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PLEURODIRAN TURTLES FROM THE EOCENE OF SAINT PAPOUL (AUDE), SOUTHERN FRANCE

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Abstract : Pleurodiran turtle remains including a well-preserved skull and isolated plates from the Eocene Saint Papoul locality (Aude, southern France) are described in detail and referred to the family Podocnemididae. The skull belongs to a new genus and species, *Papoulemys laurenti.* Its phylogenetic relationships are discussed.

Key words : Eocene, Southern France, Testudines, Pleurodira, Podocnemididae, Papoulemys laurenti, Phylogeny,

Tortues pleurodires de l'Eocène de Saint Papoul (Aude, France)

Résumé : Des restes de tortues pleurodires comprenant un crâne en bon état et des plaques isolées provenant du gisement de Saint Papoul (Aude, France) sont décrits en détail et attribués à la famille des Podocnemididae. Le crâne appartient à un nouveau genre et une nouvelle espèce, *Papoulemys laurenti.* Ses relations phylogénétiques sont discutées.

Mots clés : Eocène, Sud France, Testudines, Pleurodires, Podocnemididae, Papoulemys laurenti, Phylogénie,

INTRODUCTION

The Saint Papoul locality is a large clay pit located about 20 km northwest of Carcassonne, (Aude, Southern France). For more than twenty years, this locality has been well known for its abundant vertebrate remains, especially among amateur paleontologists and fossil collectors, but up to now, only a few shell fragments of indeterminate Pelomedusidae have been mentioned (Broin, 1977). The fossils come from continental grey clays and sandstones with plant remains containing a rich vertebrate fauna, which includes fishes, crocodiles, turtles and mammals. Although the Saint-Papoul locality has been considered as early Lutetian (Middle Eocene) in age (Cavaillé *et al.*, 1972) its mammal fauna indicates a Cuisian (Early Eocene) age (H.P. Labarrère, pers. com.). Turtle remains are extremely abundant, and both cryptodirans and pleurodirans are present. The cryptodiran turtles, which are much more abundant than pleurodiran turtles, are represented by trionychids and emydids and will be described in a separate paper. The pleurodiran turtles, including a nearly complete skull and several isolated plates, can be referred to the family Podocnemididae. The skull represents a new genus and new species. The turtle remains described in this paper have been collected by Yves Laurent, Guy Le Roux and the Musée des Dinosaures d'Espéraza (Aude, France) during 1992-1996.

SYSTEMATIC PALAEONTOLOGY

Order TESTUDINES Linnaeus, 1758
Suborder PLEURODIRA Cope, 1864
Hyperfamily PELOMEDUSOIDES Cope, 1868
Family PODOCNEMIDIDAE Cope, 1868

Genus PAPOULEMYS gen. nov.

Types species.
Papoulemys laurenti sp. nov.

Derivation of name.
from the type locality : Saint Papoul.

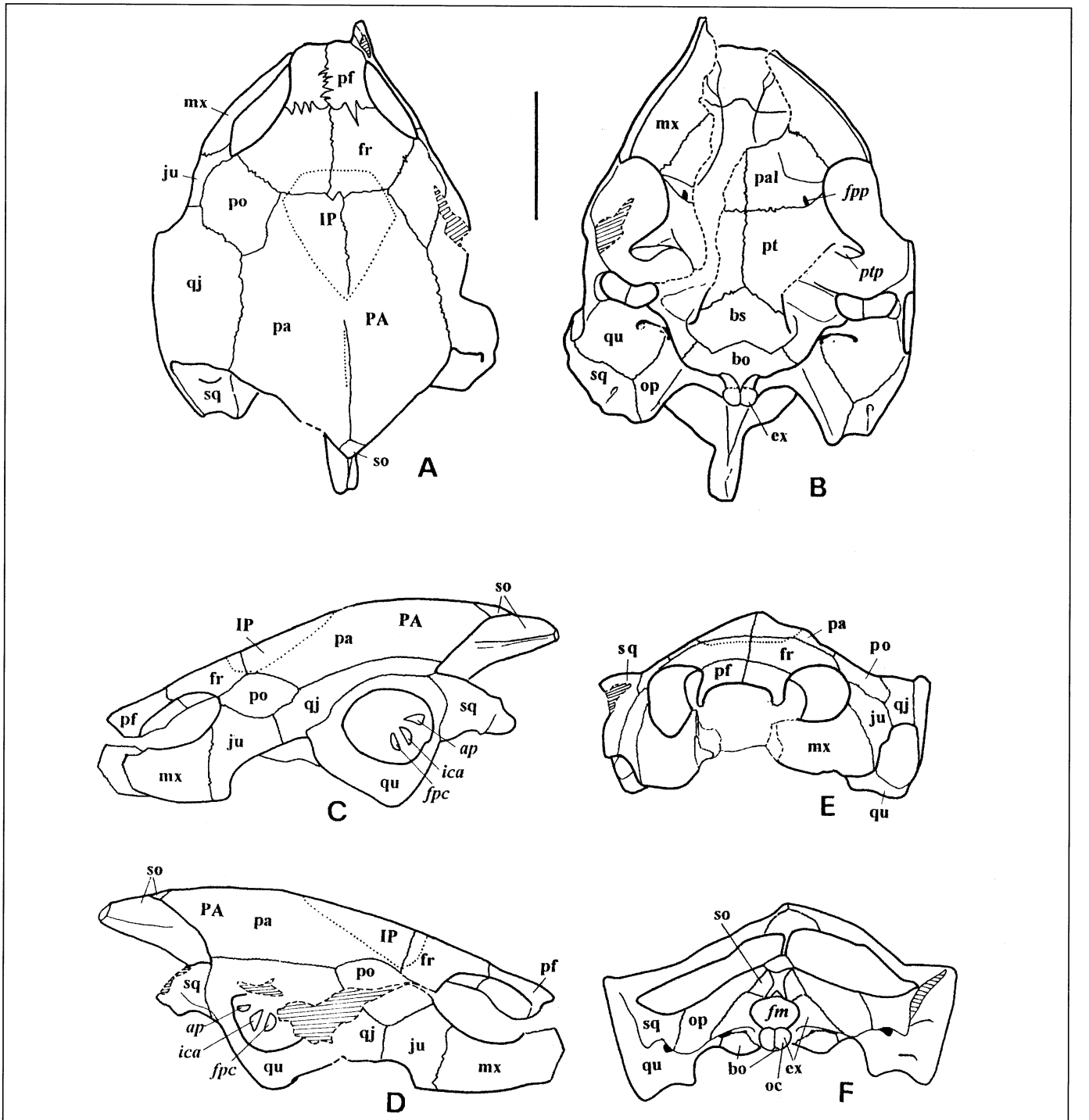

Fig. 1 : Skull of *Papoulemys laurenti* n. gen. et sp. nov. (type, n° T12, Musée des Dinosaures, Espéraza) in dorsal (A), ventral (B), left lateral (C), right lateral (D), anterior (E) and posterior (F) views. Scale bar : 2 cm. Abbreviations : ap : *antrum postoticum,* bo : basioccipital, bs : basisphenoid, ex : exoccipital, fm : *foramen magnum*, fpc : *fossa precolumellae*, fpp : *foramen palatinum posterius,* fr : frontal, ica : *incisura columellae auris,* ju : jugal, mx : maxilla, oc :occipital condyle, op : opisthotic, pa : parietal, pal : palatine, pf : prefrontal, pmc : pterygoid muscle chamber, po : postorbital, pt : pterygoid, ptp : *processus trochlearis pterygoidei,* qj : quadratojugal, qu : quadrate, so : supraoccipital, sq : squamosal.

Fig. 1 : Crâne de *Papoulemys laurenti* gen. et sp. nov. (type, n° T12, Musée des Dinosaures, Espéraza) en vue dorsale (A), ventrale (B) et latérale gauche (C) latérale droite (D), antérieure (E) et postérieure (F). Echelle : 2 cm.

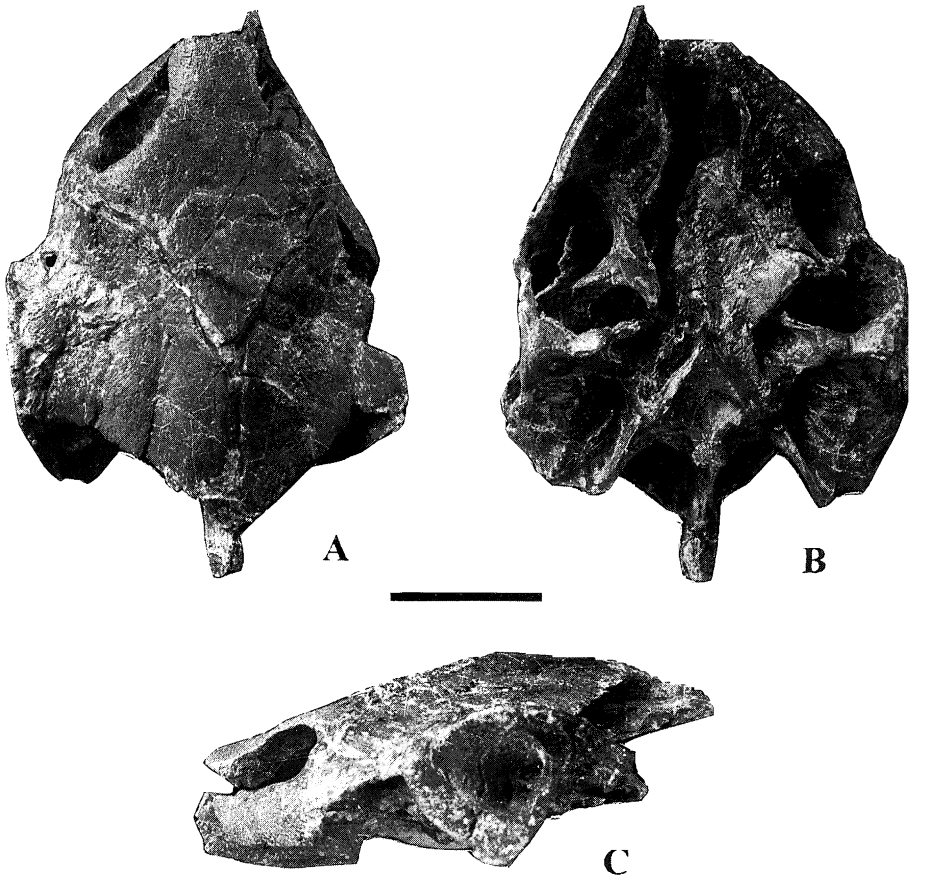

Fig. 2 : Skull of *Papoulemys laurenti* gen. et sp. nov., type, n° T12, Musée des Dinosaures, Espéraza) from Saint Papoul in dorsal (A), ventral (B) and left lateral (C) views. Scale bar : 2 cm.
Fig. 2 : Crâne de *Papoulemys laurenti* gen. et sp. nov., type, n°T12, Musée des Dinosaures, Espéraza) de Saint Papoul en vues dorsale (A), ventrale (B) et latérale gauche (C). Echelle : 2 cm.

Papoulemys laurenti sp. nov.
Figures 1-2

Derivation of name : In honor of Yves Laurent who discovered the skull.

Holotype : A nearly complete skull (n° T12, Musée des Dinosaures, Espéraza, Aude, France).

Type horizon and locality :
Cuisian, Early Eocene, Saint-Papoul (Aude, France)

Diagnosis : Podocnemidid turtle with the occipital condyle constitued mainly by the exoccipitals, the basioccipital nearly excluded from it; a large cheek emargination which is longer than high, preventing a contact between the jugal and the quadrate; short prefontals which do not completely cover the *apertura narium externa* dorsally; a long triangular skull in dorsal view, dorsolaterally directed orbits, a relatively wide and flat interorbital space, a smooth triturating surface without additional ridges and a weak temporal emargination.

DESCRIPTION

Measurements : Maximum preserved length : 7.7 cm (from the snout to the posterior end of the *crista supraoccipitalis*); maximum width : 5.5 cm (at the level of the *cavum tympani*).

Preservation : The rather well-preserved skull, without a lower jaw, is nearly complete and slightly crushed dorsolaterally; the right side including the quadratojugal and the quadrate, the posterior end of the crista supraoccipitalis, the palatal region between the triturating surfaces and the right pterygoid are damaged.

General aspect : The general aspect of the Saint Papoul turtle skull is similar to that of the living *Erymnochelys madagascariensis*. The surface of the skull roof is smooth. The skull has roughly the shape of a long triangle in dorsal view. The orbits, which are oval in shape and longer than high, are dorsolaterally directed; the oval shape of the orbits may be, at least in part, due to the deformation of the skull.

The snout region is a little damaged, the snout is narrow and is not wider than the interorbital space, the *apertura narium externa* are anterodorsally directed. In *E. madagascariensis,* the latter are anteriorly directed. The temporal emargination is weak, as in *E. madagascariensis*, and the *crista supraoccipitalis* is well developed. In lateral view, the skull is higher posteriorly and slopes down forwards. The premaxillae are not preserved, so we do not know whether the Saint Papoul specimen had a beak as in *E. madagascariensis* or not. Contrary to the latter, in which the cheek emargination is very shallow, the Saint Papoul skull has a deep cheek emargination which is longer than high.

Skull roof scales : A long pentagonal-shaped interparietal scale is present. It tapers posteriorly, and the parietal scales meet each other behind it. Other scales cannot be distinguished.

Dermal roofing elements : The prefrontals are complete and similar to those of *E. madagascariensis,* but they seem to be slightly flatter and shorter. The length of the prefrontals in our specimen is shorter than that of the frontals, the dorsal exposure of the prefrontals is square in shape, so they do not cover completely the *apertura narium externa* dorsally; whereas in *E. madagascariensis* the prefontals and the frontals have similar lengths, the dorsal exposure of the prefrontals is longer than wide, the *apertura narium externa* is not visible dorsally. Both frontals are complete and identical to those of *E. madagascariensis*, with a flat hexagonal dorsal exposure and an anterior spur on the ventral side extending forwards between the prefrontals. There is no interorbital groove, contrary to *Podocnemis*. The suture between the frontals and parietals is straight, moreover the frontal contacts the postorbital posterolaterally. In ventral view, the *sulcus olfactorius* is limited by well developed ridges. The parietals are complete but slightly deformed, they are similar to those of the Malagasy species. The parietal is a large triangular element forming much of the skull roof, it forms the large medial part of the temporal emargination and contacts the quadratojugal laterally by a long and straight anteroposteriorly directed suture. The *processus inferior parietalis* is damaged on both sides, the contacts are not distinguishable. The left postorbital is complete but the right one is a little damaged. As in *E. madagascariensis*, the postorbital of the Saint Papoul specimen is large with an anteroposteriorly elongated diamond-shaped dorsal exposure, it completely separates the jugal from the parietal and does not reach the temporal emargination. Anteriorly the postorbital forms a very small part of the posterior rim of the orbit, anterolaterally it contacts the jugal, posterolaterally the quadratojugal and posteromedially the parietal. The left jugal is the best preserved. Because of the large cheek emargination, the Saint Papoul specimen has a much smaller jugal than *E. madagascariensis* and it does not contact the quadrate, contrary to the condition in the latter. The jugal forms the posteroinferior rim of the orbit and the anterior half of the rim of the cheek emargination; it contacts the maxilla anteriorly, the postorbital dorsally, the quadratojugal posteriorly, the palatine and the pterygoid ventrally. The left quadratojugal is the best preserved, although deformed; it is an anteroposteriorly elongated element and forms a small part of the rim of the cheek emargination between the jugal and the quadrate; its contact with the jugal anteriorly is short and vertical; ventrally it contacts the quadrate and posteroventrally the squamosal. The left squamosal is complete while the right one is a little damaged posteriorly. Its lateral and ventral exposure is the same as in *E. madagascariensis* with a protuberance on the ventrolateral surface, near the posterolateral edge.

Palatal elements : Both premaxillae are missing. Both maxillae are a little damaged on the ventromedial margin. As in *E. madagascariensis*, the maxilla forms the lateral part of the *apertura narium externa*, the lower margin of the orbit and a large part of the triturating surface. The maxilla seems to be a little lower in lateral view than in *E. madagascariensis.* The triturating surface is wider posteriorly and smooth with a well developed labial ridge. The maxilla contacts the prefrontal anterodorsally by a short suture, which is much shorter than that of *E. madagascariensis*; moreover it contacts the palatine ventromedially, the jugal posteriorly. The right palatine is damaged by a fissure while the left one is complete. It is similar to that of *E. madagascariensis* : it forms the posteromedial part of the triturating surface and the posterior margin of the *apertura narium interna*, and contacts the pterygoid posteriorly. The large

foramen palatinum posterius is placed just before the palatine/pterygoid suture, posteriorly to the orbit.

Palatoquadrate elements : Both pterygoids are a little damaged but the left one is more complete. As in *E. madagascariensis*, the palate is slightly concave; the *processus trochlearis pterygoidei* is well developed and transversal. Although damaged, the pterygoid seems to present a posterior flange to cover ventrally the median part of the enlarged pterygoid muscle chamber. The suture between the pterygoid and the basisphenoid is markedly convex anteriorly. The dorsal structure and contacts of the pterygoid, as well as those of the quadrate are difficult to observe because of the skull roof. The left quadrate is complete while the right one is damaged in its anterodorsal part. As in *E. madagascariensis*, laterally the quadrate forms the funnel-shaped *cavum tympani*. The *incisura columellae auris* which is completely enclosed by bone is large and triangular in shape, including the Eustachian tube.
The *precolumellar fossa* is medium-sized and rounded in shape. The *antrum postoticum* is medium-sized and deep, its oval shape may be due to dorsoventral crushing. Ventrally the quadrate forms a transversally elongated and concave mandibular condyle and sends a medial process to contact both the basisphenoid and the basioccipital. The pterygoid muscle chamber, which is formed by the quadrate laterally, the pterygoid anteromedially and the basisphenoid posteromedially, is large and deep; its anterior end is damaged on both sides, but the left one is better preserved.
The *foramen posterius canali carotici interni is* damaged on both sides, it seems to be large. In posterior view, the *fenestra postotica* is large and continuous laterally with the *incisura columellae auris*, but separated from the *foramen jugulare posterius* by the opisthotic.

Braincase elements : The supraoccipital is nearly complete, except that the posterior end of the *crista supraoccipitalis* is broken off; it is similar to that of *E. madagascariensis*, the dorsal exposure posterior to the parietal on the skull roof is very small; the supraoccipital forms the dorsal margin oh the *foramen magnum* and contacts the parietals anterodorsally, the opisthotic laterally and the exoccipital ventrally. Both exoccipitals are complete. As in *E. madagascariensis*, the exoccipitals form most of the occipital condyle, in which a small vertical groove is present in the middle. The basioccipital is nearly excluded from the occipital condyle. The exoccipital contacts the supraoccipital dorsally, the opisthotic laterally and the basioccipital ventrally, two small *foramina nervi hypoglossi* are present in the exoccipital, near the basis of the occipital condyle. The basioccipital is complete. In ventral view, it has roughly the shape of a wide triangle and presents a concavity which occupies nearly all its ventral surface. This concavity seems to be stronger than that of *E. madagascariensis*; but the posterolateral prominence for muscle attachement is not as developed as in the latter. Posteriorly, the basioccipital sends a point between the exoccipitals and stops at the basis of the occipital condyle, thus it contributes very little to the occipital condyle, at the middle of the ventral margin only. The basisphenoid is complete, it contacts the pterygoid anteriorly, the quadrate laterally and the basioccipital posteriorly. Its roughly triangular-shaped ventral exposure seems to be a little narrower than that of *E. madagascariensis*, with an anteromedially directed groove on each side. The prootic is damaged on both sides, and difficult to be observed because of the skull roof. The left opisthotic is complete while the right one is slightly damaged on the posterior end. It is not different from that of *E. madagascariensis* : this is an anteromedially elongated element with a strong ridge on its posteromedial margin on the ventral side.

Podocnemididae indet.

Several isolated plates can be referred to the Podocnemididae. The surface of these plates is rugose, some with a light costulated ornamentation, but the "pelomedusian ornamentation" is not well marked, which is different from the bothremydids.

Nuchal : Two nuchals can be referred to Pelomedusoides by the absence of the cervical scute. The larger one (n° T13 : length = 6 cm (estimated), width = 6 cm) shows a slightly concave anterior margin, with a narrow anterior part in which the lateral margins are parallel to each other for a third of their length, and a relatively large first marginal scute which is longer than wide in the part which is located on the nuchal bone; the small one (n° T14 : length = 3.6 cm, width = 3.4 cm) is similar to the large one.

Costal 1 : One right first costal bone (n° T15 : length = 6.2 cm, width = 8 cm) is preserved, it presents the sulci for the first and second vertebral scutes on the dorsal surface and an anterolaterally directed elongated triangular scar on the lateral third of the ventral surface for the insertion of the axillary buttress.

Costal 8 : two left eighth costal bones (n° T16 : length = 2.5 cm, width = 4.5 cm; n° T17 : length = 2.7cm, width = 4.8 cm) are preserved, both present a half oval scar on the antero-ventral surface for the insertion of the ilium.

Hyoplastron : Four hyoplastra are preserved. The largest one (n° T18 : length = 9 cm, width = 9 cm) is the most complete and presents an anteriorly convex abdomino-pectoral sulcus passing at about the anterior 2/5 of the median length and its lateral end reaches the anterior tip of the mesoplastron. The median length of the hyoplastron is about one and a half times that of the entoplastron, which can be estimated from the ento-hyoplastral suture. On the dorsal side, a very strong axillary buttress is present. Other hyoplastra are less complete and similar to the large one.

Mesoplastron : One incomplete left mesoplastron is preserved (n° T19 : length = 3.8 cm), its lateral part is missing. It is cut by the pectoro-abdominal sulcus at the anterior tip.

Xiphiplastron : Two xiphiplastra are preserved. Both have two scars on the dorsal surface, the anterior one, for the pubic insertion, is long oval in shape and the posterior one is long triangular in shape and placed near the anal notch. The larger xiphiplastron (n° T20 : length = 8 cm, width = 6.5 cm), which is not complete, presents an anal notch less concave than that of the small one (n° T21 : length = 4 cm, width = 3 cm).

COMPARISONS AND DISCUSSIONS

The pleurodiran turtle skull from Saint Papoul clearly belongs to the family Podocnemididae because of the morphology of the skull, especially the much enlarged pterygoid muscle chamber and the broad quadratojugal/parietal contact, which are synapomorphies defined by Gaffney and Meylan (1988). The Podocnemididae are known from the Middle Cretaceous to the Pliocene in Africa (Wood, 1984; Hirayama, 1992; Tong & Buffetaut, 1996), the Recent of Madagascar, the Late Cretaceous to Recent in South America (see Pritchard & Trebbau, 1984; de Broin, 1994; Kischlat, 1994), the Eocene (and maybe the Oligocene) of Europe (see Broin, 1977, 1988) and the Tertiary of South Asia (see Wood, 1984).

Comparisons are made first with the European podocnemidids which are widespread in southern and western Europe (Portugal, Spain, France, Italy, Belgium and England) and very abundant during the Eocene (Broin, 1977, 1988; Jiménez Fuentes, 1993). Most of them are represented only by shell material and referred to the genus *Neochelys*. Well preserved skull and shell material of *Neochelys arenarum* de Broin, 1977 from the Sparnacian (Early Eocene) of Rians (Var, Southern France) has been described in detail (Broin, 1977). This is the only available description of the skull of this genus and it allows comparisons with the Saint Papoul skull. Although the short antorbital space, the prefrontals shorter than the frontals and the presence of a cheek emargination which separates the jugal from the quadrate are reminiscent of *Neochelys*, the Saint Papoul skull presents some differences from the latter :

1) The Saint Papoul skull is more elongated, having the shape of an elongated triangle in dorsal view, while the skull of N. *arenarum* is shorter and wider, even though the width of the type specimen figured by Broin is exaggerated (Broin, 1977).

2) One important character that de Broin used to differentiate *Neochelys* from other closely related forms such as *Erymnochelys* is that the length of the palate from the snout to the palatine/pterygoid suture (A) is shorter than the width of the palate at this suture (B) in *Neochelys* (A/B = 77-85 %), but in other forms this length is larger than the width. The Saint Papoul skull has this palatine length larger than the width, the proportion between them (A/B = 121%) is similar to that of *Erymnochelys madagascariensis* (A/B = 123 %).

3) Although the Saint Papoul skull also has the prefontals slightly shorter than the frontals, as in *Neochelys*, they do not cover completely the *apertura narium externa* dorsally contrary to the condition in the latter.

4) The occipital condyle is formed mainly by the

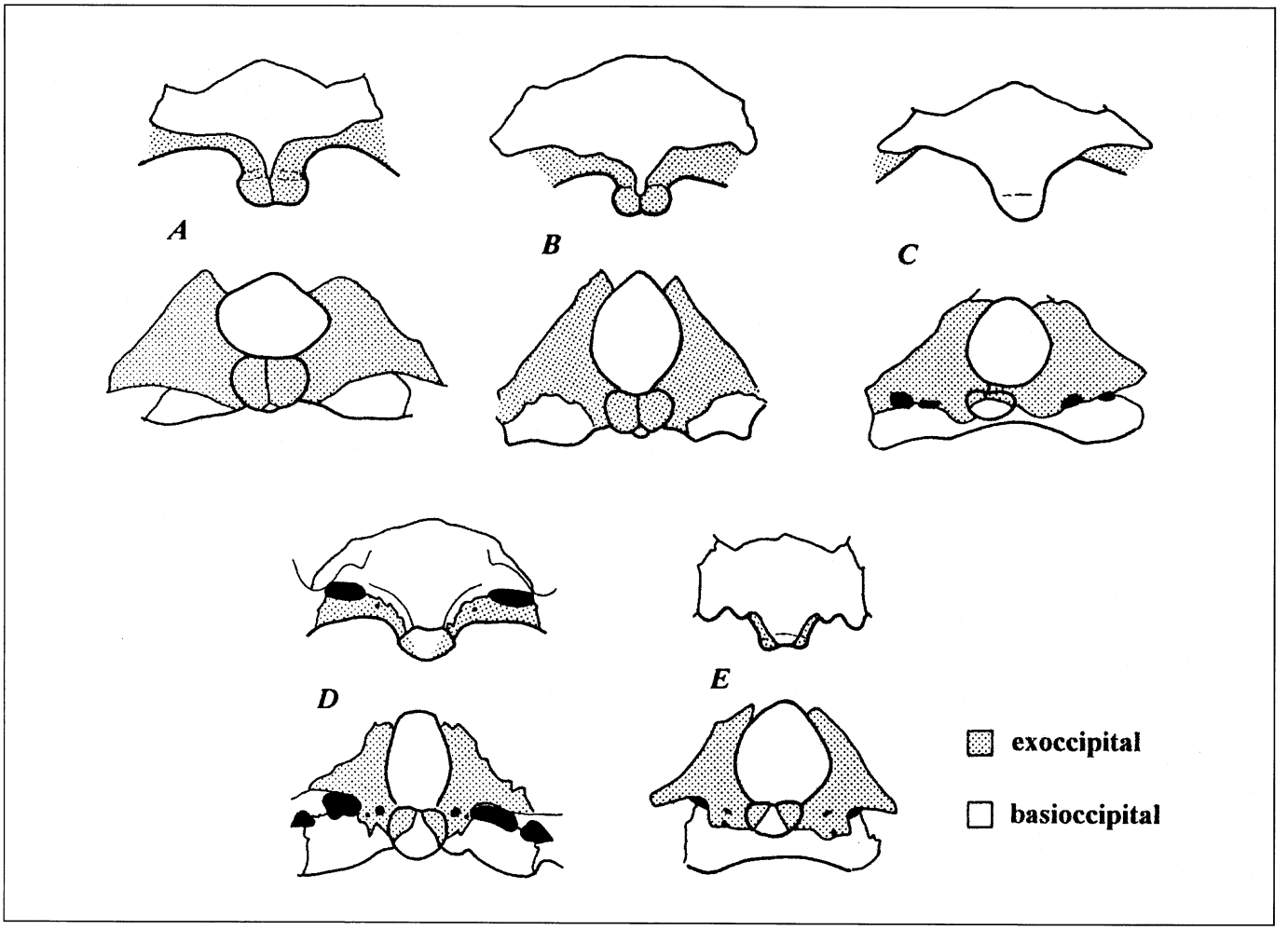

Fig. 3 : Detail of the occipital condyle in some Podocnemididae. Upper : ventral view, lower : posterior view. A : *Papoulemys laurenti* gen. et sp. nov. (n° T12, Musée des Dinosaures, Espéraza); B : *Erymnochelys madagascariensis* (after Tronc and Vuillemin, 1973); C : *Neochelys arenarum* (after Broin, 1977); D : *Peltocephalus dumeriliana* (after Gaffney, 1979); E : *Podocnemis lewyana* (MNHN 8985, type, Muséum National d'Histoire Naturelle de Paris). Not to scale.

Fig. 3 : Détail du condyle occipital chez certains Podocnemididae. En haut : vue ventrale, en bas : vue postérieure. A : *Papoulemys laurenti* gen. et sp. nov. (n°T12, Musée des Dinosaures, Espéraza); B : *Erymnochelys madagascariensisi* (d'après Tronc et Vuillemin, 1973); C : *Neochelys arenarum* (d'après Broin, 1977); D : *Peltocephalus dumeriliana* (d'après Gaffney, 1979); E : *Podocnemis lewyana* (MNHN 8985, type, Muséum National d'Histoire Naturelle de Paris). Sans échelle.

exoccipitals, the basioccipital sends a point posteriorly between the exoccipitals and stops at the basis of the occipital condyle, thus it takes very little part in the latter in the Saint Papoul skull, while in *Neochelys*, the basioccipital takes a larger part in the occipital condyle, forming all the ventral portion of the condyle under the exoccipitals (de Broin, 1977 : fig. 17).

5) The cheek emargination in the Saint Papoul skull is longer than high and larger than that of *Neochelys*.

The condition of the occipital condyle in the Saint Papoul skull is very similar to that of *Erymnochelys madagascariensis*, a living podocnemidid from Madagascar. In fact, *E. madagascariensis* has the occipital condyle formed mainly by the exoccipitals, the basioccipital occupies only a very tiny part in the middle of the ventral margin of the condyle between the exoccipitals (Tronc & Vuillemin, 1973 : pl. 8(2), 9(2), 11(1)). The reduction of the participation of the basioccipital in the occipital condyle is a derived character shared only by the Saint Papoul skull and *Erymnochelys* among the Podocnemididae, all other podocnemidids, including the most primitive

one, *Hamadachelys escuilliei* Tong and Buffetaut, 1996, from the Cretaceous of Morocco1, have the occipital condyle formed by both the exoccipitals and the basioccipital and the latter forms at least one third of the condyle. This is also a stable character at at least the generic level in Pelomedusoides and has been used to establish phylogenetic relationships (Gaffney & Meylan, 1988). In *Peltocephalus dumeriliana*, a living species from South America, the basioccipital occupies more than one third of the occipital condyle and reaches the lower margin of the *foramen magnum,* it separates the right exoccipital from the left one in posterior view (Gaffney, 1979 : Fig.141). In living *Podocnemis, P. expansa* (Gaffney, 1979 : Fig. 54) and *P. Llewyana,* the condition of the occipital condyle is the same as that of *Peltocephalus.* This may confirm that the South American podocnemidids are more closely related to each other than to the Madagascar form, as suggested by Gaffney and Meylan (1988) on the basis of features of the cervical vertebrae (Williams, 1950). In Pelomedusidae (*Pelomedusa* and *Pelusios*), the basioccipital stops before the occipital condyle and the latter is formed only by the exoccipitals (Fig. 3).

Among the podocnemidids, *Erymnochelys* seems to be the most similar form to the Saint Papoul skull. *Erymnochelys* is a fresh water turtle, of which only one species, *E. madagascariensis*, still lives in Madagascar. Fossil *Erymnochelys* have been reported from the Lutetian (Middle Eocene) of Saint Germain-en-Laye in the Paris Basin, France (Taugourdeau, 1965, Broin, 1977) and from the Oligocene to Miocene of Africa (see Pritchard & Trebbau, 1984; Broin, 1988; Hirayama, 1992). Besides the occipital condyle and the narrow palate mentioned above, both the Saint Papoul skull and *E. madagascariensis* have a long triangular skull, dorso-laterally directed orbits, a relatively wide and flat interorbital space, a shallow temporal emargination as well as a triangular interparietal scale tapering posteriorly, with the parietal scales meeting behind it. These interparietal and parietal scales are different from those of *Peltocephalus dumeriliana* in which the interparietal scale is expanded posteriorly and separates the right parietal scale from the left one (Williams, 1954). The weak temporal emargination is a derived character, the Mesozoic podocnemidids from both South America (*Roxochelys* Broin, 1991) and *Bauruemys* (Suarez, 1969; Kischlat, 1994) and Africa (*Hamadachelys* Tong and Buffetaut, 1996) as well as Tertiary and Recent South American *Podocnemis* (Pritchard & Trebbau, 1984), have larger temporal emarginations.

The living *Erymnochelys* is moreover characterized by the presence of a premaxillary beak and a very weak or absent cheek emargination with a jugal/quadrate contact. Not much skull material is known for fossil *Erymnochelys*, but the Saint Germain-en-Laye specimen includes both skull and shell material and was named *"Podocnemis eremberti"* by Taugourdeau (1965) but with neither a diagnosis nor a figure, so that the taxon cannot be considered as valid; the brief description given later by Broin mentioned the presence of a premaxillary beak and the absence of a cheek emargination, with a jugal/quadrate contact (Broin, 1977).

The condition of the occipital condyle cannot be determined in the Saint Germain-en-Laye specimen since only the anterior part of the skull is preserved. The Miocene *Erymnochelys* from Zaire in which only the anterior part of the skull is preserved, too, also presents a premaxillary beak. Thus these two characters should be considered as generic features. In the Saint Papoul skull, the premaxilla is not preserved, and it is difficult to know whether such a beak was present or not; the cheek emargination is very large and there is no jugal/quadrate contact. The jugal/quadrate contact to close the cheek emargination is considered as a derived character, also found in *Peltocephalus*. But in *Peltocephalus*, the cheek emargination is closed mainly by the posteriorly extended jugal, while in *Erymnochelys* this emargination is closed by both the posteriorly extended jugal and the anteriorly extended quadrate, thus the closing of the cheek emargination seems not to be homologous in the South American form and in the form from Madagascar. The short prefrontals which do not completely cover the *apertura narium externa* dorsally in our specimen are more primitive than in *Erymnochelys*, in which the external nares are not visible in dorsal view, and the antorbital space is longer in the latter. The comparison of skull characters between *Papoulemys* and closely related forms is shown in table 1.

In 1842, Owen described a complete carapace as *Platemys bowerbanki* and an anterior portion of a

turtle skull as *Platemys bowerbanki* ? , both from the London Clay (Lower Eocene) of Sheppey, and compared the skull to *Podocnemis expansa* (Owen, 1842). Later, Lydekker gave a brief description of the same skull as the cryptodiran turtle *Pseudotrionyx delheidi* Dollo, 1886 and compared it to the chelydryd turtle *Macroclemys* (Lydekker, 1889). After a review of the shell material, Williams (1954) included the shell of *P. bowerbanki* in the genus *Palaeaspis*, as *P. bowerbanki* (Owen, 1842). Broin (1977) reconsidered the same skull (as ? *Palaeaspis bowerbanki* (Owen, 1842)) after Owen's illustration and considered that it may be a pelomedusid similar to *Erymnochelys madagascariensis* and the Saint Germain-en-Laye specimen. According to Owen's illustration (1842 : Plate 40, figs. 1 and 2) of the not fully prepared skull (Lydekker, 1889), which showed only dorsal and lateral views, the orbits are more laterally directed, the interorbital space is wider and the antorbital space is longer than in the Saint Papoul specimen. Closer reexamination is needed to specify the systematic position of this specimen.

No shell characters can be determined in direct relation with the skull since no shell material was found in connection with it. Few shell characters can be used to distinguish *Neochelys* from *Erymnochelys*, they differ essentially in the intergular scute, for which most of the African *Erymnochelys* have been identified, and this is the part of the shell missing in our specimens. Anyway, the shape of the nuchal and the first marginal from Saint Papoul are rather different from what is known in *Neochelys* and *Erymnochelys*. The shell material from Saint Papoul is too incomplete to be identified more precisely.

In conclusion, a new genus and new species, *Papoulemys laurenti*, are erected here. This is a podocnemidid which seems to be more closely related to *Erymnochelys* than to *Neochelys,* essentially on the basis of the features of the occipital condyle, and more primitive. The analysis of the skull characters seems to confirm that the living South American podocnemidids, *Podocnemis* and *Peltocephalus*, are more closely related to each other than to the African one (*Erymnochelys*), a conclusion previously based on the characters of the cervical vertebrae (Williams, 1950; Gaffney & Meylan, 1988), and that the European podocnemidids which flourished during the Eocene are more closely related to the African ones than to the American ones.

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characters	*Erymnochelys*	*Papoulemys*	*Neochelys*	*Podocnemis*	*Peltocephalus*
skull shape	long triangular		short triangular	long triangular	
anteorbital space	long	very short		short	long
palate wider than long*	no		yes	no	
prefrontal longer than frontal	yes		no		yes
external nares direction	anterior	anterodorsal	anterior	dorsal	anterior
orbits direction	laterodorsal			dorsal	laterodorsal
interorbital space	wide			narrow	wide
interorbital groove	absent			present	absent
temporal emargination	shallow			deep	very shallow
cheek emargination	very shallow	deep		very deep	very shallow
interparietal scale	triangular and tapering posteriorly				no
ju-pa contact	absent			present	absent
ju-qu contact	present		absent		present
occipital condyle formation	mainly by ex; bo nearly excluded from it		by ex dorsally and bo ventrally	by ex and bo, and bo separating ex completely	
ptp at right angle to skull axis	yes				no
pt posterior flange	present		very weak	present	

* palate length from anterior tip of snout to pal-pt suture, width at the level of pal-pt suture.
Table 1 : Comparison of skull characters between *Papoulemys* and closely related forms. (Abbreviations see figure 1)

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