

The oldest pre-Podocnemidid turtle (Chelonii, Pleurodira), from the early Cretaceous, Ceará state, Brasil, and its environment

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RESUMEN

LAPPARENT de BROIN F. de, La tortuga pre-Podocnemidid más antigua (Chelonii, Pleurodira), Cretácico inferior, estado de Ceará, Brasil, y su entorno.

Se describe una nueva forma de tortuga pleurodira, *Brasilemys josai*, n.g., n. sp. Su posición filética se examina en relación con las filogenias establecidas anteriormente. Se sitúa también *Brasilemys* n.g. en relación con algunas formas recientemente descritas y aún no bien posicionadas en la filogenia de los Pleurodira, como son los Dortokidae, *Hamadachelys* y otra forma de la Chapada do Araripe sin nombre. En los Podocnemidoidea, *Brasilemys* n.g. aparece como el primer representante de los Podocnemidoidea, inmediatamente después de la derivación de los Bothremyidae. La aparición de este nuevo género forma parte de la extraordinaria radiación que ocurrió en los Pelomedusoides al inicio del Cretácico, cuando se separaron América del Sur y África. La fauna de tortugas de la Chapada do Araripe incluye cuatro taxones de Pelomedusoides de agua dulce, representantes de la fauna de la parte norte del antiguo continente Gondwana, además de una tortuga cryptodira, posiblemente litoral y perteneciente a un grupo más cosmopolita. De acuerdo con los datos de la estratigrafía y con los del estudio de los cocodrilos fósiles, la edad de la fauna de tortugas se situaría entre el Aptiense superior de Gadoufaoua (Niger) y el Albiense superior - base del Cenomaniense del Sáhara.

Palabras clave: Quelonios, Nuevo taxón, Relaciones filéticas, Cretácico, Brasil, Consideraciones paleoecológicas y estratigráficas.

ABSTRACT

A new form of a chelonian Pleurodira is described, *Brasilemys josai*, n.g., n. sp. Its phyletic position is examined with respect to previously established phylogenies. It is situated with respect to recently described taxa whose position is not yet clearly established, such as Dortokidae, *Hamadachelys* and an unnamed form from Araripe. In the Podocnemidoidea, *Brasilemys* n.g. represents the earliest known specimen of the Podocnemidoidea, immediately after the divergence of the

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Bothremyidae. It is part of the formidable radiation in the Pelomedusoides which occurs during the early Cretaceous when South America separated from Africa. The turtle fauna in Chapada do Araripe includes four freshwater Pelomedusoides, samples of the ancient northern Gondwana fauna, as well as a cryptodiran turtle, possibly a littoral form belonging to a more cosmopolitan group. In agreement with the stratigraphical data as well as data from the study of fossil crocodiles, this turtle fauna dates between the late Aptian fauna of Gadoufaoua (Niger) and the late Albian-early Cenomanian fauna from the Sahara.

Key words: Chelonians, New taxon, Phyletic relationships, Cretaceous, Brasil, Palaeoecological and Stratigraphical considerations.

INTRODUCTION

Brasilemys josai n.g., n. sp. is based on a specimen belonging to Joan Josa, from Barcelona, Spain, who permitted me to examine it during 1985. After a long absence from Europe, Joan Josa did the gift of the material to the Museu de Geologia de Barcelona, which allowed me to erect the new taxon. This specimen was part of a collection including various specimens of turtles which were presented to a congress in Fortaleza, Brazil (Broin e Campos, 1985). It was also presented in a congress in New York (1987) and its position was then briefly examined under the name "aff. *Teneremys* sp" in Broin (1988). Among the other turtles of the collection, two carapaces of *Araripemys* were present and a dorsal carapace of another new pleurodiran turtle, a large Podocnemidoidea (undefined Bothremyidae or Podocnemididae). For the moment, only the skull of *Brasilemys josai* n.g., n.sp. is available to study, in the wait of the arrival of the corresponding carapace in Barcelona, but all the material has been photographed previously, including that of *Brasilemys josai* n.g., n.sp. (Pls. 1-3). The authors and references (date, stratigraphical and geographical distribution) of the named Pleurodira cited below are given in annexe (not exhaustive of Pleurodira). For anatomic data see Boulenger (1889), Gaffney (1972, 1979), Lapparent de Broin and Werner (1998) and references in these works.

SYSTEMATICS

Order Chelonii Brongniart (Latreille) 1800
 Infraorder Pleurodira Cope 1864
 Hyperfamily Pelomedusoides Cope, 1868
 Superfamily Podocnemidoidea Cope, 1868
 Epifamily Podocnemidoidea Cope, 1868
 Family Brasilemydidae n. f.
Brasilemys n. g.
Brasilemys josai n.p.

Etymology

From Brazil, the country of discovery and in honour to Joan Josa for his find, loan of material and gift to the Museu de Geologia de Barcelona.

Holotype

Museu de Geologia de Barcelona, Catalunya, Spain, number MGB 37911. A carapace with a partial skull, two hyoid branches, left lower jaw; axis and 3d cervical vertebrae in the carapace.

Horizon and locality

Santana Formation, early Cretaceous, Aptian-Albian limit, Romualdo member (lower part of the upper part of the Formation), Chapada do Araripe, Ceará State, Brazil.

Diagnosis

A pleurodiran podocnemidoid turtle (particularly by the presence of a podocnemidoid fossa, developed retroarticular process crossed by the *chorda tympani*, inguinal process below the pleural 5, elongated bridge), pre-Podocnemididae by the presence of an enlarged carotid canal; but still primitive, principally by the absence of prolonged pterygoid wings, presence of open *incisura columellae auris* and Eustachian tube passage, the *foramen jugulare posterius* not separated from the *fenestra postotica*, the undifferentiated triturating surface, the articular process not horizontally or upwards directed, the neural 1 still hexagonal short sided posteriorly and the pentagonal neurals 2 and 3, the neural 7 contacting the pleurals 8 and the iliac scar contacting the suprapygal. Apomorphic by its wide anterior truncated snout, large orbits, moderately narrowed interorbital space, short maxilla below the orbits, narrow maxillare and mandibular triturating surfaces just slightly posteriorly widened, widely exteriorly extended oposthotic ventrally below the *antrum squamosum*.

Same diagnosis for the family, the genus and species by monotypy.

Description

Skull

Measurements (cm)

Skull length, medial, preserved : 2.6 on 2.85 estimated

Total estimated length up to the end of the opisthotic: 3

Width of the triturating maxillary surface: anteriorly preserved; 0.2: posterior: 0.3

Preserved width at quadrate articulation: 2.1 on 2.2 estimated.

Height at quadrate articulation: 1.4
 Height at anterior preserved part of frontal: 1.3
 Palate width anterior to trochlear process: 1.3
 Palate narrowest width posterior to trochlear process: 1
 Medial palate length posterior to quadrate articular facet, up to the condyle: 0.6
 Estimated medial palate full length, up to the condyle: 2.65
 Width at anterior preserved part (at top of external nare): 0.9
 Estimated width of external nare: 0.66
 Full length and height of orbit: 1 x 0.9
 Height of maxilla below the orbit: 0.35
 Estimated minimal width of the interorbital space: 0.65
 Ratio length carapace / skull length: 3.82

General aspect

The specimen is broken anteriorly and on the right part, and a part of the roof is missing. The first view immediately indicates that: it belongs to a pleurodiran turtle, by the presence of trochlear processes of the lower jaw muscles situated on the external process of the pterygoid (Fig. 1, ptp); and it is a Pelomedusoides by the strong skull posterior emargination (see development in relationchips chapter).

The skull is original by the shape of the snout, anteriorly wider than in other related forms. Established on the anterior preserved lateral extremity (Pl. 1, fig. 1), the reconstruction (Fig. 1) clearly indicates that the external nare was relatively wide, the anterior contour truncated, trapezoidal instead of triangular. In lateral view (Pl. 1, fig. 3), the skull is original by the large size of the orbits accompanied by the relatively short maxilla below the orbit while the interorbital space is not narrowed (Pl. 1, fig. 1; Fig. 1). That differentiates this skull from that of *Araripemys*, same locality, also relatively wide anteriorly (although less) but narrow between relatively smaller orbits and with a narrowed interorbital space. All the other Pelomedusoides have a more triangular snout, even when they have a wide interorbital space. The frontoparietal upper surface is flat, indicating that this large size of orbits is not of a juvenile, in agreement with the well sutured bones (skull and carapace).

Dorsal face (Pl. 1, fig. 1; Fig. 1)

Besides the relatively wide external nare, the interorbital space is wide, probably hardly narrower than the nare. The prefrontals are missing. The orbits are oblique, not much, oriented dorsolaterally. In the left orbit, the *foramen alveolare superius* and the *foramen supramaxillare* are visible (Fig. 1, fs, frs), situated as in Pelomedusinae and Podocnemididae (small variations of position exist). The *foramen supramaxillare* is not enlarged as it can be in Podocnemididae or reduced as it can be in Chelidae. Posteriorly to the orbits, the postorbital arch is incomplete, much broken on the right, posteriorly broken on the left, a part missing between the quadratojugal and the parietal (also partly incomplete). But the borders of these bones allow to recognize the posterior limit of the arch: the postorbital was moderately reduced

from backwards and the parietal and quadratojugal did not meet to secondarily fill the posterior emargination as they do in *Hamadachelys*, Podocnemididae and in an unnamed form from Araripe (FR 4922 of Gaffney and Meylan 1991, Meylan, 1996). The posterior emargination extended up to the level of the anterior border of the tympanic ring of the *cavum tympani*. In the broken area, the trochlear process of the pterygoid is visible, well developed laterally as in most of Podocnemidoidea (oblique anterior border, slightly oblique posterior border) except *Peltocephalus* (more oblique borders) and various Bothremyidae (see Lapparent de Broin and Werner, 1998). On the temporal dorsal surface, between the quadrate and the prootic, the *foramen stapediotemporale* is open very close to the border of the inferior fossa as in Pelomedusidae and Podocnemididae; its position is variable among Pleurodira, according to flattened skulls or not and to elongation of the pterygoid behind the trochlear process. The more anterior and the lower positions it may have been the more derived conditions. Its more advanced position is homoplastic in Pelomedusoides and Chelidae, within the branches of the two groups. In *Notochelys* it is primitively less advanced (Fernández and de la Fuente, 1994). The supraoccipital crest is prolonged backwards the parietals. The opisthotic is prolonged backwards the squamosal extremity as in Podocnemididae, not as much as in *Pelomedusa* and some species of *Pelusios* (see Bour, 2000).

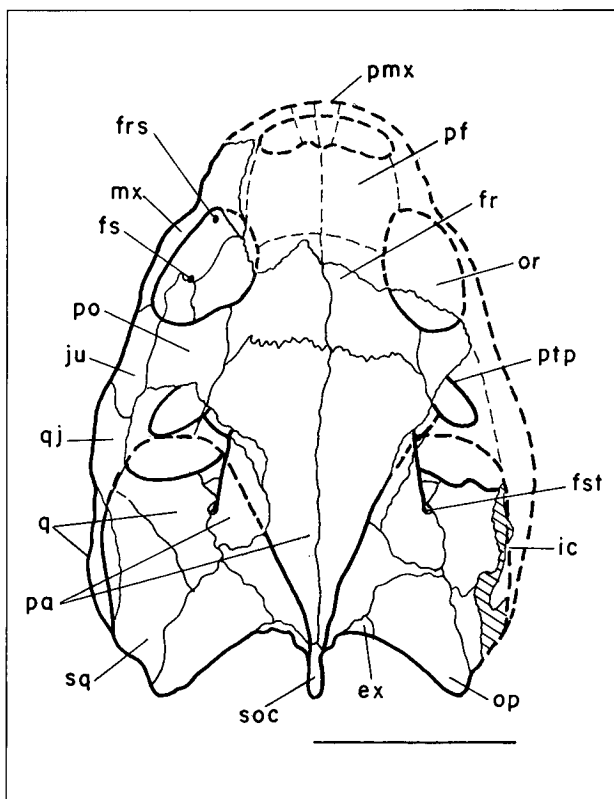


Fig. 1. *Brasilemys josai* n.g., n. sp., Chapada do Araripe, Ceará state, Brazil, early Cretaceous (late Aptian-early Albian), skull, dorsal view.

ex, exoccipital; fr, frontal; frs, *foramen alveolare superior*; fs, *foramen supramaxillare*; fst, *foramen stapediotemporale*; ic, *incisura columellae auris*; ju, jugal; mx, maxilla; op, opisthotic; or, orbit; pa, parietal; pf, prefrontal; pmx, premaxilla; po, postorbital; ptp, *processus trochlearis pterygoideum*; q, quadrate; qj, quadratojugal; soc, supraoccipital; sq, squamosum.

Scale: 1 cm.

Fig. 1. *Brasilemys josai* n.g., n. sp., Chapada do Araripe, estado de Ceará, Brasil, Cretácico inferior (Aptiense superior - Albiense inferior), crânio, vista dorsal.

Escala: 1 cm.

Lateral face (Pl. 1, figs. 2, 3; Fig. 2)

The left side (Pl. 1, fig. 3; Fig. 2) shows the relative height of the orbit with respect to the small height of the maxilla. The top of the lateral skull emargination is at the level of the top of the tympanic ring of the *cavum tympani*. This is clearly open postero-inferiorly on the *incisura columellae auris* meeting the Eustachian notch, visible on the right side (Pl. 1, fig. 2) and on the left side (Fig. 2, ic) as well as the presence of a shallow precolumellar fossa (Pl. 1, fig. 2; Fig. 2, fpc). The left side also shows the deep *antrum squamosum* behind the *cavum tympani*, well developed, constituted by the squamosum dorsally and the opisthotic at the narrowed extremity and ventrally. The anterior quadrato border of the *cavum tympani* is thin, not antero-ventrally prolonged. The articular process of the quadrate is well individualized (q,cmd). The development or regression of the process is homoplastic in turtles. In Pleurodira, the more covered skulls (dorsally or laterally) have a more ventrally salient process. The primitive condition is a slight individualization of the process from the quadrate face, but not below the inferior border of the maxilla level, as in *Brasilemys* n.g. and *Araripemys*, less developed than (apomorphically) in Bothremydidae and not regressed as in Quelidae, Pelomedusinae and most of Podocnemididae (see figures in Lapparent de Broin and Werner, 1998). The broken right side shows the long inferior process of the parietal, without epipterygoid at its base (pleurodiran character) laterally limiting

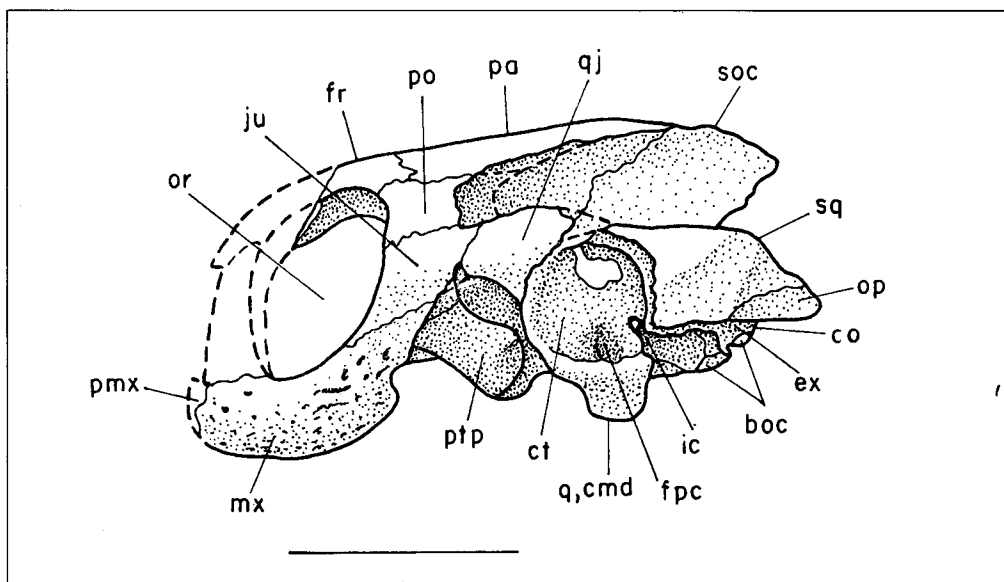


Fig. 2. *Brasilemys josai* n.g., n. sp., Chapada do Araripe, Ceará state, Brazil, early Cretaceous (late Aptian-early Albian). As in Fig. 1: boc, basioccipital; co, *condylus occipitalis*; ct, *cavum tympani*; fpc, precolumellar fossa; q, cmd, quadrate / cuadrado, *condylus mandibularis*. Scale: 1 cm.

Fig. 2. *Brasilemys josai* n.g., n. sp., Chapada do Araripe, estado de Ceará, Brasil, Cretácico inferior (Aptiense superior - Albiense inferior), cráneo, vista lateral izquierda. Escala: 1 cm.

the *cavum cranii*. The *foramen nervi trigemini* is seen open in the top of the posterior part of the vertical and lateral flange of the pterygoid, at the meeting of the prootic and the parietal descending process. The *foramen stapediotemporale* is seen behind, on the right side, in the dorsal part of the muscular infratemporal fossa, at the meeting of the prootic and quadrate (above the broken *cavum tympani*). Both sides show the trochlear processes (Fig. 2, ptp), well widely rolled up. The lateral faces show that the supraoccipital crest (Fig. 2, soc) is not as much prolonged behind as the opisthotic extremities (Fig. 2, op).

Posterior face (Pl. 2, fig. 1)

The dorsal profile of the skull is slightly domed and slightly tectiform posteriorly, at the level of the parietals. The large *foramen magnum*, roughly triangular, is surpassed by the supraoccipital crest. The exoccipitals end on the border of this foramen, at two third of its height. At the bottom of the foramen, the two exoccipitals meet ventrally with the basioccipital, this just participating to the base of the extremity of the condyle. Laterally to the condyle, on each side of the *foramen magnum*, each exoccipital bears two foramina for the hypoglossum nerve XII and minute vascular foramina. The external border of each exoccipital limits the rounded *foramen jugulare posterius*, except on the lateral border which is open on the *fenestra postotica*: a very short descending process of the dorsal part of the exoccipital, at the limit with the medial dorsal suture of the opisthotic, tends to meet a very low ascending process of the ventral part of the exoccipital, but the meeting is incomplete and the *fenestra postotica* still meets the *foramen jugulare posterius*. Laterally, inside, is the processus interfenestralis of the opisthotic descending to meet the quadrate, anteriorly limiting the recessus *scalae tympani* (here filled by the displaced *columella auris*). Laterally is the cranioquadrate passage (*canalis cavernosus* meeting the *canalis stapediotemporalis*). Still more laterally, the *fenestra postotica* is closed by the quadrate, transversally and posteriorly crossed by the notch of the columella and of the Eustachian tube behind, both going to the *cavum tympani*. Below the notch of the columella and Eustachian tube, laterally open, the articular process of the quadrate is preserved on the left, with the ventral face of the left maxilla seen in the background. The ventral face of the articular facet of the process, the *condylus mandibularis quadrati*, has a tectiform profile. In the posterior face of the quadrate, between the columellar-Eustachian tube notch and the articular process, above the medial part of the process, opens the *foramen chorda tympani inferius*.

Anterior face (Pl. 2, fig. 2)

The anterior dorsal profile is rounded at the level of the frontals. The left orbit, relatively large, is better preserved than the right one. The back face of the orbit bears, at mid-height, the *foramen supramaxillare* at the limit of the maxilla, the jugal and the palatine and ventrally the *foramen alveolare superior* (see Fig. 1, fs, frs). In the back of the orbit, on each side, the pterygoid sulcus, ovale and dorsoventrally elongated, particular to Pleurodira, is seen, which makes the communication between the orbit

and the rolled up face of the trochlear pterygoid process. It is laterally limited by the descending process of the postorbital, above and medially by the frontal and parietal and ventrally by the palatine. In the background of the pterygoid sulcus, the *foramen nervi trigemini* is seen in the external wall of the *cavum cranii*. Between the two pterygoid sulci is the medial cranial box (*cavum cranii*), roughly ovale in anterior view, and also dorsoventrally elongated but larger than the sulci. In its anterior bottom, on the floor of the posterior extremity of the meeting parietals, the medially meeting pterygoids end: these are topped by the rounded *rostrum basisphenoidale* of the basisphenoid (meeting ossified *trabeculae*) the front of which is just seen in the anterior part of the *cavum cranii*, still filled by matrix. On the right side of the view, the preserved maxilla curves medioventrally below the orbit and also bends forward ventrally. Behind, the lateral skull emargination is seen in front of the anterior border of the *cavum tympani*, constituted by the quadrate, with the articular process below.

Ventral face (Pl. 2, fig. 3; Fig. 3)

The anterior snout is partly broken as well as a good part of the right side. The area of the choanae is not preserved. Probably there was a single short vomer between the choanae, behind the premaxillae, as basically in all the Podocnemidoidea. The ventral edge of the maxilla is sharp, not rounded, and ventromedially curved. The triturating surface is narrow and very slightly posteriorly enlarged: by comparison with other turtles, beginning with *Proganochelys*, the narrow surface is a primitive condition and the condition is here hardly derived, with respect to other Podocnemidoidea. The palate is primitively wider at the palatines than at the pterygoid, contrarily to *Pelomedusa* (posteriorly wider) and some species of *Pelusios* (as wide; see Bour, 2000). The *foramen palatinum posterius* is wide, according to a relatively primitive condition. The *processus trochlearis pterygoidei* is well laterally developed, a condition of the Pelomedusoides and particularly of the Podocnemidoidea. Just behind, the pterygoid wings are developed ventrally, but they stop at the border of the pterygoid on the muscular fossa (infratemporal or palatine fossa), not prolonged medioposteriorly up to the suture of the basisphenoid, below the surface of the palate, as they are in the Podocnemididae to hide the enlarged carotid canal: just the base of the prolonged wing is indicated (Fig. 3, bw). The basisphenoid is pentagonal, its anterior tip scarcely prolonged between the two pterygoids. On each of its side is the podocnemidoid fossa, initiating the pterygoid channel or enlarged carotid canal (Gaffney, 1979; Lapparent de Broin and Werner, 1998). It is seen (Fig. 3) behind the base of the prolonged pterygoid wing, as a cavity between the border of the pterygoid on the infratemporal fossa, the lateral border of the basisphenoid medially and the descending articular process of the quadrate externally. It is basically present in Podocnemidoidea with the quadrate medioposteriorly extended up to the basisphenoid (behind the prootic) and the basioccipital covering the *processus interfenestralis* and the *fenestra postotica* ventrally. In *Brasilemys josai* n.g., n. sp., the podocnemidoid fossa is hollowed medially: prolonged by a shallow hole, the podocnemidoid fossa becomes the true enlarged carotid canal of the Podocnemididae. In the ovale (antero-posteriorly) hole is seen the triangular prootic (partly reduced basically in Podocnemidoidea),

more or less remaining external to the hole in the podocnemidoid fossa (right side), with the foramen for a branch of the facial nerve (ff) (coming from the inner skull) at the limit prootic-basisphenoid, and the foramen towards the *sulcus cavernosus* at the anterior prootic tip, opening in the bottom of the *cavum cranii* at the arrival of the *canalis cavernosus* (sc+cc) and leading the palatine carotid branch (more or less reduced) and the palatine branch of the facial nerve (Gaffney, 1979). The foramen of the internal carotid or cerebral carotid artery (fci) going to the *sella turcica* is hidden below a little blade of the basisphenoid medially bordering the podocnemidoid fossa;

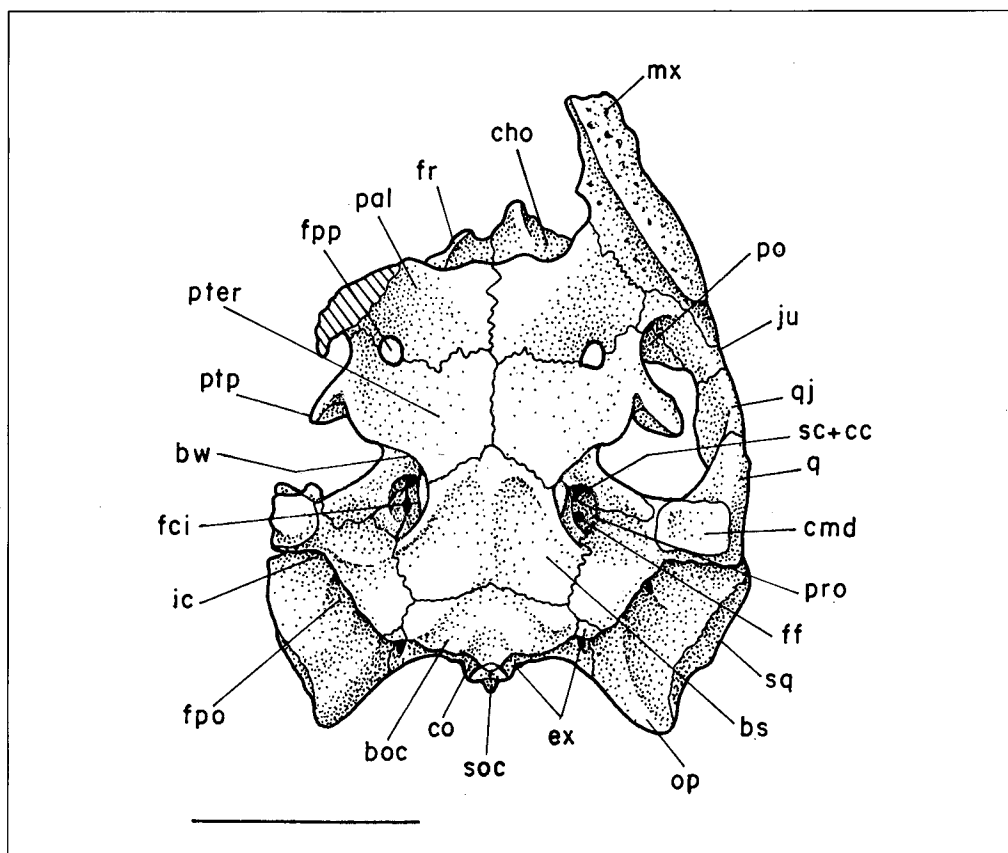


Fig. 3. *Brasilemys josai* n.g., n. sp., Chapada do Araripe, Ceará state, Brazil, early Cretaceous (late Aptian-early Albian).

As in Figs. 1 and 2 : b, basisphenoid; boc, basioecipital; bw, base for future prolonged pterygoid wings; cho, inner choana; ff, *foramen nervi facialis*; fpo, *fenestra postotica*; fpp, *foramen palatinum posterius*; pal, palatine; pro, prootic; pter, pterygoid; sc + cc, *foramen canalis cavernosi*, ventral opening of the "enlarged carotid canal" confluent with the *sulcus cavernosus*.

Scale: 1 cm.

Fig. 3. *Brasilemys josai* n.g., n. sp., Chapada do Araripe, estado de Ceará, Brasil, Cretácico inferior (Aptiense superior - Albiense inferior), cráneo, vista ventral. Escala: 1 cm.

it enters here primitively in the basisphenoid but in a more derived condition, it may enter at the limit basisphenoid-pterygoid (*Erymnochelys*). On each side of the fossa, the articular process of the quadrate, well preserved on the left, has a rectangular ventral *area articularis* or *condylus mandibularis* (cmd). This anteriorly dominates, in ventral view, the notch of the stapes and Eustachian tube. Medioposteriorly, the basioccipital, short, contributes to the occipital condyle ventrally, with the exoccipitals. The exoccipitals are prolonged ventrally between the basioccipital and the quadrate, a rare condition. The *fenestra postotica* opens laterally (fpo) below the prolonged quadrate and partly posteriorly below these exoccipital expansions, communicating with the *foramen jugulare posterius*. Above, the oposthotic forms the bottom of the large *antrum postoticum* and nearly all the ventral lateral posterior extremity of the skull. It is much extended externally with respect to other Pelomedusoides but it is not as much prolonged backwards as in *Pelomedusa* and some species of *Podocnemis*.

Lower jaw (Pl. 3, fig. 2)

Measurements (cm)

Preserved length of the left branch: 2

Height at coronoid: 0.5

Maximal width of the triturating surface, posteriorly: 0.1

The left branch of the lower jaw is preserved. The break is just posterior to the symphysis part, which allows to think that the dentaries were fused; if they were not, the separation of the two branches without break is more probable at the symphysis. There is no splenial. The external border of the triturating surface is sharp and the surface very narrow and just slightly widened posteriorly, as the maxilla (derived condition), without any secondary crest. The lingual border is also sharp, not elevated, flattened or doubled as in Podocnemididae or rounded as in Pelomedusinae. The coronoid process is not elevated. The articular is not much anteriorly sutured to the prearticular and to the surangular but it is posteriorly well sutured to the angular. The articular surface is important, forming a wide triangular facet, with a concave surface although slightly swollen, as in most of Podocnemididae, not small and rounded as in Pelomedusinae. The retroarticular process of the articular, absent in Pelomedusidae, is developed posteriorly but it is directed ventrally (Fig. 2, b, c) instead of horizontally or dorsally as, basically, in Podocnemididae (exception in *?Roxochelys vilavilensis* and *Podocnemis* where it is secondarily modified by its opening at the foramen for the *chorda tympani*). The *foramen dentofaciale majus* is present in the upper posterior part of the external face of the dentary. There are two possibly communicating foramina, one, above, in the oblique facet of the surangular, posteriorly, in front of the articular as in observed extant Pelomedusoides; one below, in the lateral face of the surangular, below the anterior border of the articular, as in Pelomedusidae, this second being absent in Podocnemididae. They may correspond to the *foramen nervi auriculotemporalis* of the Cryptodira as given in Gaffney, 1972.

Hyoid (Pl. 3, fig. 3)

The two anterior horns are preserved. They are thin, backwards curved, undifferentiated as in Pelomedusidae, *Peltocephalus*, *Podocnemis cayennensis* and *P. vogli* (not observed in other Podocnemididae). The posterior horns are not present in observed Pelomedusoides. They are also similar to the undifferentiated posterior horns of Chelidae of the *Phrynops* group, well ossified, rather than to the anterior which are less curved.

Cervical vertebrae (Pl. 3, fig. 1c)

The atlas is disarticulated, partly preserved (broken centrum). The intercentrum is small, roughly parallelepipedic and ventrally crested and slightly longer than wide conform to that of Pelomedusinae and relatively just longer than that of *Erymnochelys*. The ventral anterior border is not rounded as in Podocnemididae. The intercentrum is not shortened as in observed Podocnemidinae (*Podocnemis vogli*, *P. cayennensis*, *Peltocephalus*).

The axis and the third cervicals are preserved, still engaged in the carapace. They are procoelous with a common pedicel (process) for the postzygapophyses. They conform to most of Pelomedusoides cervicals, relatively long and low, neither secondarily elevated as in some Podocnemididae (*Peltocephalus*, *Erymnochelys*), nor particularly elongated and lowered as in *Araripemys*. The anterior point of the axis (on the right, on Fig. 1c) is strong but short as in Pelomedusinae and some Podocnemidinae. The axial prezygapophyses are horizontal: it is a primitive character (*Proganochelys*, *Notoemys*); the inclination of the postzygapophyses is variable in Pleurodira. Chelids *Hydromedusa* and *Chelodina* with very lowered and elongated cervicals also have horizontal postzygapophyses which may be secondary. The photograph (Pl. 3, fig. 1c) shows that the postzygapophyses of the third vertebra may be fused (unverified on the material), the ventral facet (seeming common to the two zygapophyses) being well elevated and without dorsal protuberances on the top of the zygapophyse.

Carapace (Pl. 3, figs. 1a,b)

Measurements (estimated: taken on photographs)

Length (preserved): 10.9

Width (preserved): 8.2

General aspect

The carapace is much eroded. Most of the plates are lost but their print is dorsally preserved, except the external part of most of the peripherals. The outline of the anterior lobe and of the bridges of the plastron is preserved. The height (not measured) is moderate as in extant *Pelomedusa*. The plates are well sutured and so is the plastron to the dorsal shell.

Dorsal face (Pl. 3, fig.1a; Fig. 4)

The shape is regularly ovale, just slightly posteriorly expanded and well rounded dorsally. There are no medial keel or protuberances. The anterior border is straight between the peripherals 1, without anterior notch or protrusion. The anterior peripheral-nuchal border is moderately elongated but not as much as in Pelomedusinae and Bothremydidae. The nuchal is approximately as wide as long, much reduced in width with respect to the primitive condition present in *Proterochersis*, *Platycheilus-Notoemys* nodes and primitive Chelidae (see de la Fuente *et al.*, 2001). The pleurals 1 are elongated with respect to the primitive condition, but moderately. The neural 1 is hexagonal posteriorly short sided (primitive condition); the second and third are pentagonal with, respectively, still a posterior short side on the left and an anterior short side on the right, which are primitive conditions: there is not yet a quadrangular neural. The neural serie is prolonged up to the heptagonal seventh, contacting the median tip of the pleurals 8. The pleurals 8 meet between the neural 7 and the roughly pentagonal suprapygal, which is derived with respect to the complete neural serie. The erosion of the pleurals allows to see: the axillary processes curved below the pleurals 1 up to nearly the mid-width of the plates; and the inguinal processes curved below the lateral part of the pleurals 5 (1/4-1/5 of their width). The thoracic rib 1 is well reduced in length and width, directed anteromedially, erecting from the medial part of the rib 2.

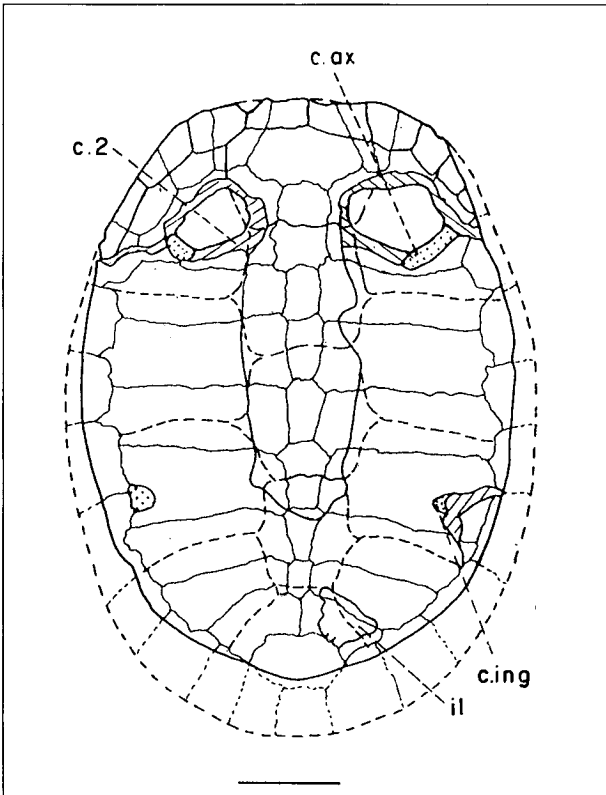


Fig. 4. *Brasilemys josai* n.g., n. sp., Chapada do Araripe, Ceará state, Brazil, early Cretaceous (late Aptian-early Albian); carapace, dorsal view; c.2, thoracic rib 2; c.ax., axillary process; c. ing., inguinal process; il, iliac scar.

Scale: 2 cm.

Fig. 4. *Brasilemys josai* n.g., n. sp., Chapada do Araripe, estado de Ceará, Brasil, Cretácico inferior (Aptiense superior - Albiense inferior); caparazón, visión dorsal.

Escala: 2 cm

The iliac scar is visible on the right side. It is roughly triangular, a short wide part below the pleural 7 and a wide and long part below the pleural 8 up to just contacting the suprapygial.

The preserved marginal scute border is relatively long on the nuchal, without cervical scute. It extends progressively a little more on the peripherals 1 and 2 which are a little elongated and reduces then posteriorly. In *Dortoka*, the anterior peripheral and nuchal border is elongated but the marginal scute border is reduced. The vertebral 1 is wide on the peripherals 1 and the pleurals 1 and reduces in width so that the vertebral serie becomes relatively narrow (scarcely the width of the nuchal), less wide than the costals (a derived condition but less pronounced than in *Dortoka*).

Ventral face (Pl. 3, fig. 1b)

The anterior lobe did not fill much of the anterior opening of the shell. It seemed to be shorter than the anterior border of the carapace. Its outline is lateroanteriorly rounded, anteriorly straight and it is not particularly wide at its base. The bridge is elongated between the inguinal and axillary notches. The bridge lateral parts of the plastron are upwards inclined, the ventral medial plastral part being positioned well below the ventral part of the bridge peripherals. The plastron is firmly sutured to the dorsal carapace.

Relationships

The relationships of *Brasilemys josai* n. g., n. sp. are expressed in a cladogram (Fig. 6), modified from the cladograms of Broin (1988) (Fig. 5) and Broin in Antunes et Broin (1988) with the data of Broin (1991), Lapparent de Broin et de la Fuente (1996), Lapparent de Broin and Werner (1998) and the cladogram of Lapparent de Broin and Murelaga (1999). The cladogram (Fig. 6) is made by hand, making just use of the previous results in the wait of a more complete study: beside *Brasilemys josai* n.g., n.sp., there are still several taxa insufficiently described, such as the taxa from the Early Cretaceous of Brazil (Chapada do Araripe) (Gaffney and Meylan, 1991; Meylan and Gaffney, 1991; Meylan, 1996), of Niger (Gadoufaoua) (Broin, 1980) and of Morocco (Lapparent de Broin and Werner, 1998). The former has been introduced in a cladogram (Meylan, 1996) although its anatomy is incompletely known, the other are still under preparation and will be progressively described. When all these works are done, it will be possible to better establish their relationships. Meanwhile, the list and matrix of characters (not yet complete) are not given. The results of the analysis with the unquestionable characters for principal nodes and the problems to be resolved are given. As in Lapparent de Broin and Werner (1998), it has been tried to analyse the skeletal structures, understand their evolution and test the homology or analogy of the previous given characters. Other cladistic studies are given in Gaffney and Meylan (1988) and Meylan (1996). The definition of the characters may be different in the cited works and the results also. The list of the named fossil Pleurodira and Cryptodira cited below (not exhaustive of the two groups) is given in annexe with their author, stratigraphical and geographical distribution.

Characters of the cladogram (Fig. 6)

1. **Pleurodira**, node of divergence of *Proterochersis*, the oldest turtle from the Triassic of Germany and the oldest turtle recognized as a pleurodiran. The outgroup is *Proganochelys*, other turtle from the same Triassic of Germany, better known and sufficiently described (Gaffney, 1990). This taxon is slightly younger than the oldest *Proterochersis* specimens (from inferior levels) and as old as the youngest specimens of *Proterochersis* (from superior levels) but it is of a more primitive evolutive stage. *Palaeochersis*, from the Triassic of Argentina, is possibly a pre-pleurodiran turtle by its beginning of sutured pelvis, although this is still very primitive, low, long and wide. It has still an hypoischion, as *Proganochelys*, a rounded (not bifid) posterior plastral lobe and a primitive skull, apparently without any pleurodiran character. But its full description is not yet published (de la Fuente in prep.). It is difficult to distinguish the apomorphies of *Proganochelys* from the primitive characters shared by the common ancestor of *Proterochersis* and *Proganochelys*. Some characters of *Proterochersis* may be of the node.

Characters at the node.

– Pelvis truly sutured to the carapace (the sutures of the pelvis make characteristic scars on the carapace), ilions to the dorsal carapace, ischia and pubis to the posterior plastral lobe, with correlative principal modifications: narrowing of the pelvis,

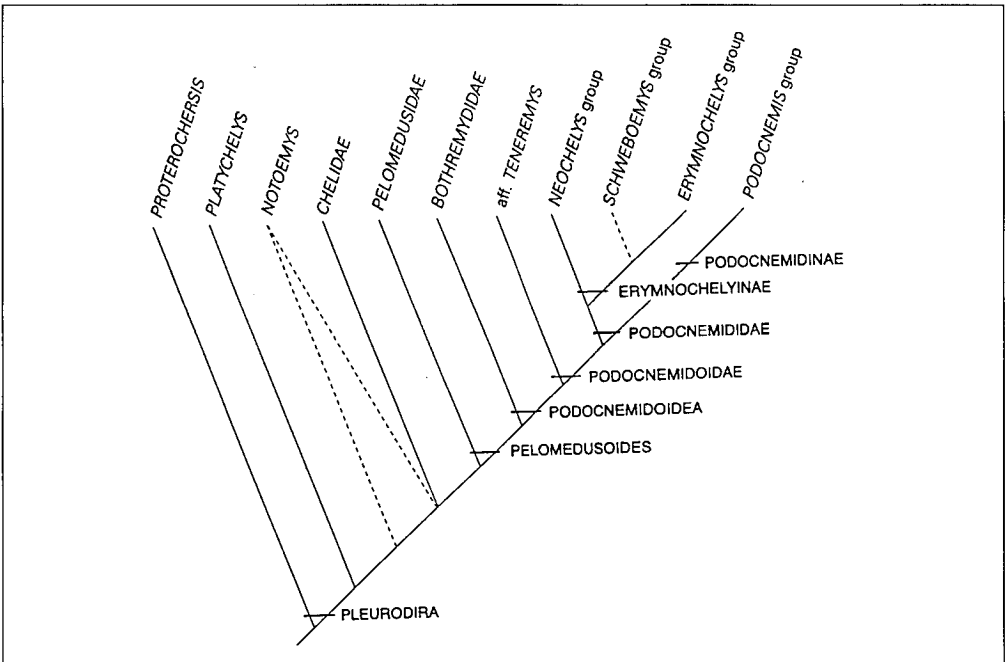


Fig. 5. Cladogram given in Broin, 1988.

Fig. 5. Cladograma propuesto por Broin, 1988.

becoming less wide than the xiphiplastral width, with reduced ventral surfaces of the ischia and pubis; elevation of the pelvis, enlargement of the close thyroid fossae (then confluent in the more derived Pleurodira of the cladogram), xiphiplastral prolonged, bifid posterior lobe receiving in each point the ischiadic sutures, reduction in width and thickness of the sacral ribs, correlative to the immobility of the pelvis, initiated here (Lapparent de Broin et de la Fuente, 1996; Lapparent de Broin and Murelaga, 1999). No hypoischion. Carapace: reduced number of marginals (and peripherals probably, but the sutures are not visible) with respect to *Proganochelys*; carapace border not anteriorly and posteriorly much dentated; sutured carapace-plastral link; less supramarginals; less inframarginals; anteriorly shorter axillary plastral processes; elevated and inclined bridge with the ventral medial part of plastron lower than the peripheral border.

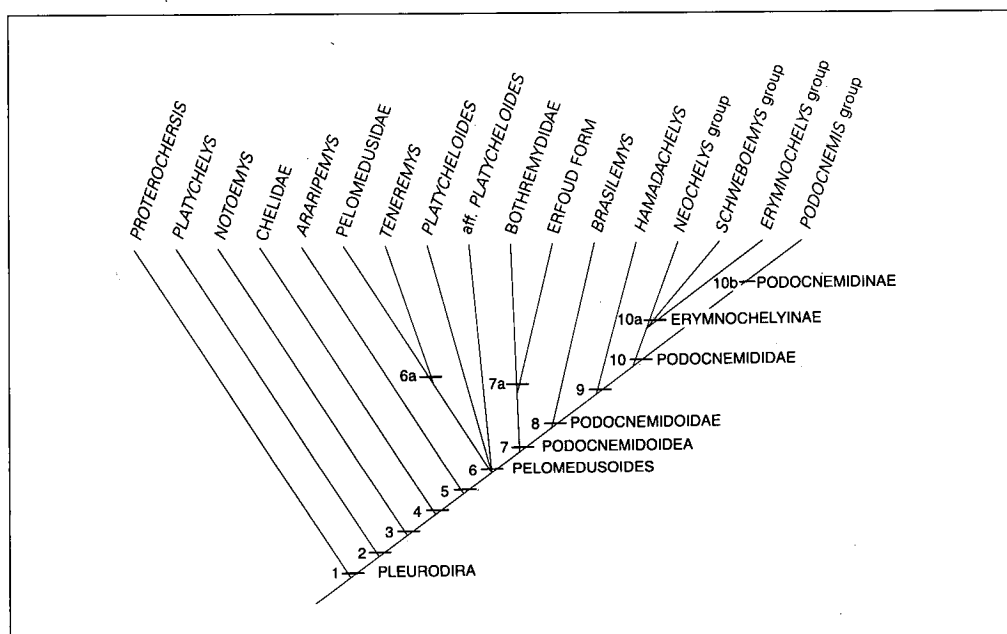


Fig. 6. New cladogram, including the resolved position of *Notoemys* with respect to *Chelidae* and the position of some taxa erected from Broin, 1988. 1, Pleurodira, divergence of *Proterochersis*. 2, node of divergence of *Platycheles* and *Dortokidae*. 3, node of divergence of *Notoemys*. 4, node of divergence of *Chelidae*. 5, node of divergence of *Araripemys*, plesion of *Pelomedusoides*. 6, *Pelomedusoides*, node of divergence of *Pelomedusidae* (unresolved position of *Platycheloides nyasae* and aff. *Platycheloides*); 6a, divergence of *Teneremys* from *Pelomedusidae* (*Pelomedusa* and *Pelusios*). Between nodes 6 and 7 possible node of divergence of FR 4922. 7, *Podocnemidoidea*: node of divergence of *Bothremyidae*; 7a divergence of the Erfoud form at the base of *Bothremyidae*. 8, *Podocnemidoidea*: node of divergence of *Brasilemys josai*, n.g., n. sp. 9, node of divergence of *Hamadachelys*, plesion of *Podocnemididae*. 10, *Podocnemididae*: 10a, *Erymnochelyinae*; 10b, *Podocnemidinae*.

Fig. 6. Nuevo cladograma con la resolución de la posición de *Notoemys* en relación con los *Chelidae* y la posición de algunos de los nuevos taxones conocidos desde Broin, 1988.

Proterochersis (unknown skull and vertebrae)

– Carapace elevated and domed; slightly rounded-dentated border; thoracic rib 1 slender than the 2d (still complete in front of the second); a round pygal notch not dentated without pygal plate; a reduced serie of three lateral supramarginals at the level of the bridge and just anteriorly; absence or reduced serie of inframarginals (according to the specimens); two triangular short intergular flat points directed forwards (not rounded anterior border as given in Broin, 1985, fig. 4, but slightly salient as in fig. 5: see Gaffney, 1990); rounded and just slightly protuberant gulars at the corner of the epiplastra (not as salient as given, reconstructed, in Gaffney, 1990, fig. 105G: a little less pointed, or rounded as in Broin, 1985, fig. 4, according to the specimens). By comparison with other Triassic turtles such as *Palaeochersis* (Argentina) and the forms from Greenland (Jenkins *et al.*, 1994) and Thailand (Broin, 1985), I consider that the intergular protrusions of the anterior border and the lateral gular angulations of *Proterochersis* are not homologous in their degree of development with the five strong points of *Proganochelys* which are exaggerated in size and apomorphic for that genus, although the presence of intergular protrusions and lateral gular angulation seems to be primitive. A part of these characters may be of the node (see above). The plastron is completely sutured to the carapace.

The skull and vertebrae are unknown: it is impossible to know if there were trochlear processes of the pterygoid for the mandibular muscles (character known in “Eupleurodira”), if the skull was emarginated from behind and laterally and how much (characters discriminating Chelidae from Pelomedusoides), if there were still two vomers, if the cervical and caudal vertebrae were still amphicoelous or if they had formed joints and, in this case, how they were constituted (characters discriminating Pelomedusoides from other Pleurodira). The probability is that the skull was still primitive as that of *Proganochelys*, *Palaeochersis*, *Australochelys* or that of *Kayentachelys* (the oldest cryptodiran known skull, early Jurassic, USA). The sutures of the plates are canceled so that the neural serie is unknown; the neurals may be long, octogon and narrow (similarly to some in the serie in Dortokidae) according to the ventral face of the specimen SMNS 17930, Staatliches Museum für Naturkunde-Stuttgart.

2. Node of divergence of the European *Platychelys* (skull unknown).

Characters at the node.

– Presence of a pygal plate (absence of a rounded pygal notch); irregular neurals, first hexagonal with short sides behind and then neurals alternately quadrate, octogon, hexagonal or pentagonal; intervertebral canal narrower posteriorly; lateral wide mesoplastra; rounded anterior border of the plastral lobe (just rounded at each scute as in extant forms); no epi- or entoplastral processes; much reduced horizontal surface of ischia, the bones being more verticalized and the thyroid fossae confluent (not known in *Notoemys*); iliac scars reduced posteriorly; partly reduced sacral ribs in size (slightly, with respect to *Proterochersis*); one intergular; epiplastral lateral posterior branches completely reduced (absent); shorter entoplastron posteriorly with shorter interclavicle part (but still longer than wide); no inframarginals; curved axillary process contacting the pleural 1 laterally; inguinal process contacts the pleural 5; no extra anal scute as present in *Proterochersis*. First attestation of constituted joints to the cervical

vertebrae. Those preserved are of the chelid type (cervicals: 2, 3 and 4 opisthocoe-
lous; 5, biconvex; 6, procoelous; 7, biconcave; 8, biconvexe): a 7th biconcave and a
8th biconvexe in *Platychelys*; four anterior preserved with three postatlas opisthocoe-
lous in *Notoemys*. But the zygapophyses are still well separated; and the transverse
apophyses are still anterior. Procoelous, amphicoelous and opisthocoeleous caudal ver-
tebrae in *Platychelys* as in primitive chelids (unknown in *Proterochersis* and *Notoemys*)
instead of amphicoelous in *Proganochelys*.

The characters “inguinal process contacts the pleural 5” and “sutured carapace-plas-
tral link” present in *Platychelys* (and *Dortokidae*) are not present in *Notoemys*: either
they are lost in *Notoemys* or the first is lost and the second not acquired. In this second
case, *Notoemys* and *Platychelys* are diverging at the same node (unresolved position).

Platychelys

–Apparent primitive straights but modified with respect to the *Proganochelys*
type: serrated border all around (long thick pointed dentations, only anteriorly and
posteriorly in *Proganochelys*); three carenae more protuberant with points, crests and
glomerules radiating from protuberances situated below the dorsal scutes. Other apo-
morphies: carapace shape: lower, narrower than that of *Proterochersis* and posteriorly
pointed (somehow as in *Notoemys*); very dentated neural sutures; reduced posterior
border of the first peripherals (narrow or contacting the pleural 1 by a point or not at
all); two lateral supramarginals, at the level of the bridge, which are approximately
homologous with the two anterior of the three of *Proterochersis*; inguinal process
contacts the pleural 5 (if not of the node and lost in *Notoemys*); the suprapygal 1 of
the Cryptodira is united to the neural 8 and the suprapygal 2 is united to the pygal;
according to specimens, the iliac scar contacts both the suprapygal part of the pygal
and the peripheral 11 or only one of them; shorter xiphiplastral points with anal notch
partly filled between the ischiadic scars; presence or absence of an extra supracaudal
scute in a slight pygal notch of the dentated border of the pygal plate; inguinal pro-
cess contacts the pleural 5; well sutured carapace-plastral link. Paedomorphic charac-
ters: a central and a posterior plastral fontanelles. Bräm (1965), Fraas (1913), Gaffney
(1990), Lapparent de Broin (in press), Lapparent de Broin and Murelaga (1999).

It is possible to think that, at this evolutive stade, the *processus trochlearis ptery-
goidei* of the Pleurodira was acquired, because of the formed joints which implicate
a modification of the neck retraction. But the zygapophyses are very separated, the
posterior not elevated on a common pedicel in *Platychelys*, the transverse apophyses
are anterior instead of medial, at the difference from *Dortoka* and from Pleurodira
situated after *Notoemys* in the cladogram, and the joints are double in *Platychelys* as
in many Cryptodira but not in known other Pleurodira. A procoelous and an opistho-
coelous caudal vertebrae (Bräm, 1965) in *Platychelys* and together procoelous,
amphicoelous and opisthocoeleous caudal vertebrae (Lapparent de Broin and Murelaga,
1999) in *Dortoka* indicate a more evolved grade than in the amphicoelous caudal ver-
tebrae of *Proganochelys*, identical to that of some chelids, fossil (*Yaminuechelys* de la
Fuente *et al.*, 2001) and extant chelid *Phrynops* spp: the tail of *Platychelys* and *Dor-
toka* has not yet the vertebrae all procoelous as in chelids other than *Phrynops* spp.
and as in all the Pelomedusoides and their plesion, *Araripemys*.

Dortokidae (*Dortoka* and *Ronella*), a strictly European group, may have had a common ancestor with *Platychelys*. Dortokidae are primitive with respect to Pelomedusoides in the low and short pelvis, and the relatively still long entoplastron (as in Jurassic forms and primitive Chelidae). They are derived with respect to *Platychelys*: no carenae and dentations, well sutured plastron to the carapace, absence of mesoplastra, either neural 8-suprapygal link or not, reduced ischiadic and pubis ventral surface of the better verticalized pelvis, iliac scar short and tribrachial not contacting the suprapygal. Very apomorphic on the very strong plastral processes and much narrowed vertebrae, curious morphology of the costal scutes (known in *Dortoka*) and neurals and strong peculiar decoration. Similarities (shared characters?) with *Platychelys*: long and narrow shape of the carapace, although ovale and not dentated, irregular neurals, alternatively quadrate and octogonal, strong reduction of the first peripheral not contacting at all the pleural 1 (known in *Dortoka*) presence of a crested decoration and partly filled anal notch (also present in Podocnemidoidea and in some lineages of Chelidae), together procoelous, amphicoelous and opisthocoelous caudal vertebrae (known in *Dortoka*) (as in primitive chelids). The known cervicals vertebrae of *Dortoka* are one opisthocoelous (3d or 4th), and one biconvexe (possible fifth), according to the chelid system as in *Platychelys*, but without the double joints of *Platychelys*, and with a common pedicel for the postzygapophyses as in Chelidae and Pelomedusoides. Indeed, Dortokidae are very derived forms with, beside their apomorphies, modern characters either of Chelidae or of Pelomedusoides that may have developed in parallel according to our present hypothesis. At a time Pelomedusoides develop in northern Gondwana (Broin, 1980; 1988) and Chelidae in southern Gondwana (Broin et de la Fuente, 1993; de la Fuente *et al.*, 2001; Lapparent de Broin y de la Fuente, 1999; Lapparent de Broin *et al.*, 1997), the Dortokidae are firstly known from the lower Cretaceous of Spain (Murelaga Bereikua, 1998). No relations with Africa are known at that time for European turtles, while Platychelidae are known in the late Jurassic and lower Cretaceous of Portugal and Spain (Bräm, 1973; Broin, 1988; Krebs, 1995; Sanz *et al.*, 1988). This indicates a more remoted Pangean common ancestor for the three groups and a possible relationships of *Dortoka* with the Jurassic European *Platychelys*. The position of Dortokidae close to *Platychelys* is an alternative to the hypothesis of their belonging to “Eupleurodira”, with Chelidae and Pelomedusoides (Lapparent de Broin and Murelaga, 1999). This hypothesis does not prevent a possible peculiar relationship of *Platychelys* and Dortokidae with Pelomedusoides, according to the palaeogeography and stratigraphy. It requires an important part of homoplasies, beginning for the characters of the *Notoemys* node, but not at all incredible.

3. Node of divergence of *Notoemys* (see Fernández and de la Fuente, 1994).

Characters at the node.

– Half reduced thoracic rib 1 in width, linked to the thoracic rib 2 and directed antero-medially towards the articulation of the thoracic vertebra 1; no supramarginals; neurals with straight borders; modern posterior neurals and suprapygal-pygals pattern (one suprapygal, well individualized from the pygal); iliac scar does not contact the peripheral 11 anymore; (all the characters also in *Dortoka*).

Notoemys (incomplete skull)

– Shape of carapace: shorter and widened, flattened and without protuberances, probably more adapted to swimming as is the elongated hand; ovoid shorter iliac suture, not contacting the suprapygal (but still long); thoracic ribs 10 not contacting the ilia (still contacting in *Platychelys* and Chelidae). Paedomorphic characters (unknown degree of adaptation of these characters to swimming): more ligamentous link carapace-plastron than in *Platychelys* and *Proterochersis* (a primitive character that can be reappeared here by paedomorphy), no sutural link inguinal process-pleural 5; a long plastral fontanelle that can be considered as the enlargement and fusion of the two fontanelles of *Platychelys*, although this characters may appear in parallel; link peripheral border-pleural disk weak and partly ligamentous (firmly sutured in *Platychelys*).

There also, the *processus trochlearis pterygoidei* of the Pleurodira was possibly present because of the preserved cervical vertebrae with formed joints. Cervical joints of the chelid type, with the axis, 3d and fourth vertebrae opisthocoelous, but here also the zygapophyses are very separated, as in *Platychelys*, the posterior not elevated on a common pedicel and the transverse apophyses anterior instead of medial as in *Dortoka* and following Pleurodira in the cladogram. The anterior zygapophyse of the axis is primitively transverse as in *Proganochelys* (and see *Teneremys* and *Brasilemys josai* n.g., n.sp. below). The partial posterior skull is the first known of the Pleurodira. The quadrate is not completely closed on itself, it is open behind the stapes (columella) and the Eustachian tube. There was no junction of the quadrate and basioccipital and the prootic was well visible between the quadrate and the basisphenoid, just in front of the break of the wide and completely open *fenestra postotica*, and crossed by the *canalis carotici interni* going to enter the braincase at the basisphenoid lateral border. There is no ventral and posterior closure of the *recessus scalae tympani* and no separation of the *foramen jugulare posterius* from the *fenestra postotica*. There is no indication of the presence of a precolumellar fossa in the preserved part of skull. It is possible that there was at least moderate lateral and posterior emarginations and also nasals, splenials and separated dentaries at the lower jaw, as they exist in chelids. As seen above, the carapace has irregular neurals, the neural 1 hexagonal with short sides behind and following alternately quadrate, octagonal, hexagonal or pentagonal similarly to the former two taxa, *Platychelys* and *Dortokidae*, although more straightly outlined.

4. Node of divergence of Chelidae from Pelomedusoides

Characters at the node, shared by Chelidae and Pelomedusoides (or partly anteriorly acquired or homoplastic?).

– Trochlear processes of the pterygoids (anteriorly acquired?). Development of the precolumellar fossa (anteriorly acquired?). Vomer single (anteriorly acquired?). Development of a pedicel (a common process) for the postzygapophyses; position of the transverse cervical apophyses at mid-length of the centrum (these two characters are also present in *Dortoka*). Reduction of the ventral horizontal surfaces of the pubis and ischia, the remaining parts being inclined and complete confluence of the thyroid fossae (as in *Dortoka*: already acquired in *Notoemys*?); sutures of the ilia with the shell reduced in length and wider (also in *Dortoka*). Carapace shape: ovale, not pointed

or expanded posteriorly; not narrowed as in *Dortoka*; without strong protuberances or keels (reversive in *Chelus*); relatively more elevated than in *Notoemys* and *Platychelys* but less than in *Proterochersis*; intervertebral canal narrowed all along; thoracic rib 1 still more reduced in width (width less than the mid-width of the pleural 1) and thickness; thoracic rib 10 and sacral ribs very reduced but still contacting the medial base of the ilia (they more reduce independently in Chelidae and Podocnemidoidea); iliac scars more rounded-triangular contacting the suprapygial (not as much reduced as in *Dortoka*). Reduced width of the vertebrae (basically not as much as in *Dortoka*).

Chelidae diversified in parallel with Pelomedusoides: many characters develop in vicariance between the two groups. For example, a descending process (generally of the opisthotic) towards the lateral basioccipital area closes the *recessus scalae tympani* and separates the *fenestra postotica* from the *foramen jugulare posterius*: there is no homology of the process in the two groups and even within Pelomedusoides, according to the different ways the closure is constructed and the fact that this process is not present in the primitive members of the Podocnemidoid branches. It is therefore difficult to be sure of the existence of a group "Eupleurodira", on the given definition because the complete skeletons of the oldest forms of the two groups (in particular of the early Cretaceous oldest Chelidae and Bahia Pelomedusoides) and the skull of *Platychelys* and complete skull of *Notoemys* are unknown.

The two groups are clearly separated on their mode of skull emargination: from laterally towards dorso-posteriorly in Chelidae, up to link the posterior emargination in *Chelodina*, and from posteriorly towards anteroventrally in Pelomedusoides, up to link the lateral emargination in *Teneremys*. Because of the absence of preserved skull in *Platychelys* and *Dortoka* and the not preserved anterior skull of *Notoemys*, it is impossible to know the basic degree of skull emargination, dorsal and lateral, if the trochlear process on the pterygoid is apomorphic or homoplastic and when the vomers become fused in a single element. While the vomer remains long between the parietals in Chelidae, it is reduced (when present) to its interchoanal part in Pelomedusoides.

The two groups are different in their mode of skull retraction, according to the different formulae of the joints of the centra. The formula of Chelidae (see above) is known in the preserved cervicals of *Platychelys*, *Dortoka* and *Notoemys* while the formula of Pelomedusoides (see below) is apomorphic.

At least a good part of their life, Chelidae retain a primitive ligamentous link between carapace and plastron and a less sutural link pleurals-peripherals, as in *Notoemys*, while all the Pelomedusoides have a firm sutural link, as *Proterochersis*, *Platychelys* and *Dortokidae*. Primitively, as in previous taxa *Platychelys* and *Notoemys* in the cladogram, the neural series is complete, the 8th contacting the suprapygial, and the iliac scar basically contacts the suprapygial.

5. Pelomedusoides. Node of divergence of *Araripemys*, plesion to Pelomedusoides

Characters of Pelomedusoides at the node.

– Dorsal posterior emargination progressing towards the level of the anterior border of the *cavum tympani*, shortening the postorbital which separated the parietal and the quadratojugal. No nasals. No splenials. Vomer reduced to its anterior interchoanal part (see above). Typical formula of cervical vertebrae of the Pelomedusoides:

biconvexe axis and procoelous 3d to 8th. Procoelous caudals (they are weakly but clearly procoelous and not amphicoelous in *Araripemys*) (parallelized in modern Chelidae, but after the primitive forms: de la Fuente *et al.*, 2001); neural 8 contacting or not the suprapygal according to the specimens (as in *Dortoka*). Rounded lateral mesoplastra; no cervical; narrowed nuchal (homoplastic in derived Chelidae); partly filled anal notch (as in *Platychelys*, *Dortoka* and evolved forms of Chelidae).

Araripemys, plesion to Pelomedusoides (see Meylan and Gaffney, 1991, Meylan, 1996).

Araripemys is primitive with respect to true Pelomedusoides by the long basisphenoid between the pterygoids up to between the palatines, posteriorly long and rounded coracoid, presence of a posterior ischiatic process as in *Proterochersis*, less reduced thoracic ribs 1 and the wide nuchal, according to the shape and width of the anterior notch and position of the peripherals 1. The vomer is unpreserved (probably absent? Unpreserved in observed specimens and erroneously reconstructed in one of them). Separate *foramen posterior canalis carotici interni* and *foramen facialis* in the prootic.

– Very curious form. Some characters, for a better adaptation to swimming, are together reversible and pedomorphic: the carapace with plastral processes not joining by their upper extremities the pleurals 1 and 5, the dorsal fontanelles (free extremities of ribs, ligamentous link peripherals-pleurals), the epiplastra returned to the shape of clavicle sticks, medial plastral fontanelles, long entopastron with the two lateral branches of the primitive interclavicle anterior to the first plastral fontanelle, and the weak ligamentous link carapace-plastron. The better adaptation to swimming is also seen in the completely flattened carapace, the flat plastron at the bridge (instead of upwards inclined as in every Pleurodiran turtle from *Proterochersis*, juveniles included), the elongated digits 2 to 5, but the fifth remaining smaller than the fourth as in other Pelomedusoides and in the cryptodiran “pre-marine” forms in which they more regularly elongate from second to fourth (littoral Jurassic European and Argentine forms and *Santanachelys* from Araripe). *Araripemys* has also very derived, autapomorphic characters such as its pitted “trionychine” decoration, the secondary wide and strong anterior notch eroding the peripherals 1 and much of the nuchal, the loss of the mesoplastra (as in Dortokidae and evolved chelids since the Palaeogene), the flat skull and the very elongated neck with all the postzygapophyses fused, a fusion also present in some chelids, FR 4922, *Teneremys*, very probably *Brasilemys* n.g. and *Podocnemis* (see above) but more complete here, from axis to eighth vertebra included, fide Meylan, 1996. The descending process of the opisthotic contacts the exoccipital intercalated between it and the basioccipital, somehow similarly to members of Chelidae and without hiding the ventral edge of the *processus interfensteralis*. *Araripemys* is more evolved than the basic Pelomedusidae by the thoracic rib 10 and the sacral ribs (integrated in the shell) no more contacting the base of the ilia, as in *Pelusios* and *Podocnemidoidea* (a character also homoplastic in *Dortoka*). The posterior skull emargination is as in Pelomedusidae basically, slightly anterior to the *cavum tympani* anterior border and a little more advanced than in the basal *Podocnemidoidea*.

The unnamed specimen FR 4922, of the same area and age as *Araripemys* and *Brasilemys josai* n.g., n.sp. (also represented by a dorsal carapace with the outline of the plastron in the Departamento Nacional da Produção Mineal, DNPM collections, Rio de Janeiro, 645-LE), is, according to Gaffney and Meylan (1991) and Meylan (1996), the

first member of the Pelomedusoides group known without a cervical scute, which becomes a constant character for all Pelomedusidae and Podocnemidoidea (the strong apomorphic anterior notch of the *Araripemys* shell does not allow to verify its potential presence). This character is already partly acquired in *Dortoka* (presence or absence of cervical according to specimens) and also acquired recently in some chelids of the Elseya group. FR 4922 is positioned with *Araripemys* by Meylan (1996), according to the presence of linked postzygapophyses of the cervical vertebrae. But this character (more or less complete in the cervical column) is homoplastic and also present in *Teneremys* (at least in two post-axial cervicals according to the preserved material), which is clearly a Pelomedusidae, very probably in *Brasilemys* n.g. n.sp. (at least 3d known vertebra), in *Podocnemis* (from 3d up to 5th or 7th) and in some Chelidae (from 3d up to 8th). The character fused postzygapophyses may therefore be primitive in Pelomedusoides (more parcimonious condition) or homoplastic and it is too much equivocal to unit *Araripemys* with FR 4922 which has not all the postzygapophyses fused (it is not said which ones are). The position of FR 4922 at the base of Pelomedusoides is not well established because of contradictory informations for its position as a plesion of Pelomedusoides. The reduction of the prootic in width, doing that the carotid is seen to enter in the basiocranium at the medial edge of the pterygoid externally (as in Podocnemididae but differently because of the absence of an enlarged carotid canal) and the single presence in the area of one foramen without indication of facial nerve foramen presence is singular, although analog in Bothremydidae. The developed retroarticular process and the chorda tympani crossing this process (Meylan, 1996) are derived characters of Podocnemidoidea. The secondary roofing of the skull by the union of the parietal and quadratojugal behind the shortened postorbital is a derived character of the Podocnemididae, known from *Hamadachelys*. The vomer is strong, which is missing in Pelomedusidae and possibly in *Araripemys*, retained and well developed in Bothremydidae and primitively present in Podocnemididae. The carapace is close to that of *Podocnemis* (although a curious shape given to the mesoplastra in the drawing) with a derived first neural quadrangular, an elongated anterior border with a straight border similar to that of Podocnemididae and many Bothremydidae (those which are not secondarily differentiated on this point), a developed bridge length and the humero-pectoral sulcus crossing the entoplastron at mid-length. FR 4922 also has the carapace-plastron link and the pleural disk-peripheral border link well sutured instead of ligamentous as in *Araripemys*. The missing characters of Podocnemidoidea are the quadrate which does not link the basisphenoid behind the prootic and the basioccipital and therefore the absence of the Podocnemidoid fossa (and the additional characters of the prootic shape and the three foramina primitively present with this fossa) and the different closure of the *foramen jugulare posterius* by the descending process of the opisthotic extended up to the fore edge of the processus interfenestralis, completely hidden (more derived condition than in *Araripemys* and Pelomedusinae). The open quadrate (it is not a Bothremydidae or a Podocnemididae from *Hamadachelys*) and the contact neural 8-suprapygal make that this taxon may be therefore immediately posterior to Pelomedusidae in the cladogram, as a plesion of the Podocnemidoidea. In this case, the contact neural 8-suprapygal has been lost independently in Pelomedusidae and Podocnemidoidea (as in Chelidae) (and that is verified later on in the cladogram) and the secondary contact quadratojugal-parietal is acquired independently in this form and in Podocnemididae from *Hamadachelys* on. This position is more parcimonious than its position just before *Hamadachelys*.

The attribution of the poorly known *Taquetochelys* Broin, 1980, which shares a part of the paedomorphic and derived characters of *Araripemys* is retained till further discussion (Lapparent de Broin in prep.).

6. Pelomedusoides, node of divergence of Pelomedusidae with respect to *Araripemys*

Characters at the node: see the characters at the node 5 and the problem of *Araripemys* and FR 4922.

Pelomedusidae

– United *foramen posterior canalis carotici interni* and *foramen facialis* in the same small hole in the middle of the ventral face of the prootic (possibly also a passage towards the *canalis cavernosus* as in Podocnemididae: to be studied). Reduction of the neural serie, never complete but nearly, basically. Small protuberances below the posterior part of the vertebral scutes (variably developed, parallelized in some *Podocnemis*). The coracoid reduces in length in most of forms but not in *Pelusios sinuatus*; may be it is a reversion, if the beginning of reduction is shared with Podocnemididae (in any case, less reduction in Pelomedusidae than in this family); it also reduces in length within Chelidae. Descending process of the opisthotic contacting the basioccipital, laterally extended, just behind the ventral edge of the *processus interfenestralis*

The postorbital-jugal and jugo-quadratojugal arches are very short, as in *Araripemys* (the postorbital-jugal arch is not elongated by a secondary roofing of the skull, as it happens in Podocnemididae, *Hamadachelys* and FR 4922). *Araripemys* and Pelomedusidae (including *Teneremys* where the lateral arch is regressed) are the most evolved Pleurodira for the dorsal emargination: the posterior skull emargination is at least a little anterior to the level of the anterior border of the *cavum tympani*. No vomer, an assertion after the hypothesized absence in *Araripemys* (an homoplastic character, also developed in many species of Podocnemididae).

At the base of Pelomedusoides are provisionally given *Platycheloides*, an African poorly known, and a form from Niger, aff. *Platycheloides* sp., which was attributed to this genus ("*Platycheloides* cf. *nyasae* in Broin, 1980). It is differently evolved from *Platycheloides* and Pelomedusinae by several characters (Lapparent de Broin and Cooper in prep.). Both lack skull and vertebrae.

6a, divergence of *Teneremys* from Pelomedusinae, *Pelomedusa* and *Pelusios*.

– Complete reduction of the dorsal roof cover, the posterior emargination joining the lateral emargination in a complete dorsolateral opening: *Teneremys* is the most evolved Pelomedusoides and pelomedusid for that point. Basisphenoid prolonged posteromedially at the anterolateral part of the basioccipital, hiding the medioanterior border of the *fenestra postotica* and the anterior part of the *processus interfenestralis* of the opisthotic. Separating the *fenestra postotica* and the *foramen jugulare posterius*, the descending process of the opisthotic contacts this extension of the basisphenoid and the *processus interfenestralis*, then completely hidden. Much developed

plastral processes up to 1/2 of the lateral width of the pleural 1 (as in basic Podocnemidoidea) while they are few developed in *Pelomedusa* and absent in *Pelusios* because of the hinge of the anterior lobe.

Primitive straights with respect to Pelomedusinae: first neural hexagonal, short sides behind; the last neural may be the eight anteriorly incomplete but contacting the suprapygal or the seventh posteriorly incomplete not contacting the suprapygal; the quadrate is still open behind both the Eustachian tube and the *incisura columellae auris*, as in *Araripemys* and FR 4922, contrarily to *Pelomedusa* and *Pelusios*. The dentaries are unfused as in *Pelomedusa*. Unknown presence of a precolumellar fossa (crushed skulls).

Pelomedusinae (*Pelomedusa* and *Pelusios*).

– Quadrate closed behind both the Eustachian tube and the *incisura columellae auris* as in *Hamadachelys* and Podocnemididae (homoplastic acquisition in Pelomedusidae, Podocnemididae and Chelidae). Rounded lingual border of the maxilla. Longer protection of the head and anterior limbs by the anterior elongation of the carapace (progressive elongation of the anterior peripherals, and the nuchal; elongation of the pleurals 1 and the neural 1) somehow as in Chelidae of the *Hydromedusa-Chelodina* group and *Phrynops* group and Bothremydidae of the *Taphrosphys* group but independently acquired because of the variable extension and shape in each line of the families. First neural quadrangular instead of hexagonal with posterior short sides as it is in Pleurodira anteriorly positioned in the cladogram, *Teneremys* included. The character is also homoplastic: the first neural becomes also quadrangular in Chelidae posterior to Cretaceous forms (most *Hydromedusa* excepted), Bothremydidae and Podocnemidoidea posterior to *Brasilemys* in the cladogram. The carapace is more elevated and rounded in transverse profile than *Teneremys* (and aff. *Platycheloides*) as in *Brasilemys josai* n.g., n.sp. and most of the Poconemididae. The last neural does not contact the suprapygal.

Pelusios, the hinged box-turtle (mobile anterior lobe, hinge through the hyoplastra) diversifies in the shape of the carapace, more or less domed, dentated or no, with stronger protuberances and carenae variably developed, the strong possible reduction of neurals (see Broin, 1969; Broadley, 1983), the enlargement of the plastral lobes, the fusion of the dentaries (as in Podocnemidoidea), the iliac scar contacting or not the suprapygal according to species (as in Podocnemidoidea) and the integration of the sacral ribs in the shell. *Pelomedusa* is derived in the enlargement of the posterior skull, widening of the palate posterior to the trochlear process and associated elongation of the prootic-quadrate area; this also happens in *Pelusios marani* Bour, 2000 (while other species have a narrowing of the posterior palate, such as *P. niger*).

7. Podocnemidoidea, node of divergence of Bothremydidae

Characters at the node

– Link quadrate-basisphenoid behind the prootic and quadrate-basioccipital, ventrally hiding the *fenestra postotica* and the *processus interfenestralis*. Podocnemidoid fossa in the area of the prootic prefiguring the pterygoideus channel (for the pterygoid

muscle) or enlarged carotid canal (Gaffney, 1979); three foramina in the fossa: one anterior, at the limit of the pterygoid, leading towards the *sulcus cavernosus* for the palatine branch of the facial nerve and eventually a palatine artery branch; one medial, below the lateral border of the basisphenoid at the contact with the pterygoid, for the carotid towards the *sella turcica*; and one, more lateral in the prootic, for the facial nerve. A marked line at the base of the future prolonged pterygoid wings which develop in Podocnemididae; *processus retroarticularis* of the articular developed behind the articular facet of the lower jaw; *chorda tympani* entering the *processus retroarticularis*. Incomplete neural serie. Elongated bridge. It is probably here that begins the character fused dentaries (unknown in primitive Podocnemidoidea *Brasilemys* and *Hamadachelys* but present in Bothremydidae as soon as Erfoud form).

Basically, the posterior emargination of the skull is that of the postorbital reduced up to the level of the anterior border of the *cavum tympani* (less derived condition than in Pelomedusidae) and, basically, this emargination is not secondary closed as later on in the cladogram. All the Podocnemidoidea manifest a widening of the triturating surfaces, either apomorphic or homoplastic within Bothremydidae and Podocnemidoidea (beginning in *Brasilemys*). Tendency to widened plastral lobes (at least the anterior; homoplastic within the groups).

Bothremydidae

– Quadrate closed around the stapes alone, in the middle of the *cavum tympani*, the Eustachian tube running posteriorly in a transversal notch of the quadrate. Much salient *processus articularis* of the quadrate below the level of the lateral border of the skull. Elongation of the skull between the orbit and the level of the *cavum tympani*. Absence of precolumellar fossa (the loss here is the more parcimonious condition and the loss happens also in some Chelidae and specimens of *Podocnemis expansa*). Carapace shape: more hydrodynamic in its rounded and low dorsal contour with more angulated tectiform peripherals of the bridge. Carapace more strongly decorated than in the other Pelomedusoides, at least, basically, deeper short dichotomic sulci similarly to marine cryptodiran turtles (*Bothremys*) or sulci often united in polygons, often much salient (*Taphrosphys*).

All the known Bothremydidae share the secondary filling of the lateral emargination and most of them have a reduced jugal: but the filling is variably constituted, homoplastic according to a common trend (contact of the maxillary with the quadratojugal or descending quadratojugal, see Lapparent de Broin and Werner, 1998, fig. 4) and sometimes homoplastic with the filling in Erymnochelyinae (see below).

7a, divergence of the Erfoud form at the base of Bothremydidae.

The undefined form from Erfoud (description in prep.; Lapparent de Broin and Werner, 1998, fig. 4a,e), Hamada of Guir, can be put at the base of the family, according to the suture of the two borders of the quadrate which is very short between the round *incisura columellae auris* and the deep Eustachian notch. It has a deep small hole at the place of the foramen for the posterior carotid (podocnemidoid fossa area), but the prootic is hidden inside by the pterygoid meeting the quadrate and there is no facial nerve foramen, in accordance with evolved bothremydids.

– In the Erfoud form, second closure of the quadrate behind the Eustachian tube, nearly realized in a specimen from the base of the Hamada serie (cited figured specimen) or realized in another specimen. Beginning of separation of the *foramen jugulare posterius* from the fenestra postotica: there is a thin short blade descending from the limit opisthotic-exoccipital as a beginning of the separation. The separation of the *foramen jugulare posterius* appears as homoplastic in Bothremydidae (see below).

Oman form: the undescribed form from the Miocene of Oman (Roger *et al.* 1994, pl. 1, fig. 1) may also be considered as primitive. It has a well rounded closed *incisura columellae auris* (bothremydid character) also shortly separated from the Eustachian notch as in the Erfoud form. But contrarily to other known Bothremydidae in the considered area of the podocnemidoid fossa, the prootic is not completely hidden by the quadrate and pterygoid and the three vascular and nervous foramina visible in the Podocnemidoidae are present in the pterygoid, the basisphenoid and the prootic, showing that the podocnemidoid fossa of Bothremydidae is homologous to that of Podocnemidoidae. In return, this form has already a clear separation of the *foramen jugulare posterius* from the fenestra postotica: as this character is homoplastic this Oman form, even if the most recent in the stratigraphy, may be the most primitively derived branch of the family.

Other Bothremydidae

– Wide suture of the two borders of the quadrate between the stapes and the Eustachian tube.

The *foramen jugulare posterius* is always strongly separated from the *fenestra postotica* by a descending process of the opisthotic, most often with the exoccipital, joining the ventral surface or meeting an ascending process variably constituted (quadrate and basioccipital or one or two of them, according to the genera). The prootic is completely hidden and the number of foramina of the podocnemidoid fossa is reduced to two (*Nigeremys*) or one (all the others) for the carotid. The podocnemidoid fossa is either derived in shape (*Nigeremys* group) or it disappears. Known vertebrae are of the Pelomedusoides type (partial procoelous cervicals and caudals of *Polysternon atlanticum*). *Polysternon provinciale* and *P. mechinorum* share the secondary opening of the suture of the quadrate in a long regular split, more or less oblique. It is a secondary in my opinion, according to the wide distance between the canal of the *columella* and the notch of the Eustachian tube, well constituted as in other Bothremydidae; it is the most parcimonious condition, according to all the bothremydid characters of the genus and in particular its characters shared with the *Bothremys* group. For details on Bothremydidae, see Broin in Antunes et Broin (1988), Lapparent de Broin, in press; Lapparent de Broin and Murelaga (1999), Lapparent de Broin and Werner (1998).

8. Podocnemidoidae, node of divergence of *Brasilemys josai*, n.g., n. sp.

Characters at the node

– “Enlarged carotid canal” (Gaffney, 1979): the podocnemidoid fossa is deepened in its tip by a relatively shallow ovale hole for the three foramina (see above). Carapace shape: more rounded in transversal profile, carapace more elevated, both characters parallelly acquired in Pelomedusinae).

Brasilemys josai, n.g., n. sp. is primitive with respect to other Podocnemidoidae according to the still open behind quadrate, the absence of prolonged pterygoid wings, the parietal separated from the quadratojugal and the position of the prezygapophyses of the axis which are horizontal as in *Proganochelys* and *Notoemys*. The inclination (more or less strong) of these prezygapophyses develops variably in parallel in Pelomedusoides (unknown in Bothremydidae) and Chelidae, except *Chelodina* and *Hydromedusa*. In these two genera, they are well horizontal but it may be secondary, according to the modifications of the lowered and very elongated vertebrae.

9. Node of divergence of *Hamadachelys*, plesion to Podocnemididae

Characters at the node.

– Quadrate closed, its two borders firmly sutured behind together the stapes and the Eustachian tube. Beginning of secondary roofing of the skull by the contact of the parietal and quadratojugal, up to approximately the mid-length of the *cavum tympani*.

The closed quadrate character is homoplastic between Podocnemididae, Chelidae and Pelomedusidae. The acquisition three times, in these three families, is more parcimonious than the loss five times at the nodes of *Araripemys*, FR 4922, *Teneremys* and *Brasilemys josai* n.g., n.sp., all forms which are primitive with respect to their groups, and *Pseudemydura*, the basic chelid according to Gaffney (1977) (where the opening appears as primitive, Lapparent de Broin and Werner, 1998, fig. 6b), adding to the reversive presence three times after the loss, in Chelidae, Pelomedusinae and *Hamadachelys*. As seen previously, when the opening is secondary, as in chelids *Chelodina* and *Hydromedusa*, the two borders of the quadrate still have a prolongation to meet each other, overall the inferior border which is upwards directed, or the inclination of the split is less pronounced such as in *Polysternon*. The secondary roofing of the skull by the contact of the parietal and quadratojugal is present in *Hamadachelys* and Podocnemididae but also in FR 4922: parallel acquisition? Synapomorphy? It is as parcimonious to think that this roofing has been lost after FR 4922 and reacquired by Podocnemididae, than independently acquired in FR 4922 and the Podocnemididae, beginning by *Hamadachelys* (but the hypothesis of the parallel acquisition is more probable, as a sign of a common trend of the group).

As in *Brasilemys josai* n.g., n.sp., *Hamadachelys* has an “enlarged carotid canal” not as much deepened as in the following forms in the cladogram and without a cover of pterygoid wings. It is not clear if the *foramen jugulare posterius* is really separated or not from the *fenestra postotica*. If it is, the character appears here for the first time in the Podocnemidoidae, but in parallel in each branch and in parallel with the Bothremydidae following the Erfoud form in the cladogram, and with various manners according to taxa (see above), which once more indicates that the closure of the foramen is a common trend but not a synapomorphy.

10. Podocnemididae

Characters at the node

– Much dorsoanterior enlargement of the hole in the podocnemidoid fossa, becoming the true “enlarged carotid canal” or “pterygoideus channel” (Gaffney, 1979),

forming a deeper fossa inside the skull, below the level of the palate in ventral view. Development of prolonged pterygoid wings above the anteromedial part of the fossa, from the line already marked in the previous podocnemidoid forms in the cladogram; it is the prolongation of the lateral pterygoid wings, present since *Proganochelys*, developed here ventrally in thin blades from the posterior part of the pterygoid process up to the basisphenoid lateroanterior corner; the pterygoid wings also develop ventrally in Chelidae and Pelomedusinae but they are not prolonged, i.e. not developed backwards behind the level of the quadrate articulation of the lower jaw, where the palate is flat. Elongation backwards of the secondary roofing of the skull by union of the parietal and the quadratojugal up to ca the 2/3 of the *cavum tympani*. Coracoid shortened (already acquired? Unknown in other forms after Pelomedusidae in the cladogram). Advanced humeropectoral sulcus but only up to the mid-length of the entoplastron (already acquired in FR 4922: definitely at this taxon node or homoplastic here?). Quadrangular first neural (already acquired in *Hamadachelys*? Homoplastic in Pelomedusidae, Bothremydidae and Chelidae).

Common tendency: separation of the *foramen jugulare posterius* from the *fenestra postotica* by a descending process of the opisthotic to the basioccipital and often also the quadrate, more or less elevated in an ascending process, often with the exoccipital in the descending as well as in the ascending processes.

10a, node of divergence of Erymnochelyinae

Characters at the node

– Much eroded roof of the enlarged carotid canal, the prootic and quadrate being so much eroded that the floor of the *canalis cavernosus* is broken and this canal is anteriorly confluent with the part of “enlarged canal” leading to the *sulcus cavernosus* (not known in *Dacquemys*, homoplastic but with a less eroded roof in the podocnemidine *Peltocephalus*). Shortening of the humerals: the humeropectoral sulcus is always advanced, anterior to the mid-length of the entoplastron and anterior to the suture epi-hyo-plastral, at least laterally in the modified *Stereogenys* where the intergular is much prolonged backwards on the entoplastron. Secondary roof backwards prolonged up to behind the *cavum tympani* (*Erymnochelys*, *Dacquemys*, *Neochelys*, *Stereogenys*, *Schweboemys antiqua*; homoplastic in *Peltocephalus*). Filling (more or less complete; homoplastic in *Peltocephalus*) of the lateral emargination by the descending quadratojugal (united with the jugal in a part of the *Erymnochelys* specimens, see Lapparent de Broin and Werner, 1998; filling broken in the lateral face of *Dacquemys*, figured in Dacqué, 1912, pl. 2, fig. 8) and often by an antero-inferior protrusion of the quadrate, laterally. Iliac scars not contacting the suprapygial (but unknown in *Stereogenys* and *Carteremys* and homoplastic in advanced Podocnemidinae).

The absence of saddle shaped cervical centra and details in the way the characters are constructed show the homoplasy of these characters in *Peltocephalus*.

In the Erymnochelyinae, the widening of the skull (in dorsal view) is more abrupt and stops at the level of the anterior border of the *cavum tympani*, anteriorly with respect to *Peltocephalus* (see below) where the lateral border are progressively diverging posteriorly up to the back. From the level of the anterior border of the *cavum tympani*, the skull is slightly narrowed posteriorly (Broin, 1977, Pl. 3, fig. 1-2 and Pl. 4, fig. 3-4;

Fig. 13). *S. antiqua* shares with *Erymnochelys*, *Dacquemys* and *Neochelys* the contours of the skull, slightly narrowed anteriorly, slightly elevated posteriorly (more or less globular) from the parietal backwards. *Stereogenys* is similarly widened posteriorly as the other Erymnochelyinae but it is modified owing to the long and wide secondary palate, with a more quadrate and flattened appearance. There are apomorphies for each "group", not evidently shared, possibly developed according to common trends, for the development of the intergular, the triturating surfaces and the filling of the lateral emargination of the skull. Apomorphically, in the *Erymnochelys* group (including *Dacquemys* and *Kenyemys*) the prolonged gulars are united behind the small intergular (a character known from the late Cretaceous of Ibeceten 1, Niger, up to now). In *Neochelys*, the intergular is very variable, either as long as the gulars, or the gulars meeting or nearly meeting behind the intergular (*N. laurenti*), as in *Schweboemys antiqua*, approximating the condition of *Erymnochelys*; or the intergular is prolonged up to the humeropectoral sulcus by a point or widely (according to the specimens in *N. arenarum* and *N. eocenica*, or always, or never in another species such as *N. capellinii*) more or less widely separating the humerals as in *Stereogenys* (wide contact, up to the mid-length of the entoplastron). There is a tendency to the much enlargement of the triturating surfaces of the palate: posteriorly widened maxillae and palatines shared by *Erymnochelys* and *Neochelys* and widening variably developed up to secondary palates in other forms (*Dacquemys*, *Schweboemys* and *Stereogenys*). The *Stereogenys*-*Schweboemys* group, united by the presence of a secondary palate, have differently developed carapaces: the carapace of *Schweboemys* is rather of a "*Bothremys* type", while the carapace of *Stereogenys* is more similar to that of *Neochelys* and of the *Erymnochelys* group, etc. (see figures in Andrews, 1906, being conscious that the pl. 25, fig. 1, is of *Schwoeboemys antiqua* and not of *Stereogenys*; Dacqué, 1912; Reinach, 1903; Williams, 1954b; Wood, 1970). The roof is not preserved in most of the specimens of *Schweboemys*. In *S. antiqua* (fig. 136, Gaffney, 1979), the posterior emargination is filled, posteriorly up to the *cavum tympani*, and the lateral emargination is partly filled dorso-posteriorly by the quadratojugal. Beside the similarly widened masticatory surfaces, *Erymnochelys* and *Neochelys* share the antero-inferior prolongation of the quadrate to partially fill the lateral skull emargination. As in *Dacquemys* where it is broken, the lateral face of *Stereogenys* is not well known, not presented in authors's figures. Mio-Pleistocene *Schweboemys gaffneyi* and *S. pilgrimi* have elongated skulls. They are unknown as far as their lateral filling and dorsal roofing are concerned. It is probable that the four forms i.e. *Erymnochelys* group, *Neochelys*, *Stereogenys* and *Schweboemys*, derived from a common early Cretaceous afro-indian origin from which they retain common tendencies, distributed in mosaic. The Indian "group" of *Carteremys* seems related to the Pakistanese *Schweboemys* because of the elongated skull, wide masticatory upper surfaces and widened lower jaw, and to the African *Schweboemys* because of the large and wide intergular joining the humeropectoral sulcus (Jain, 1978, 1986; Singh *et al.*, 1998, in which the carapace and plastron of "*Pelomedusidae* indet." are clearly of *Carteremys*; Williams, 1953). In the cladogram (Fig. 6) we distinguish now, with respect to the cladogram of Broin, 1988, the *Neochelys* group (possibly with some forms from Fayum), the *Schweboemys* group (possibly with *Stereogenys* and *Carteremys*) and the *Erymnochelys* group. A particular study of the "subfamily" has to be made.

10b, node of divergence of Podocnemidinae

Characters at the node

– Cervical centra with posterior condyles horse-saddle shaped. At least in extant forms, shortened atlas intercentrum.

Peltocephalus, *Bauruemys elegans*, aff. *Roxochelys vilavilensis*, *Podocnemis* and *Stupendemys* share this character (Williams, 1950), less achieved in *Peltocephalus* (saddles to cervical 2-6) than in others (saddles to cervicals 2-7): the posterior condyle of the procoelous cervical vertebrae are in form of saddle and the ventral face of the condyle has no more salient protuberances below. The meeting of the quadratojugal and parietal, as in *Erymnochelyidae*, is less long posteriorly in Podocnemidinae except in *Peltocephalus*. As in *Peltocephalus*, the humeropectoral sulcus is posterior on the entoplastron in a large primitive late Cretaceous form from the Bauru group, “*Podocnemis*” *brasiliensis*, a form which may correspond to an undescribed large posterior skull from Peiropolis (DNPM, 1958, Rio de Janeiro). This skull is also possibly related to *Peltocephalus* because of the much roofed skull with a relatively widened posterior interparietal scute (less widened than in *Peltocephalus*). In the *Podocnemis* group, the roof is not as much secondarily completed, the interparietal is posteriorly pointed (but uncompletely in *P. sextuberculata*), and the humeropectoral sulcus is more advanced but no more than the epi-hyoaplastral suture. *Podocnemis* is a monophyletic genus particularly on the interorbital sulcus and the link jugal parietal behind the reduced postorbital. The loss of the iliac scar-suprapygal contact is acquired within the subfamily (still contact in Cretaceous forms from Brazil), in parallel to Chelidae, Pelomedusinae, Bothremydidae and *Erymnochelyinae*.

The skull of *Peltocephalus* looks similar to that of *Erymnochelys*, particularly on the the lateral emargination filling, often globally constituted as in *Erymnochelys* (Broin, 1977, Pl. 3-4; Lapparent de Broin and Werner, 1998, Fig. 6, e,f) and on the elevation of the very roofed skull. But there is evidence of homoplasy because the details differ. In *Peltocephalus*, in dorsal view, the globosity of the skull begins anteriorly and in a more oblique line up to the back and, in lateral view, the roof is more elevated and longer, doing different dorsal and lateral contours; the snout is much more prolonged with a strong premaxillary hook and a strong ventral premaxillary pit; the triturating surfaces are narrower than in *Erymnochelys* and *Neochelys*; there is no antero-ventral prolongation of the quadrate to fill the lateral emargination; the enlarged canal is not as much eroded dorsally, so that a part of the roof of the *canalis cavernosus* remains present; medial dorsal expansions of the pterygoid united to a dorsal crest of the basisphenoid cover the rodlike *rostrum basisphenoidale*, and the trochlear face of the pterygoid process is directed posteriorly. The vertebrae saddle shaped centra and the shortened atlas intercentrum are different and clearly show its belonging to the Podocnemidinae. As in *Erymnochelys*, the vertebrae are relatively high and the postzygapophyses are not linked in extant *Peltocephalus*. However, there are large vertebrae with linked postzygapophyses in the material from Peiropolis, probably corresponding to “*Podocnemis*” *brasiliensis* which is possibly related to *Peltocephalus* (see above). The humeropectoral sulcus is never anterior to the suture epi-hyoaplastral in this form and in *Peltocephalus*.

Statements on the cladistic analysis

There is an approximate consensus for the phyletic relationships of the Pleurodira examined in the presented cladogram, except for details in Podocnemididae. Except also that, from their erection, the phyletic interrelationships of some new taxa have not yet been discussed: Dortokidae, FR 4922 and *Hamadachelys*. This work is the first to integrate these new taxa with *Brasilemys josai* n.g., n.sp. in the phylogeny. This new taxon is surely correctly situated as the first known pleurodiran podocnemidoid with a basic "enlarged carotid canal". It is surely situated before *Hamadachelys*, according to the absence of closed quadrate, and therefore it is also not a bothremydid. *Hamadachelys* also appears as well situated, without prolonged pterygoid wings. Problems evidenced in this study is the situation of *Araripemys*, Dortokidae and FR 4922. I propose new positions: that of the Dortokidae related to Platychelyidae, according to the data of the palaeogeography, and that of FR 4922 closer to Podocnemidoidea which implies homoplasies (and requires more study of the specimens). The position of *Araripemys* at the base but not included in the Pelomedusidae is better.

The most important problem existing now is the divergence Chelidae-Pelomedusoides. Either they constitute a clade "Eupleurodira" or, according to palaeogeography and stratigraphy, each one is the sister group of another taxon such as, respectively, *Notoemys* and *Platychelys* (or other unknown taxa). There is no solution to recognize the homoplasies if the two groups are studied separately. More researches on partly undescribed specimens and on chelids are necessary and it is one more reason not to establish now a new cladogram with a program of parcimony.

PALAEOECOLOGICAL AND STRATIGRAPHICAL CONSIDERATIONS - CONCLUSION

Brasilemys josai n.g., n. sp. is part of the famous fauna and flora of the Chapada do Araripe (Maisey ed., 1991), from the upper part of the Romualdo member, Santana Formation, limit Aptian-Albian. The turtle fauna includes five taxa of turtles, four Pleurodira (one of the two still extant infraorders of chelonians) and one Cryptodira (the other extant infraorder).

The Pleurodira are *Araripemys* Price, 1973, *Brasilemys josai* n.g. n.sp., the new undefined taxon presented in Gaffney and Meylan, 1991 (Senckenberg specimen, FR 4922, in Meylan, 1996) and the Podocnemidoidea indet. of the Josa collection. The cryptodire is *Santanachelys* Hirayama, 1998, a primitive protostegid. The Araripe turtle pleurodiran fauna is phyletically related to the continental African fauna of the early Cretaceous. It is continental, as most of the other members of the fauna except, eventually, some marine fishes trapped in the Araripe lake (? Maisey, 1991) and the Echinodermata found (not often in place) in a very upper level of the final Albian transgressive stage of the Santana Formation.

The cryptodiran *Santanachelys* has an anteriorly protruded carapace, alleviated as the plastron, and still a short fore limb but that is derived by a small hand-paddle (elongated digits 2 to 5) as in late Jurassic littoral forms (Europe, Argentina) with

more or less regressed articulations. It has also a postero-inferiorly enlarged foramen interorbitale (as much as in the Jurassic *Solnhofia*, at least the specimen from Quercy, France, and more enlarged than in *Plesiochelys*), which allows Hirayama (1998) to think that it had a salt gland and was adapted to salt water. The protostegid group is then known in estuarian and littoral sediments with *Rhinochelys* in the Albian of France and Albian-Cenomanian Greensands of England (references in Lapparent de Broin, in press) and *Cratochelone* and *Notochelone* in the Albian of Australia (Gaffney, 1991; undescribed new material in the Queensland Museum, Brisbane). True marine Chelonioidea with not only alleviated carapace and plastron, and eventually an anterior protrusion of the carapace, but also with elongated and flattened digits 2 to 5, modified humerus, elongated fore arm much longer than hind limb, etc., are found in marine environments during the upper Cretaceous in Europe, Asia and North America (Hay, 1908; Hirayama, 1994; Hirayama and Chitoku, 1996; Zangerl, 1953 and others). It is possible that *Santanachelys* was a littoral form (issued from littoral Jurassic forms or from ancestors of all these forms) and having been trapped in the lake of Araripe communicating with the sea. But its fore hand is too short and the articulations too much preserved (fingers 1-2) to be derived from the littoral *Neusticemys* Fernández and de la Fuente, 1993, from the lower-middle Tithonian of Argentina. This has an anteriorly protruding carapace, alleviated as the plastron and a similar elongated hand, and it is probably also a primitive Protostegidae as *Santanachelys* but, besides, it has a much more elongated fore arm and no more hand articulations. We note that, although potentially adapted to sea, *Santanachelys* is surely not a marine turtle because of "the depositional environment of the fossil" which is continental (Maisey ed., 1991) and it is surely not "the oldest sea turtle" because of the Jurassic records.

The oldest chelonians were terrestrial as shown by *Proganochelys*, from the Triassic of Germany, *Palaeochersis*, Triassic of Argentina and *Australochelys*, from early Jurassic of South Africa. *Proganochelys*, better preserved and known, has a typical aspect of a terrestrial heavy primitive form (high and roofed skull; carinated carapace with protuberances, protection of pointed osteoderms on the neck, members and tail; dentated carapace and plastron; short hands and feet; thick bones etc.). The low carapace, at the height of the body (as for the shield of the crocodiles), is just primitive and has nothing to do with the lowering of the carapace for adaptation to water, as produced in aquatic more recent forms (not all the aquatic forms) but also in terrestrial forms. *Proterochersis*, older than *Proganochelys*, has a domed shell but it is clear that *Proganochelys* is of a more primitive stage. The chelonians firstly adapted to freshwater before to marine water: the adaptation to freshwater began as early as late Triassic of Thailand (freshwater environment of aff. *Proganochelys rucha* Broin, 1985, in a locality without any terrestrial form). The strong adaptation of the carapace for better swimming is known in Eurysternidae from Jurassic of Europe (Broin, 1994; Lapparent de Broin *et al.*, 1996). In Brazil, it is evidenced in *Araripemys* (firstly represented in the continental late Aptian of Gadoufaoua, Niger) which has a very low and alleviated carapace and long fingers. The first Trionychoids, with paddled limbs, long neck and flattened and alleviated carapace, are also found in continental deposits of the late Jurassic-early Cretaceous of Asia (Yeh, 1963; new finds in Laos) and they remained continental, although able to follow a littoral stream.

As far as the pleurodirans from Araripe are concerned, they are typical continental forms as they exist in continental areas of the very early Cretaceous of Bahia, late Aptian from Gadoufaoua, Niger, and late Albian-early Cenomanian from Sahara, early Cenomanian of Baharija, Egypt (see maps in Broin, 1988). Later, a branch (the Bothremydidae) adapted to littoral environment from the Cenomanian of Israël (Haas, 1978a,b) up to the Miocene (Lapparent de Broin and Werner, 1998). Some are apparently more swimmers, such as the very flattened *Araripemys*, while other are less, such as *Brasilemys josai* n.g., n.sp.: with a regular ovale carapace not keeled, not posteriorly particularly expanded and not flattened, it is a turtle with the habits of a freshwater turtle as some of the small extant South American species of *Podocnemis* and of the chelid *Phrynops* group, but also as the African Pelomedusinae. Without the limbs, it is difficult to see if *Brasilemys josai* n.g., n.sp. was more or less terrestrial. These pleurodiran forms of turtles are intertropical now. The continental various branches of the group never adapted to climatic change (cooling) during the end of the Eocene in Europe and Patagonia and the littoral branch (Bothremydidae) also disappeared during the Miocene of Mediterranean countries and North America: although some adapted to dryness and possible nocturnal cold, those which still exist now are approximately in the same warm climates as during the Cretaceous times.

Brasilemys josai n.g., n.sp., as all the fauna of turtles from the Chapada do Araripe, is very important. With the fauna of Aptian-Albian-early Cenomanian of the northern part of Africa, this fauna is part of the formidable radiation of the hyperfamily Pelomedusoides, which are the Pleurodira of the northern part of the ancient Gondwana continent, which occurred in a short geological time, the early Cretaceous. The fauna from the Chapada do Araripe includes three taxa situated at important nodes of the phyletic relationships of the Pelomedusoides: *Araripemys*, diverging at the base of the Pelomedusoides, the unnamed form of Gaffney and Meylan (1991), proposed as diverging at the base of the Podocnemidoidea and *Brasilemys josai* n.g., n. sp., diverging at the base of the epifamily Podocnemidoidea leading to the Podocnemididae (Podocnemidinae of South America and Erymnochelyinae of Africa-Europe-Madagascar-Indian subcontinent up to Burma). Their spring was part of a unique continent and the moment of the break and drift is just anterior and contemporaneous with this explosion of forms. However, the fauna of Araripe was never completely identical in genera with that known of Africa: if the basins may have communicated during the very early Cretaceous of Bahia, as soon as during the Gadoufaoua times the genera are different, except for *Araripemys* which is different at the specific level, just showing that they have close common ancestors. The fauna of turtles from Bahia-Tucano basin (DNPM, Rio de Janeiro) is very poorly preserved and consists of undefined Pelomedusoides, possibly related to *Teneremys* (including a flattened medium-sized form with 6 neurals only). It just indicates the presence of the Pelomedusoides group, already well differentiated before the continental break.

As far as the age is concerned, the fauna of turtles from the Chapada do Araripe is well situated between: - the fauna of the late Aptian of Gadoufaoua, Niger, and other corresponding Algerian and Tunisian localities, late Aptian, lower level of the upper part of the "Continental Intercalaire du Sahara" (itself considered as younger than the fauna from Bahia); - and the fauna from the Hamadas of Kem-Kem and Guir, Morocco and other Saharian countries, late Albian-early Cenomanian, terminal level of the upper part of the "Continental Intercalaire du Sahara". It is different from the fauna of the early

Cenomanian from Baharija, Egypt (Gmira, 1995; Lapparent de Broin, 2000). There is an increase of size in *Araripemys* which can be considered as significative: from the smallest in Gadoufaoua, the middle-sized *Araripemys barretoii* in Araripe, the largest in Morocco and a possible much larger in Baharija (Stromer, 1934). The other elements are not truly conclusive but they are concordant. The unnamed Araripe form of Gaffney and Meylan (1991) is more advanced than the Pelomedusoides from Gadoufaoua; the pre-Podocnemidid *Hamadachelys* from Morocco is posterior in age and more evolved than *Brasilemys josai* n.g., n.sp., from Araripe, which could fit with the different ages. But if the Erfoud form, from Morocco, one of the first recognized bothremydids, is smaller than and different from the form from Baharija, *Apertotemporalis* Stromer, 1934 (a locality with a different known fauna of turtles and crocodiles), there are also poor remains of large undefined Pleurodira in Morocco and in other Albian localities (see Tikarkas, Mali in Bergounioux et Crouzel, 1968, Kem Kem in Gmira, 1995, and various localities from Sahara, cited in Lapparent de Broin, 2000). As the Bothremydidae, firstly known in Morocco, diverged before *Brasilemys josai* n.g., n.sp., from Araripe and as Podocnemididae evolved separately after the early Cretaceous in Africa and South America because of the break of the Gondwana, I wait for the found of a (pre-) Podocnemididae and a (pre-) Bothremydidae in Araripe: the undefined podocnemidoid of the Josa collection surely corresponds to one of them.

The age of the fauna of Araripe younger than that of Gadoufaoua is in agreement with the data of the fauna of crocodiles, comparing South-America and Africa. For example, *Sarcosuchus* Broin et Taquet (1965) is present during the early Cretaceous (Barremian-Aptian) of the Bahia basin (Mawson and Woodward, 1907) and the late Aptian from Niger, Algeria and Tunisia. It disappeared and is not present during the Albian of Araripe, Morocco and other Saharian localities of the same stratigraphic zone. But, as the turtles, the crocodiles of those localities have diverged after the break with different forms in America and Africa. For example (among others) the crocodile aff. *Araripesuchus wegneri* (Buffetaut, 1981), from Gadoufaoua is not a true *Araripesuchus* Price, 1959, as are those from Araripe (type locality) and Argentina (Michard *et al.*, 1990; Ortega *et al.*, 2000) and the longirostrine "Mesosuchian" "*Thoracosaurus*" *cherifiensis* Lavocat, 1955, from the African late Albian level (Broin *et al.*, 1971; Lapparent de Broin in prep.) is unknown in South America. However, in Africa and South America, most of the crocodiles from the Albian-very early Cenomanian level are "Mesosuchian" in stage of evolution (Broin *et al.*, 1971; Gasparini, 1971; Ortega *et al.*, 2000, and others) with amphicoelous vertebrae, and not "Eusuchian", i.e. more "modern" because of procoelous vertebrae. Mesosuchian disappeared during the lower Eocene while "Eusuchians" developed up to now. The procoely appeared independently several times during the late Jurassic-early Cretaceous times (in particular during the early Cretaceous of Cameroun, Michard *et al.*, 1991) but, curiously, procoelous crocodiles are rare in the late Albian "Continental Intercalaire du Sahara" from Morocco, Algeria, Tunisia, Niger and Mali and absent from the Cretaceous of South America: among hundreds of specimens, only one procoelous vertebra from the upper level, late Albian-early Cenomanian, of Algeria and two from the same level from Morocco (new material) are known, while most of the crocodiles of the early Cenomanian fauna from Baharija are procoelous (Stromer, 1925, 1933). The "Mesosuchian" of the Saharian countries are not evidenced in the locality, according to the figures of Stromer (although possibly present, but Stromer's material is

lost): if the age of Baharija was the same as that of Morocco (at least the very upper levels) and of other countries, nevertheless the known fauna is different and more advanced in Baharija.

The comparison of the African fauna with the fauna from the Chapada do Araripe clearly evidences two facts: – that the Gadoufaoua stratigraphic zone in Sahara is oldest than the Romualdo member of the Chapada do Araripe which produced the turtle fauna and – that, even if not far in age, this Araripe time is older than the extreme upper part of the “Continental Intercalaire du Sahara”, which is older than, or in any case different from, the Baharija fauna.

Endly, the break of the Gondwana produced divergent faunas of crocodiles and turtles in the two new continents as soon as the early Cretaceous. The time of the fauna of turtles of Araripe is that of an important radiation of forms, as particularly evidenced by the presence and study of *Brasilemys josai* n.g., n.sp.

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ANNEXE

List of the above cited fossil turtles (not exhaustive of the known taxa of the groups) with the genus, type species, author, age, locality and distribution. References above and in Lapparent de Broin, 2000; in press; Broin, 1988; Broin et de la Fuente, 1993; Lapparent de Broin and Werner, 1998; for type species, authors and distribution of extant forms, see Wermuth und Mertens, 1977; Iverson, 1992.

Ordo Chelonii Brongniart (Latreille) 1800

Infraordo Proganochelydia Romer, 1966, Proganochelyidae Hay 1908: *Proganochelys*, *P. quenstedti* Baur, 1887, upper Keuper, upper Stubensandstein, Triassic, Neuenhaus (holotype) and various localities of Württemberg and Halberstadt, upper Stubensandstein, and Knollenmergel Germany (Fraas, 1899; Gaffney, 1990; Jaekel, 1918). Aff. *Proganochelys ruchae* (Broin, 1985) (Lapparent de Broin, 2000), Norian, Thailand.

Infraordo indet.

Australochelyidae Gaffney and Kitching, 1994: *Australochelys*, *A. africanus* Gaffney and Kitching, 1994, Early Jurassic, Hettangian, Bormansdrift, Orange Free State, Karroo, South Africa (Gaffney and Kitching, 1995).

Incertae familiae: *Palaeochersis*, *P. talampayensis* Rougier *et al.*, 1995, late Triassic, Los Colorados Formation, Norian, La Rioja, Argentina.

Infraordo Pleurodira Cope, 1864

Proterochersidae Nopcsa, 1928: *Proterochersis*, *P. robusta*, Fraas, 1913, upper Keuper, lower bed of Stubensandstein, Rudesberg North of Schorndorf (holotype); lower and upper beds of Stubensandstein, upper Triassic, Baden-Württemberg and other localities, Württemberg, Germany.

Platychelyidae Bräm, 1965: *Platychelys*, *P. oberndorferi* Wagner, 1853, upper Jurassic, probable lower Tithonian, Kelheim, Germany. Upper Kimmeridgian, Solothurn, Switzerland-Tithonian Bavaria, Germany. Indet. forms during the Kimmeridgian of Portugal (Bräm, 1973) and early Cretaceous of Spain (Krebs, 1995; Sanz *et al.*, 1988).

Dortokidae Lapparent de Broin and Murelaga, 1996: - *Dortoka*, *D. vasconica* Lapparent de Broin and Murelaga, 1996, upper Campanian, Laño, North of Iberian Peninsula. Campanian-Maastrichtian South of France, Iberian Peninsula (Lapparent de Broin and Murelaga, 1999). - *Ronella*, *R. botanica*, Lapparent de Broin, 2000, in Gherbrandt *et al.* 2000, upper Paleocene (limit lower Eocene), "calcaires de Rona", Jibou (and Rona), Romania. Indet. form, lower Cretaceous Spain (Murelaga-Bereikua, 1998).

Notoemydidae Broin et de la Fuente, 1993: *Notoemys*, *N. laticentralis* Cattoi and Freiberg, 1961, Formation Vaca Muerta, early-middle Tithonian, late Jurassic, Las Lajas, and other localities, Neuquén province, Argentina (Fernández and de la Fuente, 1994).

"Eupleurodira"

Chelidae Gray, 1825, from early Cretaceous of Patagonia to extant South America and Australasia, South Gondwanian in origin. Fossil and extants (among others): in Australasia, *Elseya* Gray, 1867 of the *Emydura* group; *Pseudemydura* Siebenrock, 1901; *Chelodina* Fitzinger, 1826; in South America, *Hydromedusa* Wagler, 1830; *Phrynops* Wagler, 1830 group; *Chelus* Duméril, 1806. See references in Broin et Fuente, 1993, Fuente *et al.*, 2001; Lapparent de Broin y Fuente, 1999; Lapparent de Broin *et al.*, 1997; Lapparent de Broin and Molnar, 2001).

Pelomedusoides (sensu Broin, 1988 and Broin, in Antunes et Broin, 1988)

Araripemydidae Price, 1973

- *Araripemys*, *A. barretoii* Price, 1973, early Cretaceous, limit Aptian-Albian, Santana Formation, Romualdo Member, Chapada do Araripe, Ceará state, Brazil. *Araripemys* spp., Aptian, Albian, early Cenomanian: Algeria, Morocco, Niger, probably Egypt and Ethiopia (Lapparent de Broin, 2000). - ?Araripemydidae Price, 1973: *Taquetochelys*, *T. decorata* Broin, 1980, late Aptian, Gadoufaoua, Niger. Possibly Anoual, early Cretaceous, Morocco.

Plesions to Pelomedusidae Cope, 1868: Aff. *Platycheloides* sp.: “*Platycheloides* cf. *nyasae*” in Broin (1980) (Lapparent and Cooper in prep.): Gadoufaoua, Niger, Late Aptian. *Platycheloides*, *P. nyasae* Haughton, 1928: early Cretaceous, “Nyasaland”, Malawi.

Pelomedusidae Cope, 1868: - *Teneremys*, *T. lapparenti* Broin, 1980: Gadoufaoua, Niger, Late Aptian. - Pelomedusinae Cope, 1868: *Pelomedusa* Wagler, 1830, extant Africa except Maghreb; Saudi Arabia; Madagascar; fossil early Miocene Namibia, Plio-Holocene Africa. *Pelusios* Wagler, 1830, Africa except Maghreb, Madagascar; neighbouring islands; fossil early Miocene Uganda-Kenya up to know in Africa.

Plesion to Podocnemidoidea Cope, 1868: g. sp. indet., FR 4922, Gaffney and Meylan, 1991; Meylan, 1996; early Cretaceous, limit Aptian-Albian, Santana Formation, Romualdo Member, Chapada do Araripe, Ceará state, Brazil.

Podocnemidoidea Cope, 1868

Bothremydidae Baur, 1891 (among others, Lapparent de Broin and Werner, 1998): - primitive forms, Oman form: g., sp. indet., early Miocene-earlier Middle Miocene, Orleanian, ar. 18 MY, Ghaba, Sultanate of Huqf (Roger *et al.*, 1994), Erfoud form: g. sp. indet., Hamada du Guir, Morocco, Albian-Cenomanian, anterior to Cenomanian of Baharija and to Cenomanian transgression (Lapparent de Broin and Werner, 1998); - *Taphrosphys* group: *Taphrosphys* Cope, 1869, *Platemys sulcatus* Leidy, 1856, upper Cretaceous, New Jersey, USA. Cretaceous USA - Eocene Peru. Europe: Campanian and Montian France; - Pre-*Bothremys* group: *Polysternon* Portis, 1882, *?Pleurosternon provinciale* Matheron, 1869, Campanian (Fuvelian) Fuveau, Fuveau-Valdonne basin, France. *Polysternon atlanticum* Lapparent de Broin and Murelaga, 1996, late Campanian, northern-western Iberian Peninsula. *P. mechinorum* (Tong *et al.*, 1998), Maastrichtian, Fox-Amphoux, France; - *Bothremys* group: *Bothremys*, *B. cooki* Leidy, 1865, late Cretaceous, New Jersey. *Bothremys* spp. in Alabama and Gulf coastal Province, Arkansas and Epicontinental province, Kansas, USA; Cenomanian, Israel. *Nigeremys* Broin, 1977, *Potamochelys gigantea* Bergounioux & Crouzel, 1968, Maastrichtian, Ibéceten 2, Niger; - Incertae sedis group: *Apertotemporalis*, *A. baharijensis* Stromer, 1934, early Cenomanian, Baharija, Egypt.

Podocnemidoidea Cope, 1868

Brasilemys n.g., *B. josai* n. p., early Cretaceous, limit Aptian-Albian, Santana Formation, Romualdo Member, Chapada do Araripe, Ceará State, Brazil.

Plesion to Podocnemididae Cope, 1868: *Hamadachelys*, *H. escuillei* Tong and Buffetaut, 1996, Albian-Cenomanian, anterior to Cenomanian of Baharija and to Cenomanian transgression, Hamada du Guir, Morocco.

Podocnemididae Cope, 1868

- Erymnochelyinae Broin, 1988: - *Erymnochelys* Baur, 1888, group: extant *Dumetilia madagascariensis* Grandidier, 1867, Madagascar; *Dacquemys* Williams, 1954b, *Podocnemis fajumensis* Andrews, 1903, Early Oligocene, Birket El Kurun beds, Fayum, Egypt; *Kenyemys*, *K. williamsi* Wood, 1983, Late Miocene, ca. 6 MY, Lothagam 1, Kerio River Basin, Kenya; indet. forms, Mio-Pliocene of Africa, Oligocene of Oman.

Neochelys Bergounioux 1954, *Emys capellinii* Zigno, 1889, middle Eocene, MP 10-11, Purga di Bolca, Monte Bolca, Italy, *N. arenarum* Broin, 1977, Rians, MP 7, *N. laurenti* (Tong, 1998), Saint-Papoul, MP 9, *N. eocenica* (De Stefano, 1902), Pépieux, MP 12, France, and others in Europe (Belgium, Germany, Spain), MP 7-12 (Lapparent de Broin, in press), late Eocene Fayum, "*Stereogenys*" *podocnemidoides* Reinach, 1903. - *Stereogenys*, *S. cromeri* Andrews, 1901: Late Eocene, Fayum, Qasr El Sagha beds, Egypt and *S. libyca* Andrews, 1903, Early Oligocene, Fayum, Birket El Kurun beds, Egypt and indet. forms, Oligocene, Oman, Miocene, Arabia. - *Schweboemys* Swinton, 1939, *Podocnemis antiqua* Andrews, 1903, Late Eocene Fayum, Qasr El Sagha beds, Egypt; *S. pilgrimi* Swinton, 1939, Pliocene-Pleistocene, Burma, *S. gaffneyi* Wood, 1970, lower Miocene, Bugti Hills, Pakistan, and indet. form, Miocene, Oman, Arabia. - *Carteremys* Williams, 1953, *Testudo leithi* Carter, 1852, upper Cretaceous, Intertrappean of Bombay; also upper Cretaceous, Pisdura Formation, Central India.

- Podocnemidinae Cope, 1868: *Bauruemys* Kischlat, 1994, *Podocnemis elegans* Martín-Suarez, 1969, upper Cretaceous, Bauru Group, Presidente Prudente, Brazil. *Roxochelys*, *R. wanderleyi* Price 1953, upper Cretaceous, Bauru Group, Brazil. *?Roxochelys vilavilensis* Broin, 1971, Palaeocene, Vila-Vila-Tiupampa, Bolivia (Broin, 1991). *Podocnemis* Wagler, 1830 (see Williams, 1954a): among other extants, *P. expansa* and *P. sextuberculata* and fossil *Podocnemis* spp., Mio-Pliocene, Colombia (Broin, 1991), Peru (Williams, 1956), Acre (Brazil) (Lapparent de Broin *et al.*, 1993). Extant *Peltocephalus dumerilianus* (Shweigger, 1812). "*Podocnemis*" *brasilensis* Price, 1953, upper Cretaceous, Bauru Group, Brazil. *Stupendemys*, *S. geographicus* Wood, 1976, Huayquerian, Urumaco Formation, Mio-Pliocene, "Capa de huesos", Venezuela and *S. sp.*, Mio-Pliocene, Acre, Brazil (Lapparent de Broin *et al.*, 1993).

Infraordo Cryptodira Cope, 1868.

Kayentachelyidae: *Kayentachelys*, *K. aprix* Gaffney *et al.*, 1987, early Jurassic, Arizona, USA.

Plesiochelyidae Baur, 1888: *Plesiochelys* Rüttimeyer, 1873, *P. solodurensis* Rüttimeyer, 1873, upper Kimmeridgian, Solothurn, Switzerland. Upper Jurassic-lower Tithonian, England, France, Germany (Hannover; Hildesheim), Switzerland.

Eurysternidae Dollo, 1886: *Solnhofia* Gaffney 1975, *S. parsonsi* Gaffney, 1975, upper Jurassic (probable lower Tithonian, Hybonotum zone), Solnhofen area, Germany. Upper Kimmeridgian - lower Tithonian, Germany, France, Switzerland.

Chelonioidea s.l. Oppel, 1811: Primitive Protostegidae Cope, 1872: *Neusticemys* Fernandez y Fuente, 1993, *Eurysternum? neuquinum* Fernández y Fuente, 1988, lower- middle Tithonian, Neuquén, Argentina; *Cratochelone*, *C. berneyi* Longman, 1915, and *Notochelone* Lydekker, 1889, *Notochelys costata* Owen, 1882, Albian, Toolebuc Formation, Queensland, Australia; *Santanachelys*, *S. gaffneyi* Hirayama, 1998, early Cretaceous, limit Aptian-Albian, Santana Formation, Romualdo Member, Chapada do Araripe, Ceará State, Brazil. Protostegidae: *Rhinochelys* Seeley, 1869, *Chelone pulchriceps* Owen, 1842, upper Cretaceous, middle Albian-lower Cenomanian, Cambridge upper Greensand, England. Europe: Albian, France, upper Albian-lower Cenomanian (Gault, upper Greensand) England.

REFERENCES

- Andrews, C.W. 1901. Preliminary note on some recently discovered extinct Vertebrates from Egypt. *Geol. Mag.*, **IV** (8), part II (448): 440-444.
- Andrews, C.W. 1903. On some pleurodiran Chelonians from the Eocene of the Fayum, Egypt. *Ann. Mag. Nat. Hist.*, Ser. 7, **11**: 115-122.
- Andrews, C.W. 1906. *A descriptive Catalog of the Tertiary Vertebrata of the Fayum, Egypt*. Order Chelonia: 275-306. Trustees of the British Museum Eds, London.
- Antunes, M.T. et Broin F. de 1988. Le Crétacé terminal de Beira Litoral, Portugal: remarques stratigraphiques et écologiques; étude complémentaire de *Rosasia soutoi* (Chelonii, Bothremydidae). *Ciênc. Terra (UNL)*, **9**: 153-200.
- Baur, G. 1887. Ueber den Ursprung der Extremitäten der Ichthyopterygia. *Bericht Vers. Oberr. geol. Ver.* **20**: 17-20.
- Baur G. 1888. Osteologische Notizen über Reptilien. *Zool. Anz.*, II Wissensch. Mitt., Jahr. II, 269-296, Fortsetz. III, Juin 1888: 417-424.
- Bergounioux, F.M. 1954. Les Chéloniens fossiles des terrains tertiaires de la Vénétie. *Mem. Ist. Geol. Miner. Univ. Padova*, **18**: 1-115.
- Bergounioux, F.M. et Cruzel, F. 1968. Deux tortues fossiles d'Afrique. *Bull. Soc. Hist. Nat. Toulouse*, **104** (2): 1-2.
- Boulenger, G.A., 1889. *Catalogue of the Chelonians, Rhynchocephalians and Crocodiles in the British Museum (Natural History)*: I-IX, 1-311, fig. 1-73, pl. 1-6, Trust. Brit. Mus. (Nat. Hist.), London.
- Bour, R. 2000. Une nouvelle espèce de *Pelusios* du Gabon (Reptilia, Chelonii, Pelomedusidae). *Manouria*, **8**: 1-32.
- Bräm, H. 1965. Die Schildkröten aus dem oberen Jura (Malm) der Gegend von Solothurn. *Schweiz. Paläont. Abh.*, **83**: 1-190.
- Bräm, H. 1973. Chelonia from the Upper Jurassic of Guimarota Mine (Portugal). In: Contribuição para o conhecimento da Fauna do Kimeridgiano da Mina de Lignito Guimarota (Leiria, Portugal). *Serv. Geol. Portugal*, 22 (N.S.), **7**: 135-141.
- Broadley, D.G. 1983. Neural Pattern. A Neglected Taxonomic Character in the genus *Pelusios* Wagler (Pleurodira : Pelomedusidae). In : A.G.J. Rhodin & K. Miyata Eds., *Essays in Honor of Ernest E. Williams, Advances in Herpetology and Evolutionary Biology*: 159-168. Mus. Comp. Zool., Cambridge, Mass.

- Broin, F. de 1969. Sur la présence d'une Tortue, *Pelusios sinuatus* (A. Smith) au Villafranchien inférieur du Tchad. *Bull. Soc. géol. Fr.*, 3e sér., **11**: 909-916.
- Broin, F. de 1971. Une espèce nouvelle de Tortue pleurodire (? *Roxochelys vilavilensis* n. sp.) dans le Crétacé supérieur de Bolivie. *Bull. Soc. géol. France*, Sér. 7, **13** (3-4): 445-452.
- Broin, F. de 1977. Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. *Mém. Mus. ntn. Hist. nat. Paris. C.*, **38**: I-IX, 1-366
- Broin, F. de 1980. Les Tortues de Gadoufaoua (Aptien du Niger): aperçu sur la paléogéographie des Pelomedusidae (Pleurodira). *Mém. Soc. géol. Fr.*, N.S., **139**: 39-46.
- Broin, F. de 1985. *Proganochelys rucha* n. sp., Chélonien du Trias supérieur de Thaïlande. *Studia Geologica Salmanticensia*, vol. espec. I, *Studia Palaeocheloniologica*, **1**: 87-94.
- Broin, F. de 1988. Les Tortues et le Gondwana.- Examen des rapports entre le fractionnement du Gondwana et la dispersion géographique des Tortues pleurodires à partir du Crétacé. *Stud. Geol. Salm.*, *Studia Palaeocheloniologica* **2** (5): 103-142.
- Broin, F. de 1991. Fossil Turtles from Bolivia. In: Fósiles y Facies de Bolivia, R. Suarez-Soruco ed., vol.1, Vertebrados, *Rev. Técn. YPF*, **12** (3-4): 509-527.
- Broin, F. de 1994. Données préliminaires sur les Chéloniens du Tithonien inférieur de Canjuers (Var, France). Table Ronde Internationale, Calcaire Lithographique, Lyon Juillet 1991. *Geobios*, **16**: 168-175
- Broin, F. de e De Almeida Campos, D. 1985. *Araripemys barreto*, uma tartaruga pleurodira do Cretaceo Inferior da Chapada do Araripe, Nordeste Do Brasil. *IX Congresso brasileiro de Paleontologia, Resumen das Comunicações*, Soc. Brasil. Paleont. ed., Rio de Janeiro: 14.
- Broin, F. de et Fuente, M.S. de la 1993. Les tortues fossiles d'Argentine. *Ann. Pal.*, **79** (3): 169-231.
- Broin, F. de et Taquet, Ph. 1966. Découverte d'un crocodylien nouveau dans le Crétacé inférieur du Sahara. *C. R. Acad. Sc. Paris*, **D**, **262** (22): 2326-2329.
- Broin, F. de, Grenot, Cl. et Vernet, R. 1971. Sur la découverte d'un nouveau gisement de Vertébrés dans le Continental Intercalaire Saharien: La Gara Samani (Algérie). *C. R. Acad. Sc. Paris*, **D**, **272**: 1219-1221.
- Buffetaut, E. 1981. Die biogeographische Geschichte der Krokodilier, mit Beischreibung einer neuen Art, *Araripesuchus wegneri*. *Geol.Rundschau*, **70** (2): 611-624.

-
- Carter, H.J. 1852. Geology of the Island of Bombay. *Journ. Bombay branch Roy. Asiatic Soc.*, **21**: 161-215.
- Cattoi, N. y Freiberg, M.A. 1961. Nuevo hallazgo de Chelonia extinguidos en la República Argentina. *Physis*, **22** (63): 202.
- Dacqué, E. 1912. Die fossilen Schildkröten Aegyptens. *Geol. Palaeont. Abh.*, **14**, (N.S. 10), (4): 275-337.
- De Stefano, G. 1902. Cheloniani fossili cenozoici. *Boll. Soc. geol. ital.* **21**: 263-304.
- Fernández M.S. y Fuente M.S. de la 1988. Nueva tortuga (Cryptodira: Thalassemydidae) de la formación Vaca Muerta (Jurásico, Tithoniano) de la Provincia del Neuquén, Argentina. *Ameghiniana*, **25** (2): 129-138.
- Fernández, M .S. y Fuente, M. S. de la 1993. - Las Tortugas casiquelidias de las calizas litográficas titonianas del área Los Catutos, Neuquén, Argentina. *Ameghiniana*, **30** (3): 283-295.
- Fernández, M.S. and Fuente, M. S. de la 1994. Redescription and phylogenetic position of *Notoemys*: The oldest Gondwanian pleurodiran turtle. *N. Jb. Geol.Paläont. Abh.*, **193** (1): 81-105.
- Fraas, E. 1899. Proganochelys Quenstedtii Baur (Psammochelys Keuperina Qu.). Ein neuer Fund der Keuperschildkröte aus dem Stubensandstein. *Jahr. Ver. vaterl. Nat. Württemberg*, **60**: 400-424.
- Fraas, E. 1913. *Proterochersis*, eine pleurodire Schildkröte aus dem Keuper. *Jahr. Ver. vaterl. Nat. Württemberg*, **69**: 13-30.
- Fuente M. de la, Lapparent de Broin, F. de and Manera de Bianco, T. in press. The oldest and first nearly complete skeleton of a chelid, of the *Hydromedusa* sub-group (Chelidae, Pleurodira), from the Upper Cretaceous of Patagonia. *Bull. Soc. géol. France*, **172** (2).
- Gaffney, E.S. 1972. An Illustrated Glossary of Turtle Skull Nomenclature. *Amer. Mus. Nov.*, **2486**: 1-33.
- Gaffney, E. S. 1975. *Solnhofia parsonsi*, a new Cryptodiran Turtle from the Late Jurassic of Europe. *Amer. Mus. Nov.*, **2576**: 1-25.
- Gaffney, E.S. 1977. The Side-Necked Turtle Family Chelidae: A Theory of Relationships Using Shared Derived Characters. *Amer. Mus. Nov.*, **2620**: 1-28.
- Gaffney, E.S. 1979 . Comparative Cranial Morphology of Recent and Fossil Turtles. *Bull. Amer. Mus. Nat. Hist.*, **164** (2): 65-376.

- Gaffney, E.S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bull. Amer. Mus.Nat.Hist*, **194**, 1-263.
- Gaffney, E.S. 1991. The fossile turtles of Australia. Ch. 19: 704-720. In: Vickers-Rich P., M. Monaghan, R. Baird and T.H. Rich (eds.), *Vertebrate Palaeontology of Australia*, 1437 p. Pioneer Design Studio, Lilydale, Victoria.
- Gaffney, E.S., Hutchinson, J.H., Jenkins, F.A. and Meeker, L.J. 1987. Modern Turtle Origins: The Oldest Known Cryptodire. *Science*, **237**: 289-291.
- Gaffney, E.S. and Kitching, J.W. 1994. The most ancient African turtle. *Lett. Nature, Nature*, **369** (6475): 55-58.
- Gaffney, E.S. and Kitching, J.W. 1995. The morphology and Relationships of *Australochelys*, an early Jurassic Turtle from South Africa. *Amer. Mus. Nov.*, **3130**: 1-29.
- Gaffney, E.S. and Meylan, P.A. 1988. A phylogeny of turtles. In: *The Phylogeny and Classification of the Tetrapods*. Vol. 1: Amphibians, Reptiles, Birds, 5: 157-219, figs. M. J. Benton Ed. Systematics Association Special Volume N 35A, Clarendon Press, Oxford.
- Gaffney, E.S. and Meylan, P.A. 1991. Primitive Pelomedusid Turtle. In: *Santana Fossils, An Illustrated Atlas*. In: J.G. Maisey ed., TFH Publ. Inc., 335-339. Neptune City, N.J.
- Gasparini, Z. B. de 1971. Los Notosuquia del Cretácico de America del Sur como un nuevo infraorden de los Mesosuchia (Crocodilia). *Ameghiniana*, **8**: 83-103.
- Gheerbrant, E., Codrea, V., Hosu, A., Sen, S., Guernet, C., Lapparent de Broin, F. de et Riveline, J. 2000. Découverte de vertébrés dans les Calcaires de Rona (Thanétien ou Sparnacien), Transylvanie, Roumanie: les plus anciens mammifères cénozoïques d'Europe Orientale. *Eclog. geol. Helv.*, 1999, **92** (3): 517-535.
- Gmira, S., 1995. *Etude des Chéloniens fossiles du Maroc. Anatomie. Systématique. Phylogénie*: 140 p. Cahiers de Paléontologie, CNRS Ed., Paris.
- Grandidier, A. 1867. Liste des Reptiles nouveaux découverts, en 1866, sur la côte Sud-Ouest de Madagascar. *Revue Mag. Zool.* (2) **19**: 232-234.
- Haas, G. 1978a. A Cretaceous Pleurodire Turtle from the Surroundings of Jerusalem. *Israel J. Zool.*, **27**: 20-33.
- Haas, G. 1978b. A new turtle of the genus *Podocnemis* from the lower Cenomanian of 'Ein Yabrud. *Israel J. Zool.*, **27**: 169-175.
- Halstead, B. 1979. A Taxonomic Note on New Fossil Turtles. In: *The Nigerian Field. The International Field Studies Journal of West Africa*, Monograph No. 1. (Suppl. to Vol. 44): 48-49. Arthurs Press Ltd, Woodchester, Stroud, Glos, U.K.

-
- Haughton, S.H. 1928. On some reptilian remains from the dinosaur beds of Nyasaland. *Trans. Roy. Soc. South Africa*, **16**: 67-75.
- Hay, O.P. 1908. The Fossil Turtles of North America. *Pub. Carnegie Instit.*, **75**: 568 pp.
- Hirayama, R. 1994. Phylogenetic systematics of chelonoid sea turtles. *The Island Arc*, **3** : 270-284.
- Hirayama, R. 1998. Oldest known sea turtle. *Nature*, **392** (6677): 705-708.
- Hirayama R. & Chitoku T. 1996. Family Dermochelyidae (Superfamily Chelonioidea) from the Upper Cretaceous of North Japan. *Trans. Proc. Palaeont. Soc. Japan*, N.S., **184**: 597-622
- Iverson, J.B. 1986. *A Checklist with Distribution Maps of the Turtles of the World*. Paust Printing, Richmond (Indiana): 1-283, maps.
- Jaekel, O. 1918. Die Wierbeltierfunde aus dem Keuper von Halberstadt. Serie II, Testudinata. Teil 1, *Stegochelys dux* n.g., n.sp. *Palaeont. Zeitschr.*, 1915-1916, **2**, (1): 88-214.
- Jain, S.L., 1978. A new fossil Pelomedusid Turtle from the Upper Cretaceous Pisdura sediments, Central India. *Jr. Palaeon.Soc. India*, **20** (1977): 360-365.
- Jain, S.L. 1986. New Pelomedusid turtle (Pleurodira: Chelonia) remains from Lameta Formation (Maastrichtian) at Dongargaon, Central India, and a review of Pelomedusids from India. *Jr. Palaeon. Soc. India*, **31**: 63-75.
- Jenkins, JR., F.A., Shubin, N.H., Amaral, W.W., Gatesy, S.M., Schaff, C.R., Clemmensen, L.B., Downs, W.R., Davidson, A.R., Bonde, N. & Osbaeck, F. 1994. Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. *Meddelelser om Grønland, Bioscience*, **32**: 2-24.
- Kischlat, E.E. 1994. Observações sobre *Podocnemis elegans* Suárez (Chelonii, Pleurodira, Podocnemidae) do Neocretáceo do Brazil. *Acta Geol. Leop.*, 39/1, **17**: 345-351.
- Krebs, B. 1995. *The Barremian Vertebrate Locality Uña (Province of Cuenca). Material for a comparison with Las Hoyas: II International Symposium on Lithographic Limestones*. Lleida-Cuenca (Spain), 9th-16th July 1995. Extended Abstracts: 95-97. Ed. Univ. Autónoma Madrid, Madrid.
- Lapparent de Broin, F. de 2000. African chelonians from the Jurassic to the Present. A preliminary catalog of the African fossil chelonians. *Palaeont. Afr.* **36**: 43-82.
- Lapparent de Broin, F. de (in press). The European fauna of turtles from Triassic to Present: a short review. *Dumerilia*, **4** (3).

- Lapparent de Broin, F. de, Bocquentin, J. and Negri F. R. 1993. Gigantic Turtles (Pleurodira, Podocnemididae) from the Late Miocene-Early Pliocene of South Western Amazon. *Bull. Inst. fr. ét. andines*, **23** (3): 657-670.
- Lapparent de Broin, F. de and Fuente, M. de la 1996. The analysis of the character "fused pelvis". Abstracts of papers, 56 Ann. Meeting, SVP, Amer. Mus. Nat Hist., New York, oct. 16-19, 1996, *J.V.P.*, 16, suppl. N° 3: 47A. Lawrence, Kansas.
- Lapparent de Broin, F. de y Fuente, M.S. de la 1999. Particularidades de la fauna continental de tortugas del Cretácico de Argentina. Res. Com. XIV Jornadas Argentinas de Paleontología de Vertebrados, 18-20 Mai 1998, Neuquén, *Ameghinina*, **36** (1): 104
- Lapparent de Broin, F. de, Fuente, M. S. de la y Calvo, J. O. 1997. Presencia de los más antiguos quélidos (tortugas pleurodiras) en el Cretácico inferior de "El Chocón", provincia del Neuquen, Argentina. XIII Jornadas Argentinas de Paleontología de Vertebrados, La Rioja, 11-15 Mai 1997, *Ameghiniana*, **34** (4): 538.
- Lapparent de Broin, F. de et Murelaga, X. 1996. Une nouvelle faune de Chéloniens dans le Crétacé supérieur européen. *C. R. Acad. Sc. Paris*, sér. IIA, **323**, (8), a: 729-735
- Lapparent de Broin, F. de and Murelaga, X. 1999. Turtles from the Upper Cretaceous of Laño (Iberian Peninsula). In: Geology and palaeontology of the Upper Cretaceous vertebrate-bearing beds of the Laño Quarry (Basque-Cantabrian Region, Iberian Peninsula), H. Astibia *et al.* coords. *Estudios del Museo de Ciencias Naturales de Alava*, **14** (Num. Esp. 1): 135-211.
- Lapparent de Broin, F. de and Molnar, R., in press. Eocene chelid turtles from Redbank Plains, southeastern Queensland, Australia. *Geodiversitas*, **23** (1).
- Lapparent de Broin, F. de and Werner, C. 1998. New late Cretaceous turtles from the Western Desert, Egypt. *Ann. Pal.*, **84** (2): 131-214.
- Lavocat, R. 1955. Découverte d'un Crocodilien du genre *Thoracosaurus* dans le Crétacé supérieur d'Afrique. *Bull. Mu. Nat. Hist. Nat.* 2e sér., **27** (4): 338-340.
- Leidy, J. 1856. Notices of remains of extinct turtles of New Jersey, collected by Prof. Cook, of the State Geological Survey, under the direction of Dr. W. Kitchell. *Proc. Acad. Nat. Sci. Philadelphia*, **8**: 303-304.
- Leidy, J. 1865. Memoir on the extinct reptiles of the Cretaceous formation of the United States. *Smiths. Cont. Knowledge*, **14**, (6): 1-135.
- Longman, H.A. 1915. On a giant turtle from the Queensland Lower Cretaceous. *Mem. Queensland Mus.* **3**: 24-29.
- Lydekker, R. 1889. Chelonia. In: *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History)*. Part III, V-XVIII, 1-239, Trustees of the British Museum of Natural History Eds., London.

-
- Maisey, J.G. ed. 1991. *Santana fossils. An Illustrated Atlas*. J.G. Maisey ed., TFH Publ. Inc.:1-459. Neptune City, N.J.
- Martín Suarez, J. 1969. Um Quelônio da Formação-Bauru. Anais do XXIII Congresso Brasileiro de Geologia: 167-176, 7 fig. *Bol. Dep. Geog. Fac. Filos. Cienc. Let. Presidente Prudente*, **2**: 35-54.
- Matheron, P. 1869. Notice sur les reptiles fossiles des dépôts fluvio-lacustres créacés du bassin à lignite de Fuveau. *Mém. Acad. Imp. Sc. B.-L. Arts Marseille*: 1-39.
- Mawson, J. and Woodward, A.S. 1907. Cretaceous Formation of Bahia and its vertebrate fossils. *Quat. J. Geol. Soc. London*, **63**: 128-139.
- Meylan, P.A. 1996. Skeletal morphology and relationships of the early Cretaceous side-necked turtle, *Araripemys barretoii* (Testudines: Pelomedusoides: Araripemydidae), from the Santana Formation of Brazil. *J. V. P.*, **16** (1): 20-33.
- Meylan, P.A. and Gaffney, E.S. 1991. *Araripemys* Price, 1973. In: Maisey J.G. ed., *Santana Fossils. An Illustrated Atlas*: 326-334. T.F.H. Pub., Neptune, N.J.
- Michard, J.-G, Broin F. de, Brunet, M. et Hell, J. 1990. Le plus ancien crocodylien néosuchien spécialisé à caractères "eusuchiens" du continent africain (Crétacé inférieur, Cameroun). *C. R. Acad. Sci. Paris*, II, **311**: 365-371.
- Murelaga-Bereikua, X. 1998. Primeros restos de tortugas del Cretácico inferior (Barremiense superior) de Vallipón (Castellote Teruel). *Mas de las Matas*, **17**: 189-200.
- Ortega, F., Gasparini, Z., Buscalioni, A.D. and Calvo, J.O. 2000. A new species of *Araripesuchus* (Crocodylomorpha, Mesoeudrocodylia) from the lower Cretaceous of Patagonia, Argentina. *J. V. P.*, **20** (1): 57-76.
- Owen, R. 1842. Report on British fossil reptiles. Part II. *Report Brit. Assoc. Advanc. Science, 1841*: 60-204. London.
- Owen, R. 1882. On an Extinct Chelonian Reptile (*Notochelys costata*, Owen), from Australia. *Quart. Journ. Geol. Soc.* **38**: 178-183.
- Portis, A. 1882. Les chéloniens de la molasse vaudoise conservés dans le Musée géologique de Lausanne. *Mém. Soc. Paléont. Suisse*, **9**: 1-78.
- Price, L.I. 1953. Os Quelônios da formação Bauru, Cretaceo terrestre do Brasil meridional. *Bol. Div. Geol. Min. D. N. P. M.*, **147**: 1-34.
- Price, L.I. 1959. Sobre um crocodylídeo notossúquio do Cretácico brasileiro. *Bol. D.N.P.M., Div. Geol. Min.*, **188**: 1-55.
- Price, L.I. 1973. Quelônio Amphichelydia no Cretaceo inferior do Nordeste do Brasil. *Rev. Brasil. Geoc.*, **3**: 84-96.

- Reinach, A. von, 1903. Schildkrötenreste aus dem ägyptischen Tertiär. *Abh. Senckenb. natur. Gesell.*, **29**: 1-64.
- Roger, J., Pickford, M., Thomas, H., De Lapparent de Broin, F., Tassy, P., Van Neer, W., Bourdillon-de-Grissac, C. et Al-Busaldi, S. 1994. Découverte de vertébrés fossiles dans le Miocène de la région du Huqf au Sultanat d'Oman. *Ann. Pal.* **80** (4): 253-273.
- Rougier, G. W., De La Fuente, M.S. and Arcucci, A.B. 1995. Late Triassic Turtles from South America. *Science*, **268**, (5212): 855-858.
- Rütimeyer, L. 1873. Die fossilen Schildkröten von Solothurn und der übrigen Juraformation. *Nouv. Mém. Soc. Helv. Sc. Nat.*, **25**: 1-185.
- Sanz, J.L., Wenz, S., Yebenes, A., Estes, R., Martinez-Delclos, X., Jiménez-Fuentes, E., Diéguez, C., Buscalioni, A.D., Bardadillo, L.J. and Via, L. 1988. An early Cretaceous faunal and floral continental assemblage: Las Hoyas fossil site (Cuenca, Spain). *Geobios*, **21** (5) : 611-635.
- Seeley, H. G. 1869. *Index to the fossil remains of Aves, Ornithosauria and Reptilia from the secondary system of strata arranged in the Woodwardian Museum of the University of Cambridge*. Cambridge Univ. Press, Deighton, Bell and Daldy: i-xxiii, 1-143.
- Singh, S.D., Sahni, A., Gaffney, E.S. and Schleich, H.H. 1998. Reptilia from the Intertrappean Beds of Bombay (India). *Ver. Fuhlrott-Museum*, **4**: 307-320.
- Stromer, E. 1925. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 7. Stomatosuchus inermis ein schwachbezahnter Krokodilier. 8. Ein Skelettrest des Pristichen Onchopristis numidus Hay sp. *Abh. bayer. Akad. Wiss., Math.-Nat. Abt., N.F.*, **30**, 6: 3-22.
- Stromer, E. 1933. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 12. Die procölen Crocodilia. *Abh. Bayer. Akad. Wiss., Math.-Nat. Abt., N.F.*, **15**: 55 pp.
- Stromer, E. 1934. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Aegyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 14. Testudinata. *Abh. Bayer. Akad. Wiss., Math.-Nat. Abt.*, **25**: 1-26.
- Swinton, W. E. 1939. A New Fresh-Water Tortoise from Burma. *Rec. Geol. Surv. India*, **74**: 548-551.
- Tong, H. 1998. Pleurodiran Turtles from the Eocene of Saint-Papoul (Aude), Southern France. *Oryctos*, **1**: 43-53.
- Tong, H. and Buffetaut, E. 1996. A new genus and species of pleurodiran turtle from the Cretaceous of southern Morocco. *N. J. Geol. Pal. Abh.*, **199** (1): 133-150.

- Tong, H., Gaffney, E.S. and Buffetaut, E. 1998. *Foxemys*, A New Side-Necked Turtle (Bothremydidae: Pelomedusoides) from the Late Cretaceous of France. *Amer. Mus. Nov.*, **3251**: 19 p.
- Wagner, A. 1853. Beschreibung einer fossilen Schildkröte und etlicher anderer Reptilien-ueberreste aus den lithographischen Schiefern und dem Grünsandsteine von Kelheim. *Abh. math. Phys. Cl. bayer. Akad. Wiss.*, 3e sér., **7** (1): 239-264.
- Wermuth, H. und Mertens, R. 1977. *Liste der rezenten Amphibien und Reptilien. Testudines, Crocodylia, Rhynchocephalia*. In: R. Mertens, W. Hennig & H. Wermuth. *Das Tierreich*, 100: I-XXVII, 1-74, Walter de Gruyter, Berlin-New York.
- Williams, E.E. 1950. Variation and selection in the cervical central articulations of living turtles. *Bull. Amer. Mus. Nat. Hist.* **94** (9): 505-562.
- Williams, E.E. 1953. Fossils and the distribution of chelyid turtles. 1. - "*Hydraspis*" *leithii* (Carter) in the Eocene of India is a Pelomedusid. *Breviora*, **1** (13): 1-8.
- Williams, E.E. 1954a. A key and description of the living species of the genus *Podocnemis* (Sensu Boulenger), Testudines, Pelomedusidae. *Bull. Mus. Comp. Zool. Harvard*, **11** (8): 277-295.
- Williams, E.E. 1954b. New or Redescribed Pelomedusid Skulls from the Tertiary of Africa and Asia (Testudines, Pelomedusidae). 1. *Dacquemys paleomorpha*, new genus, new species from the Lower Oligocene of the Fayum, Egypt. *Breviora*, **35**:1-8.
- Williams, E.E. 1956. *Podocnemis bassleri*, a New Species of Pelomedusid Turtle from the Late Tertiary of Peru. *Amer. Mus. Nov.*, **1782**: 1-10.
- Wood, R.C. 1970. A review of the fossil Pelomedusidae (Testudines, Pleurodira) of Asia. *Breviora*, **357**: 1-24.
- Wood, R.C. 1976. *Stupendemys geographicus*, the world's largest Turtle. *Breviora*, **436**: 1-31.
- Wood, R.C. 1983. *Kenyemys williamsi*, a Fossil Pelomedusid Turtle from the Pliocene of Kenya. In: A.G.J. Rhodin and K. Miyata Eds, *Essays in Honor of Ernest E. Williams, Advances in Herpetology and Evolutionary Biology*: 74-85. Mus. Comp. Zool., Cambridge, Mass.
- Yeh, H-k' 1963. Fossil turtles of China. *Paleont. Sin.* N. S.C, **150** (18): 1-112.
- Zangerl, R. 1953. The Vertebrate Fauna of the Selma Formation of Alabama. Part III. The turtles of the family Protostegidae. Part IV. The turtles of the family Toxochelyidae. *Fieldiana: Geol. Mem.*, **3** (3-4) : 59-277.
- Zigno, A. de 1889. Chelonii scoperti nei terreni cenozoici delle prealpi Venete. *Mem. R. Ist. Veneto, Sci. Let. Art.*, **23**: 119-129.

Plate 1

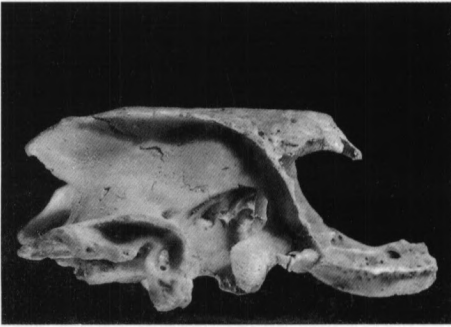
Brasilemys josai n.g., n. sp., Chapada do Araripe, Ceará state, Brazil, early Cretaceous (late Aptian-early Albian), skull, stereoscopic views: 1, dorsal; 2, right lateral; 3, left lateral. Scale: 1 cm.

Lámina 1

Brasilemys josai n.g., n. sp., Chapada do Araripe, estado de Ceará, Brasil, Cretácico inferior (Aptiense superior - Albiense inferior), cráneo, vistas estereoscópicas: 1, dorsal, 2, lateral derecha, 3, lateral izquierda. Escala: 1 cm



1



2

3

Plate 2

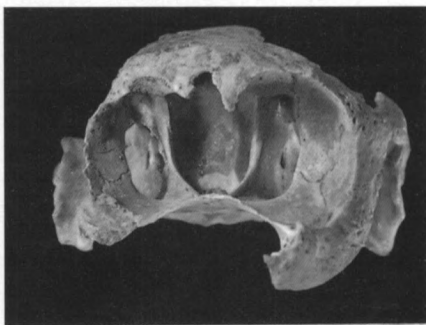
Brasilemys josai n.g., n. sp., Chapada do Araripe, Ceará state, Brazil, early Cretaceous (late Aptian-earlyAlbian), skull, stereoscopic views: 1, posterior; 2, anterior, 3, ventral. Scale: 1 cm.

Lámina 2

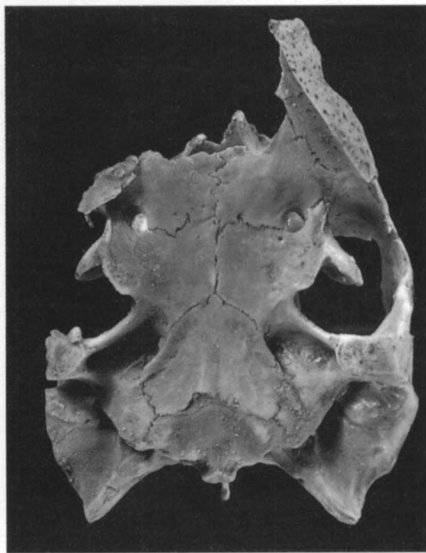
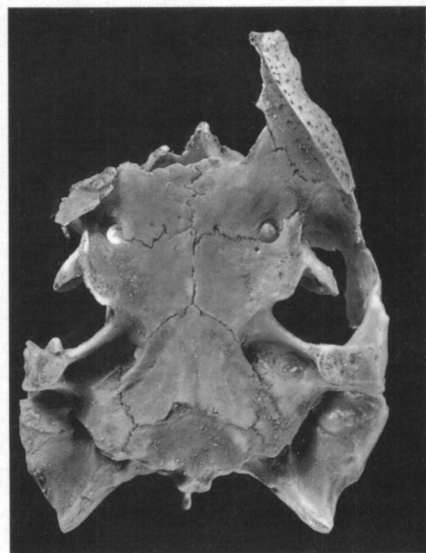
Brasilemys josai n.g., n. sp., Chapada do Araripe, estado de Ceará, Brasil, Cretácico inferior (Aptiense superior - Albiense inferior), cráneo, vistas estereoscópicas: 1, dorsal, 2, lateral derecha, 3, lateral izquierda. Escala: 1 cm.



1



2



3



Plate 3

Brasilemys josai n.g., n. sp., Chapada do Araripe, Ceará state, Brazil, early Cretaceous (late Aptian-earlyAlbian), 1, carapace, a, dorsal, b, ventral views, c, detail on axis and third cervical vertebrae. 2, left lower jaw, a, dorsal, b, medial, c, left lateral views. 3, hyoid anterior horns, a, right, b, left.
Scales: 1a,1b, 3 cm; 1c, 5cm; 2, 3: 1 cm.

Lámina 3

Brasilemys josai n.g., n. sp., Chapada do Araripe, estado de Ceará, Brasil, Cretácico inferior (Aptiense superior - Albiense inferior), 1, caparazón, vistas a, dorsal, b, ventral, c, detalle con las vértebras cervicales 2 (axis) y 3. 2, hemimandíbula izquierda, vistas a, dorsal, b, medial, c, lateral izquierda. 3, córneas anteriores del hioides, a, derecha, b, izquierda.
Escalas: 1a, 1b, 3 cm; 1c, 5 cm; 2, 3: 1 cm.

