilianus* (not examined in the other taxa of the subfamily), the carotids enter as posteriorly as in the Silveirinha specimen or more posteriorly. As in Bothremydidae, they are either not approximated when they are relatively moderate, or approximated and wider (derived conditions) in *B. elegans*, aff. *R. vilavilensis*, *P. expansa* and particularly approximated although modérate in *Peltocephalus dumerilianus*.

The foramina nervi abducentis (6th cranial nerve pair) are not present on the dorsal surface of the Silveirinha basisphenoid and no exit foramen is visible in the enlarged carotid canal on the lateroanterior border of the bone. This conforms with *Neochelys arenarum* and other observed Erymnochelyinae. In the *Erymnochelys* the foramina are laterally advanced so that they do a shallow and long notch in the thin anterolateral border of the basisphenoid, instead of a more or less posterior foramen as in the other turtles. The foramina were probably likely advanced in the fossil erymnochelyine forms, although any notch is visible (but the very thin border of the basisphenoid may be eroded). In Bothremydidae and Podocnemididae they are variably advanced and developed, inclusing individual variations between both sides, anteriorly and laterally up to a short rounded anterolateral notch (*P. dumerilianus*).

The carapace

Dorsal shell

The nuchal (fig. 8) is sufficiently preserved to hypothetize its complete shape and it conforms with the *Neochelys* nuchal. It is narrowed, as in other Pelomedusoides (more or less according to the genera) and not secondarily elongated as in many of them. It is narrow anteriorly (1.2 cm), much narrower than the midposterior width (3.2 cm) and the full medial length (approximately 2.7 cm) as in *Neochelys*. The anterior border is hardly medially drawn back, with a wide obtuse angle at the junction of the marginals 1. It does not represent a true rounded notch as present in bothremydids of the *Bothremys* group such as *Rosasia* (late Cretaceous from Portugal, Antunes & Broin, 1988) and *Bothremys* (late Cretaceous from USA, Gaffney & Zangerl, 1968; Schmidt, 1940) and some other forms. As in *Neochelys*, the lateral borders are rounded posteriorly and the posterior part of the marginals have a rounded border on the nuchal (as also often in other Erymnochelyinae and some Bothremydidae). The marginals 1 cover half the border length of the bone, which is relatively long but individually variable as seen by the two preserved peripherals 1 and other species (Tab. 2) and specifically variable. As in other Pelomedusoides, the marginals 1 shortly cover the nuchal ventrally and the surface (as anteriorly as from midlength) is not much posteriorly concave. The anterior narrowing associated with the absence of cervical are not present in the freshwater Testudinidae.

Two peripherals 1 are partly preserved (figs. 9-10). One (fig. 9a) shows growth annuli at the boundaries of the scutes. Both have a light angle at the external limit of the marginals 1 and 2, protruding from a straight transversal border, the plates being not laterally shortened as they are in freshwater testudinids. The difference with the peripheral 1 of the latter is also that the marginals 1 are much shorter than the marginals 2 and the marginal 1 is narrow, medially on the peripheral 1, because of the absence of cervical on the nuchal. The lateral border of the marginal 1 is slightly rounded. The short and narrow marginal 1 is constant in *Neochelys* and shared by some other Podocnemididae, Erymnochelyinae in particular, but with other relative proportions of the elements. The ventral part of the marginals below the peripheral 1 is short. On the preserved two peripherals 1, the marginals 1 cover a less long proportion of the corresponding nuchal than in the above described nuchal and a rather narrow medial part of the peripheral (Tab. 2). As in *Neochelys* and other Pelomedusoides, the lateral border of the vertebral 1 is lateral to the sulcus between the marginals 1 and 2 on the peripheral 1. At Silveirinha, it is straight and not close to the boundary of the nuchal, which indicates that this scute was not anteriorly narrowed as it is in *N. laurenti* (Tong, 1998) from the lower Eocene of Saint-Papoul, France, and not as wide or nearly as wide as the nuchal as it is in *N. franzeni* Schleich, 1993, from the lower Eocene of Messel, Germany (Tab. 2). In bothremydids, the peripheral 1 may be narrowed so that the wide vertebral 1 may cover the peripheral 2 or the boundary peripherals 1-2 (some specimens of *Polysternon provinciale* and *P. mechinorum*). In *Neochelys*, as in other Pelomedusoides, the marginals 1 and 2 are always shorter than the corresponding peripherals, contrarily to many testudinids.

From the nuchal and the peripherals 1, it appears that the anterior border of the shell was straight (or nearly) at the nuchal-peripherals 1 (actually in *Neochelys* between the lateral extremities of the peripherals 2, not preserved here). It is not clearly notched as in some Bothremydidae (*Bothremys* group) and some Testudinidae. In the latter family, when the border is straight it is only between the nuchal and the marginal 1 part of the peripheral 2 which is laterally shortened. The anterior part of the carapace was neither much elongated with respect to the primitive Pelomedusoides state (*Teneremys*, *Brasilemys*), not as much as in many Pelomedusoides and particularly in the Palaeogene European bothremydids, nor roundly medially protruded as in bothremydids (*Cearachelys*, *Carteremys* Williams, 1953, *Taphrosphys* group, Palaeogene European bothremydids) and in extant Pelomedusidae. Slight medial protrusion or elongation with a notched border also occurs in testudinids.

The bridge peripherals are partly broken. The open angle between the dorsal and the ventral faces of the more open peripheral 5 or 6 (n°19) and the peripherals 7 (n° 7, fig. 13 and n° 18) at the posterior extremity of the bridge, indicate an elevated shell, as in *N. arenarum* Broin, 1977, pl. V, fig. 10, for example, more than in *N. eaocaenica* which is posteriorly expanded. It ought to be elevated as in the extant *Erymnochelys* and *Peltocephalus*. The shells are generally flattened by the fossilization but actually, when living, some *Neochelys* species had a rather high and quadrangular shell while other had a more flattened and posteriorly expanded one such as *N. capellinii* and *N. eocaenica*. None is as regularly lowered and smooth as in Bothremydids.

Among the posterior preserved peripherals, the right ninth has a small external point. The tenth (fig. 14) is an element of a wide and thick shell, ca 22-23 cm long. It is short for its width, indicating a short posterior carapace border, in agreement with the preserved pygal (see below). The dorsal face is concave and the ventral face is much roundly curved, which is convenient with a shell rather elevated and with posterolaterally upward recurved borders.

The pygal (fig. 15) is slightly medially pointed (broken on the right half) and has sinuous sulci. It is more vertical than the lateral posterior peripherals. Ventrally, it bears two small and anterior concavities (for muscle attachment) as in most other Podocnemididae but not in freshwater Testudinidae where the concavities are situated below the suprapygal 2. This plate is posteriorly reduced in Pelomedusoides and represents the unique suprapygal, the suprapygal 1 of testudinids being absent. The relative length of the pygal (2.6 cm) on its width (2.4 cm), ratio 92.30%, indicates a very moderately long posterior border of the shell which is primitive for the family. But it is relatively longer than in the freshwater Testudinidae where the pygal is primitively short and wider than long (or secondarily much shorter because of the more elongated suprapygal 2). It is a little less elongated than in most other *Neochelys* species (Tab. 2) among which some have an elongated pygal as, for example in Podocnemididae, in extant *Podocnemis sextuberculata* or *Erymnochelys* (ca 72 %). It may be still longer in other species such as the more flattened *P. lewyana* (65%) and the elevated *Peltocephalus dumerilianus* (62.16%). This indicates the familial variability of the character, the ratio width on length varying from 92.30% in the Silveirinha species to ca 63% in *Peltocephalus*. But there is also an individual variation, as shown by *N. capellinii* and *N. eocaenica* that we cannot mesure for the Silveirinha species with only one preserved pygal. The length of the pygal is not related with the elevation of the shell. The elongation of the posterior border also occurs in the Bothremydidae, the border being shorter in primitive forms and in the *Bothremys* group relative to the *Taphrosphys* and *Nigeremys* groups and the Palaeogene European bothremydids. As many other characters such as the anterior elongation of the shell, the posterior elongation occurs parallelly in the taxa of the Podocnemidoidea: Bothremydidae, Podocnemidinae and Erymnochelyinae, and Pelomedusidae.

The fragments of pleurals (figs. 11-12) have irregular sinuous sulci. From the wide intervertebral sulcus on the medial pleural according to the pleural length, the vertebrals seem to be as moderately narrowed as in other *Neochelys* spp., whereas in Bothremydidae they are (as a whole) more narrowed at their junction with respect to their laterally pointed medial part between the costals, particularly in the Palaeogene European forms (London Clay, Avesa, Montoulieu). The Eocene testudinid vertebrals are also more narrowed. Ventrally, the free extremity of the ribs is narrow relative to turtles such as Carettochelyidae, but wider and shorter than in freshwater Testudinidae which, with the sinuosity of the sulci conform to that on the pygal, helps to recognize the *Neochelys* belonging of such fragments.

The anterior medial fragment of pleural 8 (fig. 16b) ventrally shows a part of a scar for the ilium which was sutured to the shell, the basic character of the Pleurodira, and anteriorly prolonged below the pleural 7 as in modern Podocnemididae. In this family, the ilium is also still primitively sutured up to the laretoanterior part of the suprapygal in a Cretaceous podocnemidid form from Brazil, but no more in all the others, including *Neochelys*. The primitive condition of the Pelomedusoides with the suture up to the suprapygal is retained in most Pelomedusidae and Bothremydidae (see Lapparent de Broin & Murelaga, 1999) but not in *"Chrysemys" montolivensis* (Oligocene, France). The condition is not known in the other Palaeogene European bothremydids. The pelvis is not sutured to the shell in Cryptodira, including testudinids.

The posterior border of the nuchal, the neurals and suprapygal are not preserved. It is probable that the neural 1 linked the nuchal as in all the Pelomedusoides, except in *Stereogenys* and some *Pelusios* spp., and the last neural did not join the suprapygal, as in all the Pelomedusoides, except in the primitive early Cretaceous forms.

The plastron

The fragmentary specimens from Silveirinha do not allow to reconstruct the whole plastral shape but they conform with the *Neochelys* elements. In *Neochelys*, the plastron has widened anterior and posterior lobes (more or less according to the species) compared to the primitive condition. The anterior is anteriorly trapezoido-rounded (more than in *Erymnochelys* and *Shweboemys*) and anteriorly not concave (fig. 2) (as it is in *Stereogenys*), moderately elongated (more than in *Shweboemys* and *Peltocephalus*, less than in *Podocnemis*), narrower than in *Peltocephalus* and *Shweboemys* in Podocnemididae. In Bothremydidae, it is wider and relatively shorter in the *Bothremys* group and much enlarged rounded or trapezoid in the *Taphrosphys* group. The *Neochelys* posterior lobe, laterally slightly rounded (fig. 4), conforms with that of various Podocnemididae. It has straighter and more convergent borders in the *Bothremys* group and in *Shweboemys*, and it is enlarged and laterally or posterolaterally more rounded in the *Taphrosphys* group.

Epiplastron. The fragmentary epiplastron (fig. 2) lacks the medial symphysis part and the lateroposterior part. The medioposterior border is part of the suture with the entoplastron and the posteromedial border is part of the suture with the hyoplastron. The anterior border is straight, does a rounded angle with the lateral border which is moderately rounded. The gular is anteriorly saliant. The epihyoplastral suture was sinuous and not straight and directed lateroanteriorly as it is in various other forms, in particular *Stereogenys* (derived condition). On the ventral face, only are visible anteriorly the gularohumeral sulcus, not the gularointergular sulcus, and posteriorly the humeropectoral sulcus. The oblique direction of the latter (fig. 2b) indicates that it was completely anterior to the epihyoplastral suture as in all the *Neochelys* spp. and in most of the Podocnemididae Erymnochelyinae, the most derived condition, more than in most of South American podocnemidines. In the family Bothremydidae, it begins posterior to the entoplastron (*Cearachelys*), then contacting it (*Rosasia*), then generally on the posterior part of the entoplastron and then rarely at the epihyoplastral suture or partly anterior (*Polysternon*, *Elochelys*) but less anterior than in Erymnochelyinae.

If we compare with other Podocnemididae, the entoplastron was quadrangular-rhomboid and large (derived condition) and the epiplastral symphysis short (primitive condition), as in other *Neochelys* spp., as deduced by the remaining parts and the posterior full width of the bone when reconstructed. The entoplastron is always large in the anterior lobe in *Neochelys*, as in the erymnochelyine line s.s., larger than in most other Podocnemididae (*Podocnemis*, *Peltocephalus*, *Stereogenys*, *"S." podocnemidoides*, *Shweboemys antiqua*). The symphysis is also short in *"Podocnemis"-Dacquemys fajumensis* from the *Erymnochelys* line, and much shorter in *S. antiqua* (shortened anterior lobe). In the other forms with a longer symphysis, either the entoplastron is shortened or the anterior lobe is elongated.

From the very oblique direction of the gularohumeral suture compared with *Neochelys* spp. (see for example Broin, 1977), the gulars were short, and well separated by the intergular, which is the primitive pattern of pleurodires from Jurassic times. There is a represented tendency in various *Neochelys* spp. (Tab. 2), for the intergular to approximate up to link the pectorals and more or less separate the humerals by a point up to a wide distance (as in *N. franzeni*) or with a large intraspecific variability (*N. arenarum*). In the *Erymnochelys* line, represented during the Ilerdian-Lutetian from France besides from Africa, the opposite tendency is the reduction of the intergular so that the gulars always meet behind it. We cannot know the complete pattern for the Silveirinha species but it was surely not the *Erymnochelys* pattern and it was probably the most primitive pattern as for example in the *Neochelys* sp. from Dormaal. The link intergular-humerals also occurs in *Stereogenys* and in bothremydids of the *Taphrosphys* group and the unsituated form *"Shweboemys pisdurensis" in* Jain (1986) (a possible bothremydid), and tends to occur in the *Bothremys* group (the Israelian form). In these cases, the posterior part of the intergular is medially posterior to the epihyoplastral suture (*Stereogenys*) and the humeropectoral sulcus is not completely anterior to the suture (*Elochelys*, *"Shweboemys pisdurensis"*) or it is completely posterior (*Taphrosphys*). Besides, the intergular is characteristically anteriorly narrowed in *Stereogenys*.

There is a very weak derived dorsal epiplastral lip, accentuated at the gularohumeral sulcus, present in *Neochelys* as in *Stereogenys* and *"Podocnemis" - Dacquemys*. It is here less pronouced than in other species (some *N. laurenti*) where it may be as strong as in freshwater testudinids such as some Eocene *Paleochelys* s.l. It is slightly and roundly saliant at the extremity of this sulcus, at the corner of the lobe, as in several *Neochelys* spp., *Stereogenys* and in some some *"Podocnemis" - Dacquemys* specimens, an individually variable character within specifically different margins (Tab 2).

Deduced from the preserved part, the anterior epiplastral border was straight on a good width and the proportion of the anterior intergular-gular border relative to the width of the anterior lobe border and of the base of the lobe was wide. This is derived, characteristic of *Neochelys* among the podocnemidid forms with a trapezo-rounded lobe (most of erymnochelyines), opposite to the forms with a more anteriorly rounded lobe and with more parallel lateral borders (*Podocnemis* group). This anterior wideness occurs in *Stereogenys* but the anterior border is concave. It also occurs by homoplasy in the *Taphrosphys* group. Sometimes in *Neochelys*, the intergular is anteriorly more protruded-rounded (Issel specimen of Gervais, 1859, pl. 53, 2, USTL coll., actually more rounded than figured; Caenes 2 specimen, Jiménez Fuentes *et al.*, 1993-1994, fig. 4E) but the gulars remain straight and the intergular-gular border part remains wide for the anterior lobe. With the slightly rounded lateral border, this wide intergularo-gular straight border produced at Silveirinha a trapezo-rounded anterior lobe as for example in the Dormaal *Neochelys* sp. or in some of the specimens of *N. salmanticensis*, but not as trapezoidal as in *N. arenarum* or in *N. zamorensis* (holotype and Valdegallina specimens) (Tab. 2). It is possible that the specific variability of the plastron with laterally more or less rounded lobes, expressed in the character "AL angle", Tab. 2, is due to the sexe, males being narrower than females, as in many extant turtles. Although the intergular part is not preserved and besides the texture and decoration, the fragment from Silveirinha cannot be interpreted as belonging to a Testudinidae (the intergular is absent in this family) because of the humeropectoral sulcus anterior to the epihyoplastral suture.

Mesoplastron: One left mesoplastron just slightly medially incomplete (13, fig. 3) is preserved, polygono-rounded as in all the Podocnemididae, *Neochelys* included. Testudinidae have no mesoplastra. The presence of small lateral mesoplastra is a character of the primitive Pelomedusoides but the more polygono-rounded shape is a more evolved grade. The less evolved grade is that of slightly shorter mesoplastra for their width, wich is the case in several specimens of *Pelomedusa* (in Africa) and in *Taphrosphys ambiguus* from the Palaeocene of France, as in the oldest Cretaceous Chelidae. In Podocnemididae, they are less lateral (compared to the base of the posterior lobe) than in most Bothremydidae, which we cannot observe here.

The pectoroabdominal sulcus meets the abdominomarginal sulcus just anterior to the mediolateral part of the mesoplastron and the latter crosses the mesoplastra longitudinally (fig. 3) and rather medially as, for example, in *N. eocaenica* (see Broin 1977, fig. 21) and in most of the species of the genus. In *N. capellinii*, the abdominomarginal sulcus is more lateral on the mesoplastron. That means that in *Neochelys* the pectoroabdominal sulci have derived to become completely anterior to the mesoplastra and the abdominomarginal rather more medial with respect to the more primitive Pleurodires with lateral mesoplastra (*Platychelys*, *Teneremys*, *Pelomedusa*, oldest chelids). The abdominals become longer anteriorly and laterally, and narrower laterally. This occurs in most of the Podocnemididae. In Bothremydidae, the pectoroabdominal sulcus, primitively less anterior laterally, arrives at the anteromedial border of the mesoplastron to cross it transversally (after doing or not yet a forward sinuosity) and then meets the abdominomarginal sulcus which runs longitudinally approximately at the boundary mesoplastron-peripherals (primitive condition of the turtles) (more or less on the mesoplastron or on the peripherals) or either completely on the peripherals (derived condition). The extreme condition of this case is that of *Elochelys* (the holotype) where the sulcus arrives completely anterolaterally to the mesoplastron and runs outside of the bone, longitudinally on the peripherals (enlarged abdominals: advanced and widened). The tendency to the lateral advancing is therefore present in Bothremydidae by homoplasy but it is rare compared to Podocnemididae where it is the rule. If both families tend to the abdominal advancing, Bothremydidae tend to the more lateral "longitudinalization" (widened abdominals) while Podocnemididae tend to the more medial "longitudinalization" (narrowed abdominals), mostly realized in Erymnocheyinae. In this progress, the Silveirinha species is advanced in grade by the medial longitudinal position of the abdominomarginal sulcus.

A medial part of hyo- or hypoplastron (11, fig. 5), among other unsituated fragments of hyo-hypoplastra, does not indicate anything and is recognized as *Neochelys* by its texture. In *Neochelys*, the bridge is elongated, as long as to longer than the posterior lobe, according to the species, which we cannot verify here. From the mesoplastron morphology, we know that the pectoroabdominal sulcus was well anteriorly positionned (derived condition) on the hyoplastron.

Xiphiplastra: A left partial xiphiplastron (21, fig. 4), a partial right xiphiplastron (10, fig. 6) and the extremity of a left xiphiplastron (12, fig. 7) show the suture of the pelvis to the carapace, which caracterizes the pleurodires: the ovale suture of the pubis (figs. 4a and 6) and the transversal-medial triangular suture of the ischium (fig. 7a) on the dorsal face of the xiphiplastron, shapes present in nearly all the Pelomedusoides except a derived shape in *Taphrosphys* (see Broin, 1977; Gaffney, 1975 and others). The anterior fragment (fig. 4) shows the rounded lateral border of the posterior lobe and the transversal femoroanal sulcus (fig. 7b).

The anal fragment (fig. 7a) shows the wide and short anal notch of the plastron, with straight borders. This shape is rather primitive, at the basic Pelomedusoides level such as in *Teneremys* Broin, 1980 (new unfigured material) and *Cearachelys* Gaffney, Campos *et al.*, 2001. It is less secondarily deep than in most of the Pelomedusoides species. It is short because the deep notch, between the pointed xiphiplastral extremities which still bear the ischiatic suture extremities, of the more primitive stade (stade present in *Proterochersis*, *Platychelys*, oldest chelids and preserved in many chelids), has been filled. The ischiatic sutures are then anterior to the secondary anal notch as in the Silveirinha species. The anal notch shape is individually and specifically variable in Pelomedusoides, including *Neochelys*. But in this genus it has generally straighter borders and it is rather shorter than in some other Pelomedusoides. It is more or less narrow and/or deep according to the species (Tab. 2) and the individuals. In some species or individuals (Dormaal) it is slightly rounded.

On the anterolateral xiphiplastral border, the dorsal part of the scales is wide (fig. 4a) as in some Fayum forms. It is narrower at the lateral posterior border and becomes wider at the extremity (fig. 7a). The dorsal part of the plastral lobe scutes are variably wide according to the species (see Broin, 1977, pl. III, IV and V). The scutes are dorsally wider than in *Erymnochelys*, *Podocnemis*, *Peltocephalus* and *Pelomedusa* but less than in *Stereogenys* or *Pelusios*.

Girdle: A proximal part of a right ischium (22) is preserved. The shape is of a pleurodire, being conform, for example, with an ischium corresponding to a carapace 15 cm long of a *Pelusios* from Madagascar.

Discussion

Neochelys is recognized by a set of various characters of the skull and shell, besides the characters of Podocnemididae Erymnochelyinae. Associated with other characters (Tab. 1) a good derived character of *Neochelys* is that of the interparietal shape of the skull, truly cordiform with a sinuous anterior border in two semi-circular parts, longer than wide but not much: its shape is homogeneous in the genus (much more variable in shape and relative proportions in the other Podocnemididae and not as regularly cordiform), differing between some species by the length (Tab. 1). It is often posteriorly prolonged by a net of diverging sulci, fine or wide (Tab. 1), not known in other genera.

	Si	Do	Ri	Ca	Lau	Fran	Eoc	Zam	Salm
Skull number	0	0	4	0	2 (1, and 1 ? + d)	3/ ?	0	6 observ. (4 meas.)	1 ? /?
Ipa L/s L	?	?	shortto middle m 44,8%	?	short m 36,83	long 46,33	?	long m 46,86	ca 40?
Post Ipa scales	?	?	net or not	?	no	net or not	?	large elong. scales	net
Lat em	?	?	?1/2 meat. h.	?	1/2 meat. h	?	?	< 1/2 meat. h	?
Precol f	?	?	narrow, weak	?	moderate	?	?	rather large, deep	?

Tab. 1 - A selection of comparitive skull characters of the *Neochelys* species, estimated on the specimens of the type localities. Si, species indet. from Silveirinha. Do, species indet. from Dormaal. Ri, *N. arenarum*. Ca, *N. capellinii*. Lau, *N. laurenti*. Fran, *N. franzeni*. Eoc, *N. eocaenica*. Zam, *N. zamorensis*. Salm, *N. salmanticensis*. Skull number: number of observed skulls; n: after photographs, d: after author's data, others: observed and measured after the specimens. *N. zamorensis*: 6 observed (observ.), 4 measured (meas.) skulls, from the Valdegallina level. *N. salmanticensis*, a slide of a dorsal view of one skull from Teso de la Flecha observed. Ipa L/s L: interparietal length on skull length; m = mean. Post Ipa scales: a deltaic net of minute scales at the posterior point or large elongated scales behind the interparietal or absence. Lat em: lateral emargination, height relative to the height of the meatus quadrati (meat. h.). Precol f: precolumellar fossa, size and depth.

Species	Si	Do	Ri	Ca	Lau	Fran	Eoc	Zam	Salm
Nuchal ant bord w	narrow	wide	narrow	wide	narrow	narrow	wide	wide	narrow
M1/nuchal	mid-long to long	short	mid-long	short	short to mid-long	mid-long	short	mid-long	long
M1w	rather narrow	?	narrow	wide	wide	narrow	narrow	wide	wide
Per points	yes	?	yes	no	yes	yes	weak	yes	yes
Per 2 width	?	?	wide	wide to mid-wide	mid-wide	mid-wide	mid-wide	wide	mid-wide
V1/nuchal	wider	wider	wider	wider	wider, anteriorly clearly narrowed in lyre	as wide or ca	wider	wider	wider
Pygal l/L%	933	?	7692	71,57-83,36	70	70278163	72,94 ca 83	9523	?
Car max size	21-28 cm	17,8 cm	25 cm	31 cm	365	24 cm	35 cm	30 cm	ca 44 cm
Plastral shape	?rather wide rounded	(narrow?) rather rounded	rather wide straight	rather wide rounded	rather wide rounded	rather wide (AL>PL) rounded	rather wide rounded	narrow straight	rather wide rounded
Saliant gular	Yes much	yes or no	no to weakly	no to weakly	yes or no	no	no	yes much (typically) to no	no (typically) to weakly
AL angle	rounded	± rounded or angular	angular	Rounded or angular	rounded	rounded	rounded	rounded or angular	rounded
Al border	Rounded	straight or rounded	straight	rounded	rounded	rounded	rather straight	straight (typically) to rounded	rounded
Ant Ig width	?	narrow	narrow	wide	narrow	wide	mi-wide	mi-wide to narrow	mid-wide
Ig/HP contact	?	no	no to narrow contact	no	no	very wide	no to ± wide	no to yes narrow	no to wide
Gul w/ Ig w	?	wide	Wide	moderate	wide	narrow	mid-wide	mid-wide	mid-wide to wide
Gul l/Ig l	?	long; ento overlap	long; ento overlap	short to mid-long; ento just contact or no	mid-long to long, Gul shorter or Ig=Gul; ento overlap or no	short, no ento contact	short-mid--long; contact or no	long; ento overlap	mid-long to long; ento overlap or no
Anal notch depth	22,91 short	31,8/43,33 mid/long	33,33 mid	25/35,71 short/mid	43,48 long	42,10/45,8 long	17,64/ (18,55) short	23,43 short	22,2 short
Anal notch outline	straight	rounded	straight	straight	straight	straight	straight	slightly rounded	straight

Tab. 2 - Comparative shell characters of the *Neochelys* species, estimated on the specimens of the type localities or of their geographical area. Characters are selected according to their possible observation on the Silveirinha fragments. Si, species indet. from Silveirinha. Do, species indet. from Dormaal. Ri, *N. arenarum*. Ca, *N. capellinii*. Lau, *N. laurenti*. Fran, *N. franzeni*. Eoc, *N. eocaenica*. Zam, *N. zamorensis*. Salm, *N. salmanticensis*. Carapace. Nuchal ant bord w: width of the nuchal anterior border with respect to the posterior nuchal width (narrow: between 35 and 40-43%; wide: between 47 and 65 %). M1/nuchal: length of the marginals 1 with respect to the lateral borders of the nuchal (short: 20-26%; mid-long: 34-40 %; long: 50->50%). M1w: width of the overlaping part of the marginal 1 on the peripheral 1 with respect to the width of the anterior border of the peripheral 1. Per points: presence or peripherals points at the external limit of marginal sulci of at least some peripherals. Per 2 width: particular width of the peripheral 2 with respect to the peripheral 1. V1/nuchal: vertebral 1 width with respect to nuchal width. Pygal l/L%: ratio posterior width on medial length. Car max. size: maximal known carapace length. Plastron. Plastral shape: either rather wide or narrow with either moderately rounded or straight lobe borders; AL, anterior lobe wider than PL, posterior lobe. Saliant gular: anterior saliant gular at the limit with the humeral or not. AL angle: shape of the angle of the anterior lobe, at the lateral extremity of the anterior border. AL l border: straight or rounded lateral border. Ant Ig width: anterior intergular width with respect to the gular width. Ig/HP contact: relation of the intergular posterior extremity with the humero-pectoral sulcus: intergular separating more or less widely or not the humerals. Gul w/ Ig w: width of the anterior border of the gular with respect to that of the intergular. Gul l /Ig l: gular length with respect to the intergular length: short or mid-long to long, not contacting or contacting or overlaping the entoplastron (ento). Anal notch depth: ratio % medial length on posterior width. Anal notch outline: straight or more or less rounded.

In the absence of the skull and from the limited shell material, the Silveirinha species is clearly a *Neochelys* species because of the united presence of : - The derived nuchal shape, anteriorly narrowed but posteriorly wider and not elongated, bearing regularly transversally shortened marginals 1 with a rounded posterior border. - The derived quadrangular-rhomboid entoplastron large in the anterior lobe, but with a short epiplastral symphysis (deduced from the epiplastral remain). - The derived wide proportion of the straight anterior intergular-gular border with regard to the anterior plastral lobe border (partly present, partly deduced). - The primitive long intergular (also deduced from the epiplastral remain). - The primitive straight and short anal notch consistent with various *Neochelys* spp. - The basisphenoid consistent with that of *Neochelys* as known in *N. arenarum*. Also convenient are the decoration, the growth annuli and the peripherals points.

The Table 2 tries to compare the specimens from Silveirinha with the other named *Neochelys* species. Several characters are not known in several species and not enough characters are preserved at Silveirinha. In particular the intergular/gular pattern which is very important. However, as seen above, the intergular had to be longer than the gulars, separating or not the humerals (probably not). The gulars ought to be relatively short. The species lacks some specialized characters found in various species: the specialized anal notch, relatively long of *N. laurenti* and *N. franzeni* and more or less rounded of *N. zamorensis* and the species from Dormaal, the specialized anteriorly narrowed vertebral 1 of *N. laurenti*, the angulous epiplastral border of *N. arenarum*, the trapezoidal anterior lobe of *N. arenarum* (always wide) and *N. zamorensis*. The other derived characters such as the relatively narrow anterior nuchal border, the saliant gular and the rounded epiplastra lateral border are also present in *N. salmanticensis*, another Iberian form. But they are also present in other different species (Tab. 2) and they may vary in a species (Dormaal). The medial abdominomarginal sulcus position on the mesoplastron is also derived but it is shared by nearly all the species. Here we have not several specimens for each of these characters. The species could be new according to all the other species and in particular to the latter Iberian one. This is not strange with regard to the difference in age between the localities, *N. salmanticensis* from the Teso de la Flecha being possibly Bartonian (MP 16) (Cuesta Ruiz-Colmenares, 1994-1995). With regard to the species from the MP7 zone from the earliest Eocene, we can exclude *N. arenarum* and the elements from Dormaal. But with so few preserved elements from Silveirinha, we cannot affirm that the species was the most primitive, despite the short pygal, the short and straight anal notch and the rather long marginals 1. If the preserved elements do not show any specialization with regard to the above named species from the lower-middle Eocene, we cannot exclude an unpreserved specialized element. It appears that, very early during the Eocene, *Neochelys* abundantly diversified. However, in the present state of the material we cannot distinguish a directive line of specialization of the Silveirinha form, even relative to the Spanish more younger elements, and the species is primitive as a whole.

Palaeogeographical implications

The families Podocnemididae and Bothremydidae originated in the continental northern part of the Gondwana, including the northern part of Africa and Brazil during the early-mid-Cretaceous. Podocnemididae, are unknown in Asia and Northern America and only invaded the western part of Europe from the early Eocene (in the state of our knowledge) up to (at least) the late Eocene in Spain (see the Annexe; Lapparent de Broin, 2000a, 2001). Podocnemididae are unknown during the European localities with turtles of the late Cretaceous and Palaeocene (which are few and northern) when only the Bothremydidae are already arrived from Africa, hypothetically by a littoral way at least as soon as the Campanian times. We do not know at which time *Neochelys* precisely diversified, and if it is in Europe or in Africa. *Neochelys* is known from the early MP7 zone of Western Europe, approximately at the same time (Escarguel *et al.*, 1997) in Belgium (Dormaal), France (Rians) and Portugal (Silveirinha) (Antunes *et al.*, 1997; Antunes & Russell, 1981). In Spain, the earliest sure records (undefined species) are from the Cuisian of La Roca, nortwestern Spain, and the records of *N. zamorensis* from the area of Valdegallina, northeastern Spain, which are not precised in age but possibly include late Ypresian as well as Lutetian (MP9-14). Then, *Neochelys* is abundant in Europe, including the Lutetian (lower and upper) from Catalunya-Tremp basins and, in the northwestern Spanish area, up to the upper Eocene at least. In France, *Neochelys* is not known from Meudon (MP7) (Russell *et al.*, 1990). It is neither known from Le Quesnoy (France) (Nel *et al.*, 1999), a locality also situated in the MP7 zone as Silveirinha. *Allaeochelys*, arrived during the early Eocene from Asia, is also absent. Two more primitive turtle taxa than in the other MP7 localities are present (very few specimens): a "chelydroid in aspect" turtle (a remnant from the Palaeocene fauna of the Belgo-French basin) and a new relict taxon, besides a very abundant new geoemydine turtle. This is a Eocene new form different from the geoemydines from Rians and other Eocene European localities. Geoemydines are new Eocene direct immigrants from Asia as *Allaeochelys*. At Le Quesnoy, also are present three trionychine taxa, also known at Dormaal and other early Palaeogene localities of the Belgo-French basin and representative of the Laurasiatic Palaeocene northern fauna, hypothetically with common ancestors with North-American forms. They are unknown in Rians and Silveirinha. The *Trionyx line* and *Allaeochelys* are known during the Ypresian (MP8-9) in southern France and northeastern (from Cuisian) and northwestern Spain. It is evident that while *Neochelys*, arrived from Africa, distributed quickly towards the North, being present as soon as the age of Dormaal in the MP 7 zone, but not in Le Quesnoy, *Trionyx* and *Allaeochelys*, arrived from the

North. They invaded the South so that the three genera meet at least at the time of the MP8-9 zones in the Iberian Peninsula. The ecology of *Trionyx* and *Allaeochelys*, freshwater forms with paddled limbs which need continuous wider and enough deep streams and are awkward on the ground, is different from *Neochelys*, a more amphibian freshwater form (from its carapace morphology and limbs) which probably migrated by rivers but also by small ponds and short dry lands between them as the extant African Pelomedusidae. *Trionyx* and *Allaeochelys* could spend more time to find convenient stream links and go southern to France and Spain, than *Neochelys* to come from Africa and southern Portugal up to south of France and up to Belgium. Nevertheless, from the absence of *Trionyx* and *Allaeochelys* in South (Portugal, France) during the MP 7 zone, we cannot deduce an older age for Silveirinha or Rians than to Dormaal and Le Quesnoy as far as *Neochelys* is concerned. Although, just for the northern part of western Europe, we can recognize an older age for Le Quesnoy than for Dormaal because of the more primitive turtle fauna. However, from the known material, the species from Silveirinha is sufficiently few differentiated to be one of the older *Neochelys* species and the older one from the Iberian Peninsula.

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Annexe

Stratigraphic distribution of the turtles of the subfamily Erymnochelyinae from the Palaeogene of Europe: Belgium, Germany, France, Portugal (stratigraphic data summarized *in* Escarguel *et al.,* 1997, and pers. com. Labarrère and Vidalenc) and Spain (stratigraphic data from Cuesta Ruiz-Colmenares, 1994-1995).

Neochelys is also present in several localities from the Cuisian, Lutetian (mainly), Eocene of Catalunya and Tremp basin (Spain) with many fragments of several large undefined species including an entoplastron of the *N. arribasi* type at la Roca, Cuisian (Material preserved in the Institut de Paleontologia "M. Crusafont", Sabadell, and in the Seminario Conciliar Museum, Barcelona).

Bothremydidae are represented by both *Bothremys* and *Taphrosphys* goups in Europe from the Upper Cretaceous. During the Palaeocene: *Taphrosphys ambiguus* (Gaudry, 1890), Mont-Aimé, France; the Ypresian: *Palaeaspis bowerbanki* (Owen, 1842), London Clay, England; the Lutetian: an indetermined form from Avesa, Italy (Broin, 1977); the Oligocene: *"Chrysemys" montolivensis* Roman, 1897 (not a *Neochelys* as suggested *in* Broin, 1977), Montoulieu, France; and eventually (?) from the Palaeogene of Spain.

Lower Oligocene

(base of Oligocene) + upper EOCENE (upper Priabonian, MP 19-20): Molino del Pico: "Pelomedusidae ind.": Jiménez Fuentes, 1984, 1992, Spain, not figured, Bothremydidae not excluded?

Eocene

Priabonian (top at 33,7 Ma): MP17-18
MP 17-18: Deza, *Neochelys* sp.: Jiménez *et al.,* 1989, Spain.
MP 16-17: Mazateron: *Neochelys* sp.: Jiménez Fuentes *et al.*, 1993-1994, Fuentesaúco (Zamora): *Neochelys* sp. and *N.* aff. *salmaticensis*: Jiménez *et al.,* 1993-1994, Spain.
Bartonian: MP 16-15
?MP 16: Area escarpes del Tormes (Salamanca): Teso de la Flecha: *N. salmanticensis* Jiménez Fuentes, 1968: Jiménez Fuentes *et al.* 1993-1994 and *P. carbajosai* Jiménez Fuentes, 1971 = *Neochelys salmanticensis*: Jiménez Fuentes, 1992 (is it a *Neochelys* species?); Cabrerizos (Los Caenes), Pelomedusidae: Jiménez Fuentes, 1984; Cabrerizos: *Podocnemis entodermica* Jiménez Fuentes, 1970 = *N. salmanticensis*: Jiménez Fuentes *et al.,* 1993-1994; Caenes 2: *N. salmanticensis*: Jiménez Fuentes *et al.*, 1993-1994. Spain.
MP16-15: Aldearrubia: *Podocnemis armuniensis* Jiménez, 1970 = *Podocnemis* sp.: Jiménez, 1971 = *Neochelys* sp. (?): Jiménez Fuentes *et al.*, 1993-1994; Aldearrubia: Teso de las Canteras: *Duerochelys arribasi* Jiménez Fuentes, 1975 = *N. salmaticensis*: Jiménez Fuentes, 1972 = *"Duerochelys" arribasi*: Jiménez Fuentes, 1992 [= *Neochelys arribasi* (Jiménez Fuentes, 1975) mihi]. Babilafuente: *Neochelys* sp.: Jiménez Fuentes & Jambrina-Leal, 1984 and *"Duerochelys" arribasi*: Jiménez Fuentes, 1992. Spain.
MP 15: Castrais, lower part: *Neochelys mengaudi* (Bergounioux, 1935) from the Molasse de Sicardens (holotype lost or specimen mentioned as *"Clemmys pougeti"* in MHNT coll?), France.

Lower Bartonian- upper Ypresian:
Zamora province, Spain:
Lutetian: MP 13-14: El Viso N, S, Sanzoles, Jambrina, Santa Clara de Avedillo, Casaseca de Campeán, Corrales del Vino, Fuente el Carnero...: *N.* aff. *salmanticensis*:

Jiménez Fuentes,1992-1993; Jiménez Fuentes *et al.*, 1989. Correses (Zamora), *Neochelys* sp. : Jiménez Fuentes *et al.*, 1988. Unclear specific differentiation between *N. zamorensis* and *N. salmanticensis* (small to large forms). And

MP ?8-?9-14: Area Cubillos-Valdegallina (Valdegallina, Valdegallina 1,Valdegallina 3 + Tardemayas 2 and Cubillos 3) including Sanzoles, Camino a Escobar, locality of the holotype, MP 13-14? (see above), of *N. zamorensis* Jiménez Fuentes, 1992: Jiménez Fuentes, 1992-1993; Jiménez *et al.*, 1993-1994.

Lutetian: MP 11-14

MP 13

Saint-Germain-en-Laye: *Erymnochelys eremberti* Broin, 1977. Guitrancourt: cf. *Erymnochelys* sp.: Lapparent de Broin *et al.*, 1993. France.

Issel: *Neochelys* sp. (*N. eocaenica*: Broin, 1977). Aiguevives II: *Neochelys* sp. (new locality, Labarrère and Vidalenc coll.). France.

MP12-13 (MP13 -) :

Grès d'Aigne: area of Pépieux-Cesseras =Azillanet (but not the Azillanet bed, top of Calcaire d'Agel, MP 10) = Olonzac: *N. eocaenica* (De Stefano, 1902): Broin, 1977. La Livinière 1: *Neochelys* sp. (and ?*Neochelys* sp.): Broin, 1977; La Livinière 2 (Marnes à tortues et mammifères): *Neochelys* sp., Broin, 1977; Félines 2 (Marnes à tortues et limnées), *Neochelys* sp. France.

MP 12

Rouzillac (new locality, Labarrère and Vidalenc coll.): *Neochelys* sp. France.

ca MP 12: Cava Valle (Avesa), *N. nicolisi* (Zigno, 1890), Italy .

MP11: Argenton-sur-Creuse: *N.* cf. *eocaenica*: Broin, 1977, France. Messel: *N. franzeni* Schleich, 1993, Germany.

Lutetian-Ypresian boundary

ca MP 10-11: Purga di Bolca, Valleco, *N. capellinii* (Zigno, 1889), type species of the genus *Neochelys* Bergounioux, 1954, Italy.

"Ilerdian" (Ypresian + Lutetian?): Coustouge (Aude): *Erymnochelys* cf. *eremberti* (L. Lacombe coll., unpublished), France.

Ypresian (base at 55 Ma): MP 7-10

MP10

Calcaire d'Agel (Niveau Azillanet): *Neochelys* sp. (USTL). Prémontré, Sables à Unios et Térédines (Cuis, Grauves, Monthelon, Mancy), Cuise-Lamothe, Mont-Bernon: *N. eocaenica*: Broin, 1977, Augé *et al.*, 1997, France.

MP 9-10 boundary: Sainte-Eulalie: *Neochelys* sp. (Labarrère and Vidalenc coll., unpublished); Saint-Papoul: *N. laurenti* (Tong, 1998) (= *Neochelys* sp.: Broin, 1977). France.

MP 8-9: Condé-en-Brie, Broyes, Avenay, Mutigny: *N. eocaenica*: Broin 1977, France.

MP 7: Dormaal: *Neochelys* sp.: Godinot *et al.*, 1978, Belgium. Rians: *N. arenarum* Broin, 1977, France. Silveirinha: *Neochelys* sp. (*N.* cf. *arenarum* Broin, *in* Antunes & Russell, 1981), Portugal.

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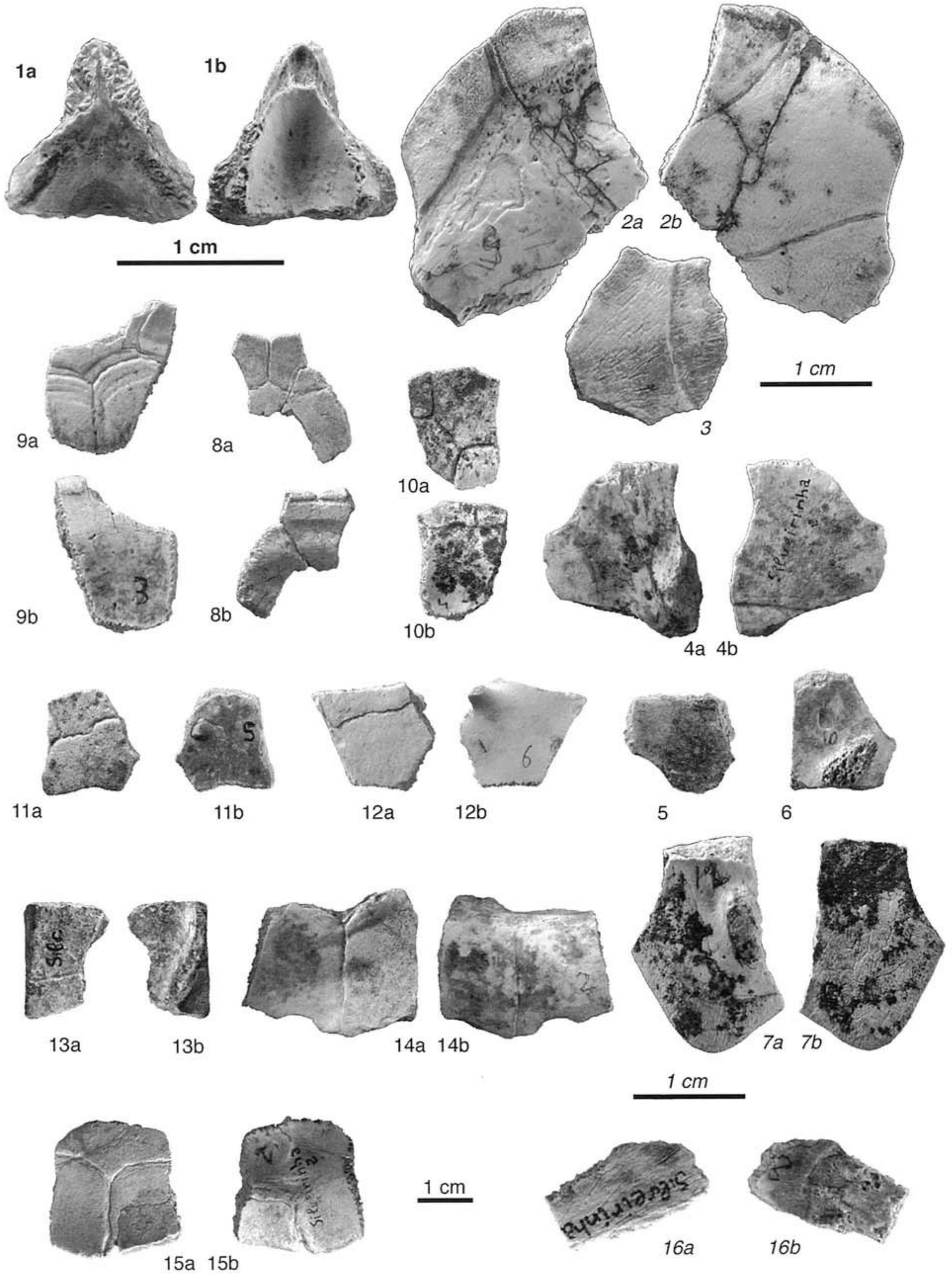
Neochelys sp., Silveirinha, Portugal, early Eocene, MP 7, UNL coll.

Skull:
Fig. 1 a, b – basisphenoid, n° 21, ventral and dorsal views.
Fig. 2 a, b – partial left epiplastron, n° 9, dorsal and ventral views;
Fig. 3 – left mesoplastron, n° 13, ventral view;
Fig. 4 a, b – left partial xiphiplastron, n° 21, dorsal and ventral views;
Fig. 5 – medial part of hyo- or hypoplastron, n° 11, ventral view;
Fig. 6 – partial right xiphiplastron, n° 10, dorsal view;
Fig. 7 a, b – extremity of left xiphiplastron n° 12, dorsal and ventral views.
Fig. 8 a, b – nuchal, n° 23, dorsal and ventral views;
Fig. 9 a, b – left partial peripheral 1, n° 3, dorsal and ventral views;
Fig. 10 – nearly complete right peripheral 1, n° 4, dorsal and ventral views;
Fig. 11 a, b, 12 a, b – proximal extremity of two pleurals 3 or 5, n° 5 and n° 6, dorsal and ventral views;
Fig. 13 a, b – fragmentary left bridge peripheral 7, n° 7, dorsal and ventral views;
Fig. 14, a, b – posterior right peripheral 10, n° 2, dorsal and ventral views;
Fig. 15 a, b – pygal, n°1, dorsal and ventral views;
Fig. 16 a, b – anteromedial fragment of a left pleural 8, n° 8, dorsal and ventral views.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