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

France de Lapparent de Broin

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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 phylaétiques 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 ubiquitous (Americas, western Europe, Africa, Indian continent).

The genus Neochelys Bergouioniux, 1954, has been recognized as a pleurodire (Broin, 1977) and included in the Podocnemidae Cope, 1868. At that time, the Bothremydidae Baur, 1891, were also included in the Podocnemidae. The restoration 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 Podocnemidae: erection of the hyperfamily Podocnemusoidea, including the Podocnemidae reserved to a early derived line of forms, fossill and extant (including Pelomedusa and Pelusios), the Bothremydidae and the Podocnemidae (with Podocnemidinae and Erymnochelyinae and their plesion aff. Teneremys now named Brasillemys 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 Podocnemusoidea, as it is here practiced (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 Podocnemusoidea in Africa and in Europe is given in Lapparent de Broin (2000a, 2001), and the characters at the nodes in the Podocnemusoidea 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 hypothesize the presence of a new species at Silveirinha, which cannot be named and precised in its relationships with the other species.

**Systematics**

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<th>Subclass</th>
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<tr>
<td>Ordo</td>
<td>CHELONII Brongniart, 1800 (Latreille, 1800)</td>
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<td>Infraordo</td>
<td>PLEURODIRA Cope, 1864</td>
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<tr>
<td>Hyperfamily</td>
<td>Podocnemusoidae Cope, 1868</td>
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<td>Subfamily</td>
<td>Erymnochelyinae Broin, 1988a</td>
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<td>Genus</td>
<td>Neochelys Bergouioniux, 1954</td>
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*Neechelys* sp. (fig. 1-16)


**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 polygons (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 sinusuous 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 fresh water Palaeogene Testudinidae. It occurs much later (from Oligocene) in some *Psychogaster* 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, as also 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 fresh water 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* podocnemoides, *S. cromeri* and *S. libyca*, *Podocnemis* - *Daqueymus fajumensis*, *Shweboemys antiqua* (less) and other taxa from Egypt and Africa (see the Fayum forms in Andrews (1906), Daqué (1912), Reinaich (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 basiethmoid (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 basiethmoid. 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 basiethmoid notch of entrance in the sella turcica, i.e. the basal preserved part of the foramen anterior canalis carotic 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 basiethmoid. 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 Mughara, 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 Podocnemididae and the Bothremydidae (when known: *Bothremys* sp. in Gaffney, 1977; the Oman skull in Roger et al., 1994; *Rossasia*, in Antunes & Broin, 1988; *Sohlafah* 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* Martin Suarez, 1969 (late Cretaceous from Brazil), aff. *Roxochelys vilavilensis* Broin, 1971, and the extant *Podocnemis cayennensis*, *P. expansa*, *P. vogli*, *P. lewyanana* and *Peltcephalus 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 moderate in *Peltcephalus dumerilianus*.

The foramina nervi abducentis (6th cranial nerve pair) are not present on the dorsal surface of the Silveirinha basiethmoid 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 basiethmoid, 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 basiethmoid may be eroded). In Bothremydidae and Podocnemididae they are variably advanced and developed, including 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 *Neocheley.* 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 *Neocheley,* 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 Bothremydididae). 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 *Neocheley* 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 1. As in *Neocheley* 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 Silverinha, 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. laurentii* (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. franzensi* 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 *Polystraton provinciale* and *P. mechinorum*). In *Neocheley,* 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 Neocheley* between the lateral extremities of the peripherals 2, not preserved here). It is not clearly notched as in some *Bothremydididae* (*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, Brasillemys,* 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. eocaenica* 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 *Neocheley* species had a rather high and quadrangular shell while other had a more flattened and posteriorly expanded one such as *N. capellini* and *N. eocaenica.* None is as regularly lowered and smooth as in Bothremydid.

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 sinusous 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 *Neocheley* species (Tab. 2) among which some have an elongated pygal as, for example in *Podocnemis* 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 *Peltoschelus*. But there is also an individual variation, as shown by *N. capellinii* and *N. eocaenica* that we cannot measure 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 *Taphrophysys* 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 vertebrales 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 vertebrales 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 Pelomedusoidae 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 Pelomedusoidae, except in *Stereogenys* and some *Pelusios* spp., and the last neural did not join the suprapygal, as in all the Pelomedusoidae, 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 trapezoid-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 *Peltoschelus*, less than in *Podocnemis*), narrower than in *Peltoschelus* and *Shweboemys* in Podocnemididae. In Bothremydidae, it is wider and relatively shorter in the *Bothremys* group and much enlarged rounded or trapezoid in the *Taphrophysys* 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 *Taphrophysys* group.

Epiplastron. The fragmentary epiplastron (fig. 2g) lacks the medial symphysis part and the lateroanterior part. The medioanterior 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 salient. The epiphyostrastral 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 epiphyostrastral suture as in all the *Neochelys* spp. and in most of the Podocnemididae Erymnochelyinae, the most derived condition, more than in most 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 epiphyostrastral suture or partly anterior (*Polysternon, Elochelys*) but less anterior than in Erymnochelyinae.

If we compare with other Podocnemididae, the entoplastron was quadrangular-rhomboïd 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*, *Peltoschelus*, *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. franzensi* or with a large intraspecific variability (*N. arenarum*). In the *Erymnochelys* line, represented during the Iberian-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 medi ally posterior to the epiphyoplastral suture (*Stereogenys*) and the humeropectoral sulcus is not completely anterior to the suture (*Elochelys*, "*Shweboemys pisdurensis*"), but 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 pronounced than in other species (some *N. laurentii*) 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 (*Podocnemis* holotype) and the anterior border is concave. It also occurs by homoplasy.

In *Neochelys* the intergular is anteriorly more protruded-rounded (*Podocnemis* holotype) and the anterior border is concave. It also occurs by homoplasy.

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, which is the case in several specimens of the *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 Bothremydididae, 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 mesoplastra. 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 Bothremydididae, 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 Bothremydididae by homoplasy but it is rare compared to Podocnemididae where it is the rule. If both families tend to the abdominal advancing, Bothremydididae 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 positioned (derived condition) on the hyoplastron.

**Xiphiplastron**: 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 characterizes 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 femoral 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.

<table>
<thead>
<tr>
<th>Skull number</th>
<th>Si</th>
<th>Do</th>
<th>Ri</th>
<th>Ca</th>
<th>Lau</th>
<th>Fran</th>
<th>Eoc</th>
<th>Zam</th>
<th>Salm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>2</td>
<td>3/?</td>
<td>0</td>
<td>6</td>
<td>1</td>
</tr>
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<td></td>
<td></td>
<td>(1, and 1</td>
<td>? + d)</td>
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<td></td>
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</table>

<table>
<thead>
<tr>
<th>Species</th>
<th>S1</th>
<th>Do</th>
<th>Ri</th>
<th>Ca</th>
<th>Lau</th>
<th>Fran</th>
<th>Eoc</th>
<th>Zam</th>
<th>Salm</th>
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<tbody>
<tr>
<td>Nuchal ant border</td>
<td>narrow</td>
<td>wide</td>
<td>narrow</td>
<td>wide</td>
<td>narrow</td>
<td>narrow</td>
<td>wide</td>
<td>wide</td>
<td>narrow</td>
</tr>
<tr>
<td>M1/nuchal</td>
<td>mid-long to long</td>
<td>short</td>
<td>mid-long</td>
<td>short</td>
<td>short to mid-long</td>
<td>mid-long</td>
<td>short</td>
<td>mid-long</td>
<td>long</td>
</tr>
<tr>
<td>M1w</td>
<td>rather narrow</td>
<td>?</td>
<td>narrow</td>
<td>wide</td>
<td>wide</td>
<td>narrow</td>
<td>narrow</td>
<td>wide</td>
<td>wide</td>
</tr>
<tr>
<td>Per points</td>
<td>yes</td>
<td>yes</td>
<td>no</td>
<td>yes</td>
<td>yes</td>
<td>weak</td>
<td>yes</td>
<td>yes</td>
<td></td>
</tr>
<tr>
<td>Per 2 width</td>
<td>?</td>
<td>?</td>
<td>wide</td>
<td>wide to mid-wide</td>
<td>mid-wide</td>
<td>mid-wide</td>
<td>mid-wide</td>
<td>wide</td>
<td>mid-wide</td>
</tr>
<tr>
<td>V1/nuchal</td>
<td>wider</td>
<td>wider</td>
<td>wider</td>
<td>wider</td>
<td>wider, anteriorly clearly narrowed in lyre as wide or ca</td>
<td>wider</td>
<td>wider</td>
<td>wider</td>
<td></td>
</tr>
<tr>
<td>Pygal I/L%</td>
<td>933</td>
<td>?</td>
<td>7692</td>
<td>71,57-83,36</td>
<td>70</td>
<td>70278163</td>
<td>72,94 ca 83</td>
<td>7294</td>
<td>9523</td>
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<tr>
<td>Car max size</td>
<td>21-28 cm</td>
<td>17,8 cm</td>
<td>25 cm</td>
<td>31 cm</td>
<td>365</td>
<td>24 cm</td>
<td>35 cm</td>
<td>30 cm</td>
<td>ca 44 cm</td>
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<td>?rather wide rounded (narrow?) rather rounded</td>
<td>rather wider straight rather wider rounded</td>
<td>rather wider rounded</td>
<td>rather wider (AL&gt;PL) rounded</td>
<td>rather wider rounded</td>
<td>rather wider rounded</td>
<td>narrow straight</td>
<td>rather wide rounded</td>
<td></td>
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<tr>
<td>Saliant gular</td>
<td>yes much</td>
<td>yes or no</td>
<td>no to weakly</td>
<td>no to weakly</td>
<td>yes or no</td>
<td>no</td>
<td>no</td>
<td>yes much (typically) to no</td>
<td>no (typically) to weakly</td>
</tr>
<tr>
<td>AL angle</td>
<td>rounded</td>
<td>± rounded or angular</td>
<td>angular</td>
<td>Rounded or angular</td>
<td>rounded</td>
<td>rounded</td>
<td>rounded</td>
<td>rounded</td>
<td>rounded</td>
</tr>
<tr>
<td>Al border</td>
<td>Rounded straight or rounded</td>
<td>straight</td>
<td>rounded</td>
<td>rounded</td>
<td>rather straight (typically) to rounded</td>
<td>rounded</td>
<td>rounded</td>
<td>rounded</td>
<td></td>
</tr>
<tr>
<td>Ant Ig width</td>
<td>?</td>
<td>narrow</td>
<td>narrow</td>
<td>wide</td>
<td>narrow</td>
<td>mi-wide</td>
<td>mi-wide to narrow</td>
<td>mid-wide</td>
<td></td>
</tr>
<tr>
<td>Ig/HP contact</td>
<td>?</td>
<td>no</td>
<td>no to narrow contact</td>
<td>no</td>
<td>no</td>
<td>very wide</td>
<td>no to ± wide</td>
<td>no to yes narrow</td>
<td>no to wide</td>
</tr>
<tr>
<td>Gul w/ Ig w</td>
<td>?</td>
<td>wide</td>
<td>Wide</td>
<td>moderate</td>
<td>wide</td>
<td>narrow</td>
<td>mid-wide</td>
<td>mid-wide</td>
<td>mid-wide to wide</td>
</tr>
<tr>
<td>Gul I/Ig l</td>
<td>?</td>
<td>long; onto overlap</td>
<td>long; onto overlap</td>
<td>short to mid-long; onto just contact or no</td>
<td>mid-long to long; Gul shorter or Ig=Gul; onto overlap or no</td>
<td>short; no onto contact</td>
<td>short-mid-long; contact or no</td>
<td>long; onto overlap</td>
<td>mid-long to long; onto overlap or no</td>
</tr>
<tr>
<td>Anal notch depth</td>
<td>22,91</td>
<td>31,8/43,33</td>
<td>mid/long</td>
<td>33,33</td>
<td>mid</td>
<td>25/35,71</td>
<td>short/mid</td>
<td>43,48</td>
<td>long</td>
</tr>
<tr>
<td>Anal notch outline</td>
<td>straight</td>
<td>rounded</td>
<td>straight</td>
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<td>straight</td>
<td>straight</td>
<td>slightly rounded</td>
<td>straight</td>
<td></td>
</tr>
</tbody>
</table>

Tab. 2 - Comparative shell characters of the **Neocheles** 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. S1, 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 overlapping 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 I/L%: ratio posterior width on mediad 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 I 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 I/Ig l: gular length with respect to the intergular length: short or mid-long to long, not contacting or contacting or overlapping 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 synphysis (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 basiaphenoid consistent with that of *Neochelys* as known in *N. arenarum*. Also convenient are the decoration, the growth annuli 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 mediolateral abdominal marginal 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 Brion, 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, northwestern 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* sp. 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 MP7 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.

Acknowledgements

I particularly thank Prof. Dr. M. T. Antunes (Silveirinha material and for his kind help), M. J. Martín Roldan and Dr. Antonio de la Peña (Valdegallina material), M.M. A. Galoyer and F. Escuillé (Saint-Papoul material), H.P. Labarrère and Dr. D. Vidalenc (Aiguevives II, Rouzillac, Sainte-Eulalie, Saint-Papoul material and stratigraphic data), B. Marandat (new material from Calcaire d’Agen and Sainte-Eulalie, USTL, Montpellier II), Dr. E. Jiménez Fuentes (slides from Teso de la Flecha material, Salamanca University), Dr. S. Calzada Badia (Seminario Conciliar, Barcelona), Dr. J. Agusti and Dr. A. Galopart i Lorente (Institut de Paleontologia “M. Crusafont”, Sabadell), S. Chapman (The Natural History Museum), E. Brahm, Dr. J. Habersetzer and Dr. S. Schaal (Naturmuseum Senckenberg, Frankfurt am Main), Dr. R. Wild (Staatliches Museum für Naturkunde-Stuttgart) for the kind permission of the observation of their fossil material; P. Loubry and D. Serrette (photographs), H. Lavina (plate), Paléontologie, MNHN.

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* groups 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


Jiménez Fuentes, 1984, 1992, Spain, not figured, Bothremydidae not excluded?

Eocene

Priabonian (top at 33,7 Ma): MP17-18


Bartonian: MP 16-15


MP 15: Castraños, lower part: *Neochelys mengaudi* (Bergouinoux, 1935) from the Molasse de Sicardens (holotype lost or specimen mentioned as "Clemmys pougetii" 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, Cassacea de Campeán, Corrales del Vino, Fuente el Carnero... *N. aff. salmanticensis*:

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MP 12 Rouzillac (new locality, Labarrère and Vidalenc coll.): Neocheles sp. France.

c Sample MP 12: Cava Valle (Avesa), N. nicolisi (Zigno, 1890), Italy .


References


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

Skull:
Fig. 1 a, b – basisphenoid, nº 21, ventral and dorsal views.
Fig. 2 a, b – partial left epiplastron, nº 9, dorsal and ventral views;
Fig. 3 – left mesoplastron, nº 13, ventral view;
Fig. 4 a, b – left partial xiphiplastron, nº 21, dorsal and ventral views;
Fig. 5 – medial part of hyo- or hypoplastron, nº 11, ventral view;
Fig. 6 – partial right xiphiplastron, nº 10, dorsal view;
Fig. 7 a, b – extremity of left xiphiplastron nº 12, dorsal and ventral views.
Fig. 8 a, b – nuchal, nº 23, dorsal and ventral views;
Fig. 9 a, b – left partial peripheral 1, nº 3, dorsal and ventral views;
Fig. 10 – nearly complete right peripheral 1, nº 4, dorsal and ventral views;
Fig. 11 a, b, 12 a, b – proximal extremity of two pleurals 3 or 5, nº 5 and nº 6, dorsal and ventral views;
Fig. 13 a, b – fragmentary left bridge peripheral 7, nº 7, dorsal and ventral views;
Fig. 14, a, b – posterior right peripheral 10, nº 2, dorsal and ventral views;
Fig. 15 a, b – pygal, nº 1, dorsal and ventral views;
Fig. 16 a, b – anteromedial fragment of a left pleural 8, nº 8, dorsal and ventral views.