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Notoemys laticentralis (Chelonii, Pleurodira), Late Jurassic of Argentina: new examination of the anatomical structures and comparisons

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Abstract

Notoemys laticentralis, a basal pleurodiran turtle of the Upper Jurassic from South-Argentina, is reconsidered with respect to the evolutionary process of some structures: proportions of the skull, anatomy of the back skull, alone preserved, and of the neck. Comparison of these structures has been leaded in different groups of turtles, previously established as monophyletic. Before, some remarks are given, with examples, on the difficulty to establish the homologies, what appears in the comparisons. The family Notoemydidae is supported as distinct from the family Platychelyidae and considered as including *Notoemys laticentralis*, *N. zapatocaensis* and *Caribemys*.

Key words

Notoemys laticentralis, back skull, neck, comparisons pleurodires-cryptodires.

Résumé

***Notoemys laticentralis* (Chelonii, Pleurodira), Jurassique supérieur d'Argentine: nouvel examen des structures anatomiques et comparaisons.-** L'étude de *Notoemys laticentralis*, tortue pleurodire basale du Jurassique supérieur du sud de l'Argentine, est reprise en se focalisant sur le processus évolutif de certaines structures: les proportions relatives du crâne et l'anatomie de l'arrière du crâne, seul préservé, et du cou. La comparaison de ces structures a été menée entre différents groupes de tortues, dont la monophylie a été précédemment établie. Auparavant, des remarques avec exemples sont faites sur la difficulté d'établir les homologies, ce qui apparaît aussi au cours des comparaisons. La famille des Notoemydidae, avec *Notoemys laticentralis*, *N. zapatocaensis* et *Caribemys*, est maintenue séparée de celle des Platychelyidae.

Mots-clés

Notoemys laticentralis, arrière-crâne, cou, comparaisons pleurodires-cryptodires.

INTRODUCTION

Notoemys laticentralis CATTOI & FREIBERG, 1961, is a pleurodiran turtle described on specimens recovered from three localities of the Neuquén Province, Argentina: Las Lajas, Los Catutos and Cerro Lotena, in the Formation Vaca Muerta, late Lower Tithonian, Late Jurassic.

WOOD & FREIBERG (1977) attributed *Notoemys laticentralis* to the cryptodiran Plesiochelyidae according to the characters of the carapace, then alone known. Two of us (DE LA FUENTE & FERNANDEZ, 1989; FERNANDEZ & DE LA FUENTE, 1994) fully redescribed *N. laticentralis*, with the help of the better preserved specimen MOZP 2487 from Cerro Lotena and correctly attributed it to Pleurodira. A further observation of the skull and cervical vertebrae of this specimen led us to modify our opinion on this taxon with respect to some of the characters given in these works. In this paper, we detail the principal new elements leading to these new deductions, particularly after the study of other pleurodires including forms recently named. In addition, the analysis of the evolution of the pleurodiran pelvis (LAPPARENT DE BROIN & DE LA FUENTE, 1996) has given us the opportunity to analyse the morphology of the sacral area of *N. laticentralis*, which is basically pleurodiran by the way the pelvis is sutured to the carapace and plastron. Some of the new results have already been shortly integrated in papers (DE LA FUENTE, 2003; DE LA FUENTE & ITURRALDE-VINENT, 2001; LAPPARENT DE BROIN, 2000a; LAPPARENT DE BROIN & DE LA FUENTE, 1993; LAPPARENT DE BROIN & MURELAGA, 1999). In addition to the characters of the skull and neck, detailed below, we figure the carapace

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of the specimen from Cerro Lotena, including the iliac preserved area, and we figure the newly observed anterior plastral lobe of the holotype, from Las Lajas (Fig. 1). Among the known forms of primitive pleurodires (i.e. previous to the Eupleurodira, which include Chelidae and Pelomedusoides and their plesions), in addition to the anterior neck of *N. laticentralis*, only some isolated cervical vertebrae are known in few taxa including the Upper Jurassic *Platychelys* (late Kimmeridgian of Swiss and early Tithonic of Germany) and *Caribemys* DE LA FUENTE & ITURRALDE-VINENT, 2001 (Oxfordian of Cuba). Some vertebrae of the Cretaceous *Dortoka*, Dortokidae, from the Basque Country (LAPPARENT DE BROIN & MURELAGA, 1996; 1999; LAPPARENT DE BROIN *et al.*, 2004) are also known. The Triassic German *Proterochersis* FRAAS, 1913, is not considered (unknown skull and cervical vertebrae). The systematic position of *Notoemys* is examined help to the newly known form *N. zapatocaensis* CADENA RUEDA & GAFFNEY, 2005.

The partial skull of *N. laticentralis* is the oldest described pleurodiran skull (see references in LAPPARENT DE BROIN, 2000a, b) which gives it much interest. The present work particularly concerns the examination of some skull structures which can be seen in *N. laticentralis* by comparison with other taxa of Pleurodira, and also of some Cryptodira. They concern the general morphology of the skull (emarginations, proportions) and the development of the ear area by: 1), the development of the *cavum tympani* with the rolling up of the quadrate, its associated structures (i.e. formation of an *incisura* or a *foramen columellae auris* and eventually the presence of a precolumellar fossa), the realization of an *antrum postoticum*, and the consequent modifications for the attachment of the *depressor mandibulae* muscle in the ventral postero-lateral skull area; 2) the ventral closure of the cranio-quadrate passage and of the *fenestra postotica*, with the covering of the *cavum acustico-jugulare* and the modifications introduced by the reduction of the paroccipital process of the occipital and its complete suture with the quadrate.

Homology - The notion of false homoplasy or false synapomorphy: The primitive completely roofed skull of turtles, anapsid without lateral and posterior emarginations, is associated with a neck that is not retractile, composed of amphicoelous vertebrae with heavy cervical ribs. After the Triassic forms, the emargination of the skull, linked to the formation of cervical joints, the reduction of the cervical ribs and development of transverse apophyses, accompany the above mentioned skull structures, developing within all turtle groups. In addition, some other adaptative characters may develop also in parallel, such as the skull flattening or its secondary posterior elevation, a further elongation (anterior and/or posterior), a secondary roofing of the back skull and a shortening of the basicranium with the development of the triturating surfaces. It is important to define here the details in which the evolutionary trends differ in their expression, so that the not-monophyletic groups of taxa which have just a superficial similarity between them, can be separated: their union in previous papers is based on these common evolutionary trends which are expressed by characters not exactly homologous (examples in GAFFNEY *et al.*, 1991; GAFFNEY, DE ALMEIDA CAMPOS & HIRAYAMA, 2001; GAFFNEY & WOOD, 2002; MEYLAN, 1996; SHAFFER *et al.*, 1997, etc.). Such an incomplete way of analyzing the characters is unfortunately widely spread in all the extant studies (see LAPPARENT DE BROIN, 2002, as indicated for

Fig. 1: *Notoemys laticentralis* CATTOI & FREIBERG, 1961, Cerro Lotena, Neuquén province, Argentina. Formation Vaca Muerta, Late Jurassic. A-F, MOZP 2487, Cerro Lotena. A, Carapace, dorsal view. B, Carapace, left lateral view. C, Carapace without the plastron, reconstruction of the ventral view. D, Plastron, ventral view. E, Posterior part of the inner carapace, detail showing the insertion of the ilium below the pleural 8, partly covering the extremity of the thoracic rib 9, and the sutures of the sacral ribs 1 and 2; the sacral rib 1 is anterior and ventral (in an low plan) to the sacral rib 2. F, lateral part of posterior lobe, dorsal view. G, Holotype, MACN, 18043, Las Lajas, anterior plastral lobe, ventral view. a, anal; ab, abdominal; ano, anal notch (encoche anale); ap, axillary process suture below the pleural 1 (suture du processus axillaire sous la pleurale 1); b, bridge (pont); bb, lateral bombing, weak, lowered post-mortem (bombement latéral faible, déprimé post-mortem); ce, cervical; cr, medial carina, low (carène médiale basse); e, epiplastron; en, entoplastron; f, fontanelle; f+ap, fontanelle with a part of the axillary process extremity (fontanelle recevant partiellement l'extrémité du processus axillaire); fe, femoral; g, gular; h, hyoplastron; hp, hypoplastron; hu, humeral; ig, intergular; il, ilion; ip, inguinal process suture below the peripheral 8 (suture du processus inguinal sous la périphérique 3); is, ischium (ischion); ivc, intervertebral canal; la, axillary process suture below the peripheral 3 (suture du processus axillaire sous la périphérique 3); ma1, marginal 1; me, mesoplastron; n1, neural 1; nu, nuchal; p3, p7, p10, p11, peripherals (périphériques) 3, 7, 10, 11; pec, pectoral; pl 8, pleural 8; pro, protuberance; pu, pubis; py, pygal; r1, r2, r9, r10, thoracic ribs (côtes thoraciques) 1, 2, 9, 10; s1, s2, sacral ribs (côtes sacrées) 1, 2; sp1, sp2, suprapygals 1, 2; vs2, sacral vertebra 2 (vertèbre sacrée 2); x, xiphiplastron.

Fig. 1: *Notoemys laticentralis* CATTOI & FREIBERG, 1961, Cerro Lotena, province du Neuquén, Argentine. Formation Vaca Muerta, Jurassique supérieur. A-F, MOZP 2487, Cerro Lotena. A, Carapace, vue dorsale. B, Carapace, vue latérale gauche. C, Carapace sans le plastron (dossière), reconstitution de la vue ventrale. D, Plastron, vue ventrale. E, Partie postérieure interne de la carapace, détail montrant l'insertion de l'ilion sous la pleurale 8, couvrant en partie l'extrémité de la côte thoracique 9, et les sutures des côtes sacrées 1 et 2; la côte sacrée 1 est antérieure et ventrale (dans un plan inférieur) à la côte sacrée 2. F, lobe postérieur partie latérale droite, vue dorsale. G, Holotype, MACN, 18043, Las Lajas, lobe plastral antérieur, vue ventrale.
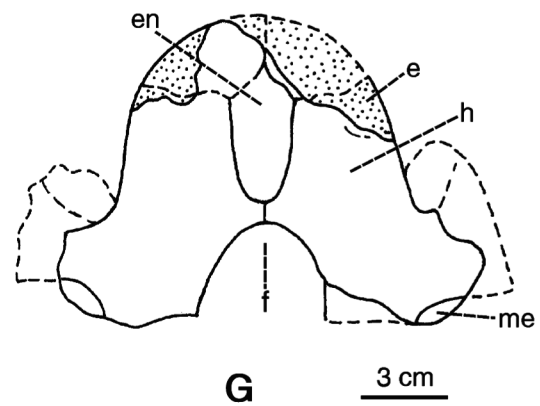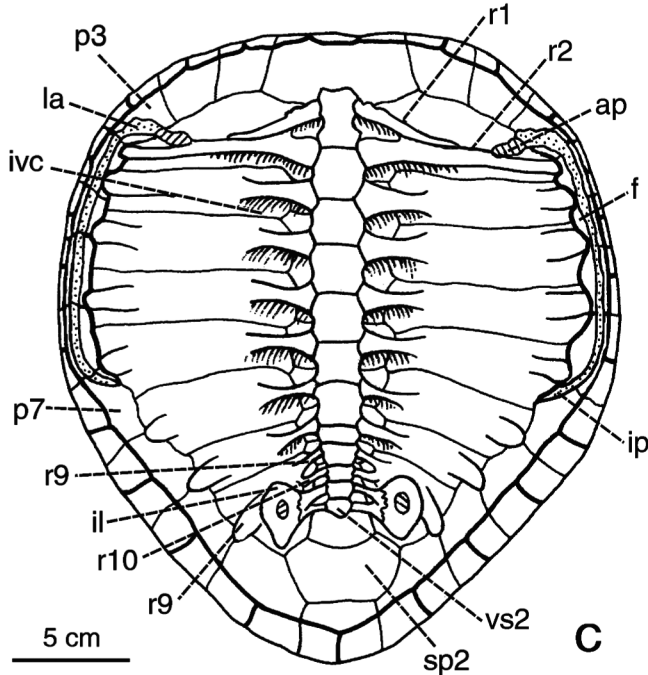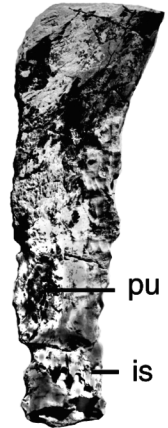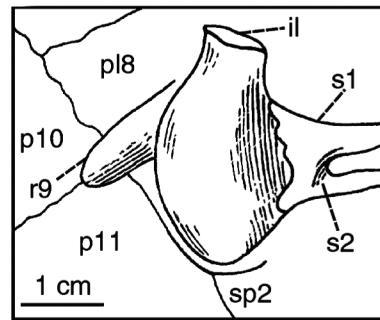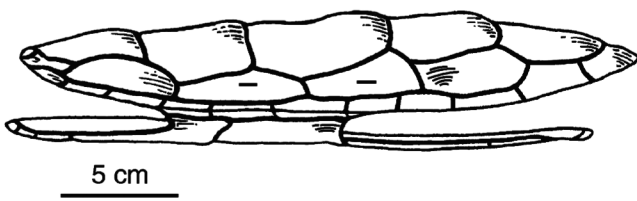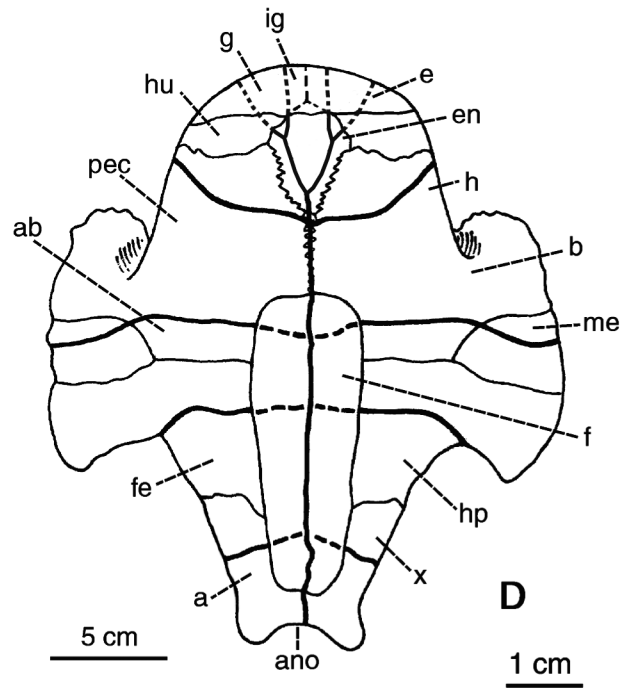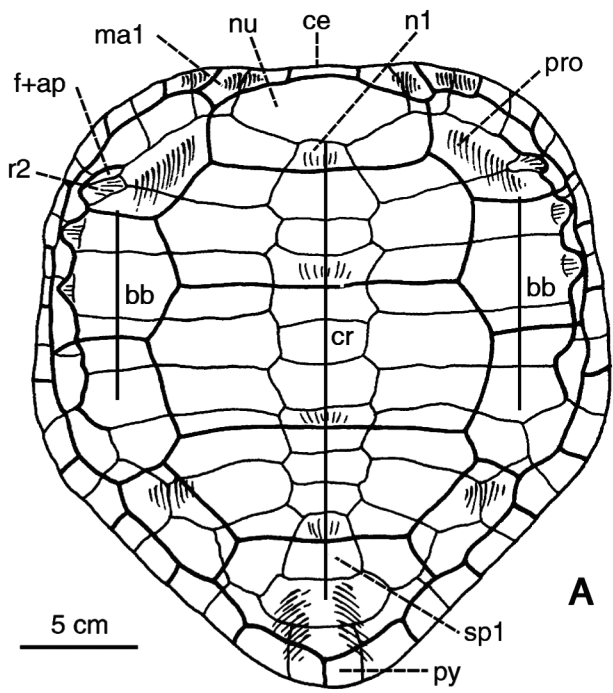
crocodile studies) and the resulting cladograms may be considered with caution. If the definition of the characters and their states is not enough accurate, the characters or the character states may be not homologous ("falsely" homologous); in this case, the result may produce a "false synapomorphy" or a "false homoplasy". Two problems are frequently encountered in the cladistic analysis: 1) the insufficient definition of the characters, with a two low number of evolutionary states; 2) the comparison of a new studied taxon with some groups taken as a whole: for example, a family or a group of genera, or even a genus, are defined on the derived state of a character of the extant forms, without having studied the fossils which have a less progressive state for this character than the extant forms; or a family is coded by a double state (0-1) on the two possible states found in the family, which, in our opinion, evidently falsifies the resolution.

It is possible to take the example of the rolling up of the quadrate, analysed in *Notoemys laticentralis* (see below). In works introducing or not the Pleurodira, in the definition for the character "closure of the quadrate" (HIRAYAMA & CHITOKU, 1996) or "*incisura columellae auris*", (MEYLAN & GAFFNEY, 1989; SHAFFER *et al.*, 1997), there are generally two states (first definition): (0) "no" and (1) "yes" (or "open" or "closed" quadrate). In works not introducing the Pleurodira, the character "closure of the quadrate" could be better defined (second definition) by three states such as: "(0) absent closure, quadrate not bent over the *columella*, no *incisura*; (1) partial closure, but unclosed *columella* (open *incisura*); and (2) "closed quadrate around the *columella* (by a *commissura quadrati*) or closed *incisura* ". If the work introduces the Pleurodira, it is necessary to modify the state (2) as (for example): "closed around the *columella* alone" (*incisura* becoming a rounded *foramen columellae auris* with a quadrate suture behind, the *commissura quadrati*); and add the state (3): "closed together around the *columella* and the Eustachian tube" (i.e. closed *incisura*: an elongated ovoid *foramen columellae auris* and a *commissura quadrati* posterior to the Eustachian tube extremity). In the first definition, the state (1) "yes" (for example) results in the cladogram either by the possible union by synapomorphy of two taxa that have, for example, the two last different conditions (2 and 3), or the possible attribution of a homoplasy between these two taxa. This union of the states (2) and (3), clearly not homologous, represents what we understand as a "false" homology resulting in the cladogram in a "false" homoplasy or a "false" synapomorphy. But actually, when the quadrate is already bent up but remains unclosed in the state (1) of the second definition, there are various shapes of open *incisura*, characteristic of taxa and possibly indicating an independent acquisition or a secondary modification, which do not always represent exact homologies, particularly touching characters ontogenetically developed. In this case, the shape of the *incisura* may be considered. The *incisura* is (in Cryptodira, see figs in GAFFNEY,

1979a, BRINKMAN & PENG, 1993b): either wide, open in U, moderately downwards inclined (in relation with the articular quadrate process) such as in Dermochelyidae; or wide, open in a V widely open and moderately inclined downwards as in *Sinemys*; or in a V less widely open and moderately downwards inclined as in extant Cheloniidae; or open in a long and descending glove finger as in most Baenidae (more or less wide); or open in a thinner split, horizontally directed as in *Mesochelys*; or (frequently) open in a narrow V, moderately downwards inclined, in some primitive Pelomedusoides such as *Araripemys barretoi* PRICE, 1973, from the Lower Cretaceous, late Aptian at the Albian boundary of the Chapada do Araripe, Brasil (MEYLAN, 1996) and *Teneremys lapparenti* BROIN, 1980, from the Lower Cretaceous, late Aptian, of Gadoufaoua, Niger (see below). A problem concerns the Chelidae (LAPPARENT DE BROIN & MOLNAR, 2001): most genera have an ovoid closed *incisura* (with a more or less strong *commissura*). But *Pseudemydura* and some observed specimens of *Emydura macquariae* have a rather straight unclosed *incisura*, the borders of which are not inferiorly converging. While *Hydromedusa* and some species of *Chelodina* have an ovoid unclosed *incisura,* the borders of which are converging: compared to the majority of Chelidae, this *incisura* has already the potential shape of the closed ovoid chelid *incisura* but it remains unclosed presumably by paedomorphosis (figs in BOULENGER, 1889; GAFFNEY, 1977, 1979a), while in *Pseudemydura*, the not converging borders may indicate a more primitive state or a paedomorphic undevelopment. In any case, the state of unclosure of *Hydromedusa* and some species of *Chelodina* is not the same as in *Pseudemydura* which has a state closer to that of *Araripemys*. But the *incisura* is already vertically downwards directed as in other chelids and not primitively moderately inclined as in *Araripemys*. These variations may result in a more or less restricted definition according to the authors, which has to be clearly explained. Another difference between taxa is the length of the *commissura*. The *incisura* may be very short with the two quadrate borders very close together, horizontally directed such as in *Pyxis planicauda* and in freshwater Testudinoidea and Dermatemydidae (with some supplementary variations within the groups). But in *Pyxis arachnoides,* there is no closure: that is considered as paedomorphic by BOUR (1981) and representing the primitive condition. In all these cases, the state "unclosed *incisura*" for freshwater Testudinidae, primitive Pelomedusoides (such as *Araripemys* and *Teneremys*), *Hydromedusa* or *Pseudemydura*, *Dermochelys* or Baenidae can be considered as "primarily homologous" in term of "identical structure" but the type of *incisura* being not truely homologous, it rather conduces to an eventual "false" homoplasy or "false" synapomorphy in the analysis. It is possible to examine other parameters of the *cavum tympani* which can help to the modification of the definition, or may constitute other characters, for

finding the good relationships between the taxa. In addition to the proportions of the *incisura columellae auris*, other neglected parameters are, for example: the position of the *columella* in the *cavum quadrati*, either closer to the back or to the center of the *cavum* and the *incisura* downwards directed (as seen above for Chelidae) or horizontally inclined in relation with the articular quadrate process. Other *cavum* character is the presence either of a secondary depression in the *cavum tympani* around the *columella* up to the entrance of the *antrum postoticum*, or only below the *incisura* (see the Chelydridae and Testudinoidea) or a well delimited precolumellar fossa (most of Pleurodira) etc. The complete quadrate suture (*commissura quadrati*) may be either short to medium (in a *cavum* higher than long), as in terrestrial Testudinidae (except in *Pyxis* without closure), Chelydridae and *Platysternon*. Or the *commissura* may be a longer suture, as in various Trionychidae and Carettochelyidae (in a longer *cavum*), and as in some Bothremydidae in Pleurodira. In addition, the suture may be smooth (*Carettochelys,* some Trionychidae such as *Apalone mutica*) or thickened and underlined by a crest, the "*crista falciformis*" sensu WALTHER, 1921, variably developed (*Allaeochelys*, other Trionychidae, terrestrial Testudinidae, Chelydridae, *Platysternon* and some Bothremydidae such as *Galianemys* GAFFNEY, TONG & MEYLAN, 2002, from the Albian-Cenomanian boundary of Morocco. In Pleurodira with an *incisura* enclosing the Eustachian tube behind the *columella*, the suture is either: slight or thick, short or eventually longer, and the shape of the *insisura* is variable (see below). For the quadrate closure, it is therefore possible to separate the character of closure in more states and eventually separated characters, taking into account the shape of the *incisura*. The result is that it could elevate the number of states in a matrix including all the turtle groups. Actually, the variability within the characters is often so wide that it is difficult to separate the states and delimit the homologies, and the notion of homology varies with each author. But if an accurate examination of all the known members of the groups is leaded first, before a synthetic analysis of taxa, the distinction in the different processes may conduce to find the exact similarities between the members of a group, resulting in a better definition of the states. The cases with a similar morphology will only remain as possible homologous comparable structures in the comparison of various groups, and possibly resulting either in synapomorphies or homoplasies, the autapomorphies being evidenced. This examination of the *incisura* also shows that in general it is no more possible to admit analysis taking groups as a whole such as "Chedidae" and "Pelomedusoides" for example for this character.

We could as well take examples in the carapace: the way the first thoracic rib laterally reduces, becomes or not attached to the second rib and becomes medially upwards curved, more or less thin or widened, is much more variable than estimated in the published works such as the character "first thoracic rib" with two states: "extends to peripherals" and "fails to reach peripherals" (GAFFNEY *et al.*, 1998); it is even more diversified than in LAPPARENT DE BROIN & MURELAGA, 1999 (four selected states); it is differently leaded in marine forms (Chelonioidea), Plesiochelyidae and Chelydridae in Cryptodira, Chelidae and Podocnemididae in Pleurodira, for example. The same happens with many other characters representing modifications for more protection of the body, anteriorly and posteriorly, by elongation of the carapace and plastron, etc. or modifications without visible interest such as the reduction in width of the vertebral scutes, or the reduction of the mesoplastra: in the last case, a definition is given in: two characters with two states in GAFFNEY *et al.*, 1991, not modified in SHAFFER *et al.*, 1997; in three states of one character in CADENA RUEDA & GAFFNEY, 2005; in four states of one character in LAPPARENT DE BROIN & MURELAGA, 1999, in an analysis reserved to Pleurodira, with a definition for the state 1 not distinguishing the variability in shape in *Platychelys*, the primitive chelids, *Pelomedusa* and *Teneremys*, and not adapted to Cryptodira such as baenids and *Solemys*.

The same elements of the above evocated structures vary in Pleurodira as in Cryptodira, with particularities for *Notoemys laticentralis*, primitive Pelomedusoides, Pelomedusidae, Podocnemididae, Bothremydidae and Chelidae (with variability between the *Phrynops* group and the *Hydromedusa* group, for example). We propose here to follow their evolution in the preserved parts of *Notoemys laticentralis* compared with each of these monophyletic pleurodiran groups (already established as monophyletic in previous works), eventually briefly comparing them with Cryptodira.

Relationships between groups of turtles: Based on anatomical characters, they are examined in many works. Most include very few taxa of each group. They are either dedicated to Cryptodira alone, such as HIRAYAMA, 1985, 1994, 1994, 2000; HIRAYAMA & CHITOKU, 1996; MEYLAN & GAFFNEY, 1989; YASUKAWA *et al.,* 2001, or principally to Cryptodira (Pleurodira being included at a very high level of taxa) such as GAFFNEY, 1985, 1996; GAFFNEY *et al.,* 1987; GAFFNEY *et al.,* 1998; HIRAYAMA *et al.,* 2000; ROUGIER *et al.,* 1995; WOOD *et al.,* 1996. Some works are more inclusive of pleurodiran taxa beside the cryptodiran taxa, such as GAFFNEY *et al.,* 1991; GAFFNEY & MEYLAN, 1988; SHAFFER *et al.,* 1997. Some other works are reserved to Pleurodira such as BROIN, 1988a, b; CADENA RUEDA & GAFFNEY, 2005; DE LA FUENTE, 2003; DE LA FUENTE & ITURRALDE-VINENT, 2001; GAFFNEY, 1977; LAPPARENT DE BROIN, 2000a; LAPPARENT DE BROIN & MURELAGA, 1999; MEYLAN, 1996; TONG *et al.,* 1998 (phylogenetic analysis restricted to the skull) and in works without phylogenetic analysis but with comparative information in works such as GAFFNEY *et al.,* 2002; GAFFNEY & WOOD, 2002; LAPPARENT DE BROIN *et al.,* 2004; LAPPARENT DE

BROIN & WERNER, 1998 and others. They include as well Pelomedusoides as chelids but rarely with an extensive examination of the members of each group and without most of the primitive Cretaceous members.

In Pleurodira, the remaining problems consist in relationships between the groups, which are not always well supported. The analysis have often considered the taxa "Chelidae" or "Pelomedusoides" each one as a whole for a character state: now that primitive chelids have been described (DE LA FUENTE, 2003; DE LA FUENTE *et al.,* 2001; LAPPARENT DE BROIN & DE LA FUENTE, 2001, LAPPARENT DE BROIN, 1997; LAPPARENT DE BROIN & MOLNAR, 2001) and that Dortokidae have been discovered (LAPPARENT DE BROIN in GHEERBRANT *et al.*, 2000; LAPPARENT DE BROIN & MURALAGA, 1996, 1999; LAPPARENT DE BROIN *et al.,* 2004), it is no more possible to take these groups as a whole and to ignore the Dortokidae, as seen above. Chelidae may present some primitive characters also found in Pelomedusoides such as: lateral mesoplastra in Cretaceous forms (wider than long, closer in shape to those of *Teneremys* and many *Pelomedusa* specimens); procoelous – amphicoelous – opisthocoelous caudal vertebrae series (Cretaceous forms, some extant species of *Acanthochelys*) as also found in *Dortoka* (Dortokidae); a wide nuchal in relation to its length (Cretaceous forms); a complete neural series up to the suprapygal (Cretaceous forms i.e. not only *Hydromedusa* in the family) or a nearly complete series in the oldest *Chelodina* known species (*Chelodina alanrixi* LAPPARENT DE BROIN & MOLNAR, 2001) or in the Albian Argentine forms; ischitatic scars still inserted up to into the xiphiplastral points in Cretaceous forms as in *Proterochersis,* etc. There are more possible homoplasies than previously established. For example, some analysis (such as MEYLAN, 1996) postulated the loss of mesoplastra as a synapomorphy of Chelidae and, consequently, the taxon "Chelidae" was taken as a whole. But the primitive chelids have still mesoplastra, and there are also missing in the Pelomedusoides *Araripemy*s (see MEYLAN, 1996) and in Dortokidae (LAPPARENT DE BROIN in GHEERBRANT *et al.,* 2000; LAPPARENT DE BROIN & MURALAGA, 1996, 1999; LAPPARENT DE BROIN *et al.,* 2004). The lateral emargination of the skull is united with the posterior emargination in *Chelodina* as in the Pelomedusoides *Teneremys* (see below): actually the break process is opposite in the two groups, the anterior emargination being dominant in chelids and the posterior one in Pelomedusoides so that the fully broken state is not homologous (see below). The procoely of the caudal vertebrae has proved to be independently acquired, from a primitive state of amphicoely (Triassic forms), in most of Chelidae and all known Pelomedusoides, because an intermediate state, uniting amphicoelous, procoelous and opisthocoelous or concavo-platycoelous vertebrae in the tail, is present in some Chelidae, as well in the *Hydromedusa* group in *Yaminuechelys,* as in the *Phrynop*s group (DE LA FUENTE *et al.,* 2001), in

Dortokidae (LAPPARENT DE BROIN & MURALAGA, 1999; LAPPARENT DE BROIN *et al.,* 2004) and also in various Cryptodira such as Chelydridae (GAFFNEY & MEYLAN, 1988; LAPPARENT DE BROIN, 2000c). The reduction of the neural series up to the loss of neurals is independently acquired in South-American chelids and in the *Chelodina* lineage (LAPPARENT DE BROIN & MOLNAR, 2001), as within the Pelomedusoides Podocnemididae (GAFFNEY & WOOD, 2002) and Bothremydidae in "*Eusarkia*", a member of the *Taphrosphys* group (BROIN, 1977; LAPPARENT DE BROIN & WERNER, 1998).

In Pleurodira, the next analysis to be leaded must include more characters and more states. The relative position of the Podocnemididae *Peltocephalus* and *Erymnochelys* is not the same in MEYLAN, 1996 and LAPPARENT DE BROIN, 2000a, because the way the secondarily covered roof has been constructed and the way the podocnemidid fossa is eroded below the pterygoid wings are different and have not been examined in the first work. For the first one, both genera are included in the same clade, for the last, they belong to two distinct groups. Between the members of the Bothremydidae, there are still divergent points of views traducing a divergency in the appreciation of the characters, synapomorphic or erroneously synapomorphic: The *Taphrosphys* group (sensu LAPPARENT DE BROIN & WERNER, 1998) is different from that of GAFFNEY & TONG, 2003. *Taphrosph*ys (see GAFFNEY, 1975) is linked with *Nigeremys* BROIN, 1977, in GAFFNEY & TONG, 2003, on two skull characters, without taking into account the carapacial elements; but *Nigeremys* is part of an independent group in LAPPARENT DE BROIN & WERNER, 1998, according to the shape of the skull (see below) and to the shape of the carapace (see below). In the last work, no particular value is given to two characters given by the first authors and allowing the integration of the *Nigeremys* group in the *Taphrosphys* group, because of their definition, considered as too weak and not significant. We do not link *Taphrosphys* and *Phosphatochelys* GAFFNEY & TONG, 2003 to the *Nigeremys* group: the postorbitary wall is, in both groups, partly more open than in the *Bothremys* group. Actually, in the last one, the bony postorbital wall is particularly developed with the much posteriorly widened and depressed maxillary surfaces; therefore, there is a comparatively less open wall than in the others and that does not constitute a synapomorphic character for both first groups. In both groups, *Nigeremys* and *Taphrosphys* (including *Phosphatochelys*), the palate is wide and deeper. But we estimate that this deepening is not homologous in *Nigeremys* group (known in *Nigeremys*, *Arenila* LAPPARENT DE BROIN & WERNER, 1998 and *Azabbaremys* GAFFNEY, MOODY & WALKER, 2001) and the two others, because the constitution of the palate and masticatory surface is completely different in both groups. In the *Taphrosphys* group with *Phosphatochelys*, there is no strong and thick enlargement of the snout, with a sub-triangular shape and crested and thick maxillary border.

Nigeremys group is also distinguished by the tectiform dorsal roof, and the shell characters are different in both groups. These are known, in the *Nigeremys* group, by isolated shells as well as by several fragmentary shells associated with the skulls in Africa or present in their type-localities (although not attributed to the genera in the original descriptions of the genera). They show : converging borders of the posterior lobe, not enlarged as they are in the *Taphrosphys* group, flattened shell with peripherals posteriorly long and expanded, short pleurals 1 instead of elongated and anteriorly rounded ones, no elongated anterior peripherals doing with the elongated pleurals and nuchal an ovoid anterior shell as seen in *Taphrosphys* (see BROIN, 1977 ; 1988b, GAFFNEY, 1975 ; LAPPARENT DE BROIN & WERNER, 1998 ; references in these papers), no strong polygonal decoration, no elongated pubic scars and no rounded ischiatic scars close to the rounded anal notch (see GAFFNEY, 1975). The identity of each group is recognized but their close inter-relationships are not, no more than with the *Bothremys* group. Within both *Bothremys* and *Nigeremys* groups, the latter restricted as seen above, the reduction of the back skull is independent and cannot constitute a synapomorphy or a homoplasy, as shown by the gradient of reduction within each group, reduction which is not exactly similar in both.

In the present work, our aim is not to propose definition and states of characters for the examined structures, which obligatorily vary in the different analysis according to the included taxa ; we just hope that further studies will integrate the necessity to reexamine the anatomy of the groups in the details, before leading a complete analysis of the turtles. We want to show the diversity that may cover an apparent simple character.

SYSTEMATICS

Ordo Chelonii LATREILLE, 1800
Infra-Ordo Pleurodira COPE, 1864
Notoemydidae BROIN & DE LA FUENTE, 1993
Notoemys **CATTOI & FREIBERG, 1961**

Notoemys laticentralis **CATTOI & FREIBERG, 1961**

Revised material : Holotype : MACN, 18043, Las Lajas, Picunches Department, Neuquén province, Argentina, carapace and anterior plastral lobe, figured in WOOD & FREIBERG, 1977, Formation Vaca Muerta, late Jurassic, Tithonian. MOZP 2487, Cerro Lotena, Zapala Department, Neuquén province, Argentina, Formation Vaca Muerta, lower levels, late Jurassic, upper part of lower Tithonian, carapace and plastron, posterior skull, four anterior cervical vertebrae ; right humerus, left forelimb : radius, ulna, hand ; right femur ; left tibia, tarsus, figured in DE LA FUENTE & FERNANDEZ, 1989 ; FERNANDEZ & DE LA FUENTE, 1994 ; see also DE LA

FUENTE & FERNANDEZ, 1986. A specimen from Los Catutos, Neuquén province, Argentina, Formation Vaca Muerta, lower levels late Jurassic, lower Tithonian, exists, unstudied. References and data on most of the compared taxa are given in the Annexe in LAPPARENT DE BROIN, 2000a. Anatomical terminology of the skull and comparative skulls particularly in GAFFNEY (1972a ; 1977 ; 1979a), LAPPARENT DE BROIN (2000a) LAPPARENT DE BROIN & WERNER (1998) ; WERMUTH & MERTENS (1961) ; BOULENGER (1889).

Skull (Pl. I, A to F, Figs 2 to 4)

General view : relative proportions, elongation, flattening :
The skull of *Notoemys laticentralis* was relatively low (Pl. I, A, B ; Fig. 2 A, B) in relation to the Triassic and early Jurassic forms : *N. laticentralis* was derived by its skull flattening. The skull of *N. laticentralis* was probably relatively short and wide, although the derived constitution of the *cavum tympani* and of the *antrum postoticum* (Pl. I, F ; Fig. 2 F) show a moderate posterior elongation was present by comparison with the Triassic forms. *N. laticentralis* had derived short and thin paroccipital processes, well sutured to the basicranium and the quadrate, wide, posteriorly rounded, slightly longer than the short and thin extremities of the *antra squamosa*, and very slightly ventrally concave. *N. laticentralis* had no shortening of the ear and basioccipital-basiphenoid area, and the skull is not elevated. We cannot say if the anterior part of the skull was elongated and/or widened, probably not (Fig. 3).

In *Notoemys laticentralis*, being anteriorly incomplete, the height of the skull relatively to its full length cannot be measured. The skull was already posteriorly elongated, in relation to the Triassic genera, by the realized constitution of the *antrum postoticum*, posteriorly prolonged behind the rolled up *cavum tympani* and protruding in relation to the quadrate, as the paroccipital processes, (Pl. I, C, E, F ; Fig. 2, C to F ; Fig. 4) as in Pleurodira and Cryptodira (more or less, see below).

The posterior part of the skull is preserved. Anteriorly and ventrally, it is transversally limited from the partial right quadrate, in the articular area with the lower jaw, up to the anterior point of the basisphenoid, medially, and obliquely toward the left quadrato-opisthotic suture. Dorsally and medially, the supraoccipital is exposed with the suture for the missing parietal roof. Posteriorly, the supraoccipital crest is slightly broken (it was probably short) just in front of the posterior exposition of the two exoccipitals. We cannot say how long the skull was anteriorly, if the postorbital arch was long or short, if the orbits were small or large, more dorsal or more lateral and which was the shape of the external nare. Taking into account the preserved part, the length of the skull from prootic to opisthotic extremities and the
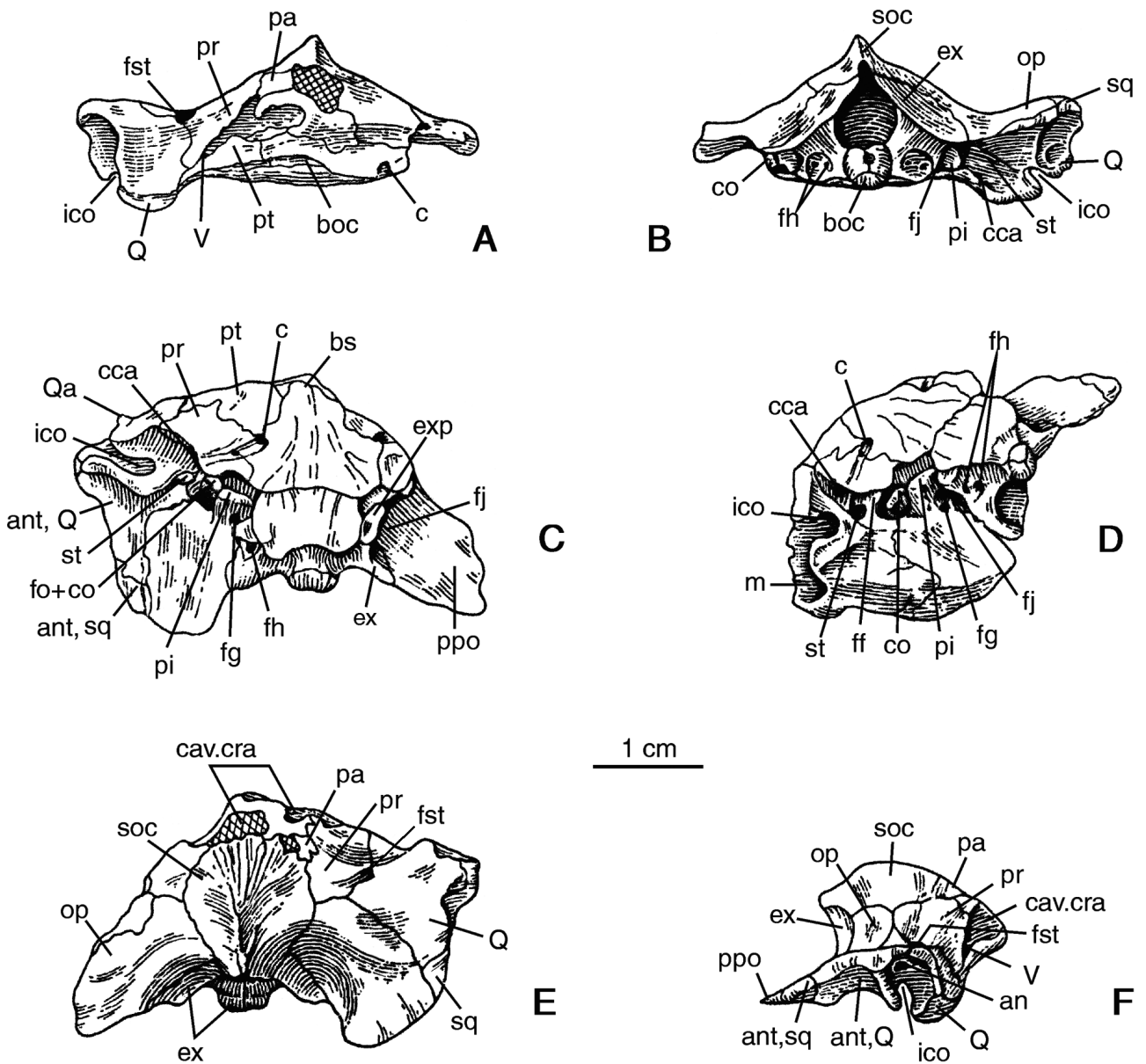
Fig. 2 : *Notoemys laticentralis* CATTOI & FREIBERG, 1961, MOZP 2487, Cerro Lotena, Neuquén province, Argentina. **Formation Vaca Muerta**, Late Jurassic, A-F, skull, anterior, posterior, ventral, ventro-latero-posterior (from above), dorsal, right lateral views. an, *apertura antri postotici* ; ant, *antrum postoticum* ; boc, basioccipital ; bs, basisphenoid ; c, foramen of the inner carotid canal (foramen du canal de la carotide interne) ; cav.cra, *cavum cranii* ; cca, *foramen posterior canalis cavernosi* ; co, *columella auris,* ex, exoccipital ; exp, exoccipital process (processus exoccipital) ; ff, *foramen nervi facialis* (VII, hyomandibular) ; fg, *foramen externum nervi glossopharyngei* (IX) ; fh, *foramen externum nervi glossopharyngei* (IX) ; fj, *foramen jugulare* ; fo +co, *fenestra ovalis + columella auris,* medial extremity (extrémité médiale) ; fst, *foramen stapedio-temporale* ; ico, *incisura columellae auris* ; m, *meatus quadrati* ; op, opisthotic ; pa, parietal ; pi, *processus interfenestralis opisthotici* ; ppo, paroccipital process of the opisthotic (processus paroccipital de l'opisthotique) ; pr, prootic ; pt, pterygoid ; Q, quadrate (carré) ; soc, supraoccipital ; sq, squamosal ; st, *foramen posterior canalis stapedio-temporalis* ; V, *foramen nervi trigemini.*

Fig. 2 : *Notoemys laticentralis* CATTOI & FREIBERG, 1961, MOZP 2487, Cerro Lotena, province du Neuquén, Argentine. Formation Vaca Muerta, Jurassique supérieur. A-F, crâne, vues antérieure, postérieure, ventrale, ventro-latéro-postérieure (vue de dessus), dorsale et latérale droite.
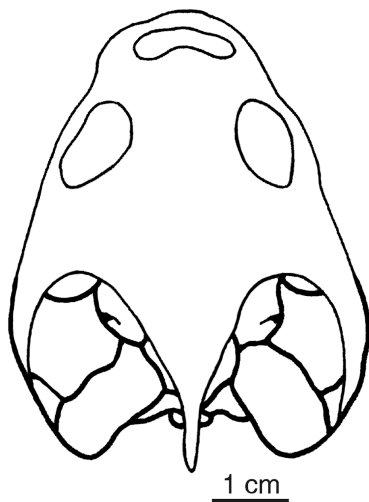
Fig. 3 : *Notoemys laticentralis* CATTOI & FREIBERG, 1961, MOZP 2487, Cerro Lotena, Neuquén province, Argentina. Formation Vaca Muerta, Late Jurassic. Hypothetic reconstruction of the outline of the skull, dorsal view ; preserved part in bold.

Fig. 3 : *Notoemys laticentralis* CATTOI & FREIBERG, 1961, MOZP 2487, Cerro Lotena, province du Neuquén, Argentine. Formation Vaca Muerta. Reconstitution hypothétique du contour du crâne en vue dorsale ; partie préservée en gras.

primitiveness of the taxon in Pleurodira, as a whole, a tentative reconstruction of the outline in dorsal view (Fig. 3) has been done. It better could agree with, in fossils, a rather primitive short shape such as that of the pre-podocnemidid *Brasilemys josai* LAPPARENT DE BROIN, 2000a. This form is recovered from the late Aptian, Albian boundary, of the Chapada do Araripe, lower Cretaceous of Brazil, which is the same locality as that of the basal Pelomedusoides (s.l.) *Araripemys barretoi* PRICE, 1973, and of *Cearachelys placidoi* GAFFNEY *et al.,* 2001, the oldest bothremydid known by its skull. The outline of the posterior part of *Brasilemys* conforms that of *N. laticentralis* and the direction of the anterior sides better agrees with it than with a narrow shaped anterior snout, as in most other derived pleurodires. The anterior snout of *N. laticentralis* might have been primitively wide, with a wide interorbitary space, as in *Brasilemys*, closer to the Triassic and early Jurassic forms. *Brasilemys* skull had to be primitively anteriorly wide, and not secondarily as it was erroneously stated in its diagnosis. A short snout with a rather wide interobitary space is also present in the late Jurassic *Platychelys*, as observed in the photograph of the new skeleton, recently found in Bavaria, Germany (H.-V KARL pers. comm. ; KARL & TICHY in press).

The preserved posterior part of the skull is low (Pl. I, A, B ; Fig. 2, A, B) and apparently lowered in relation to the most primitive turtle skulls, such as, from the late Triassic, the Argentine *Palaeochersis talampayensis* ROUGIER *et al.,* 1995 (Los Colorados Formation,

Norian, La Rioja) and the German *Proganochelys* BAUR, 1887 (Keuper beds from Germany, see GAFFNEY, 1990), and those from the early Jurassic, the South-African *Australochelys* GAFFNEY & KITCHING, 1994 (and 1995) (from the Karroo) and the North-American *Kayentachelys* GAFFNEY *et al.,* 1987 (from Arizona). The skull is unknown in other Triassic forms (*Proterochersis* and affine forms to *Proganochelys*, BROIN *et al.,* 1982 ; JENKINS *et al.,* 1994).

Comparisons : In the three first primitive forms, *Palaeochersis*, *Proganochelys* and *Australochelys*, the skull is wide and high for its length and the back part is short in relation to the anterior masticatory part : the back part becomes relatively elongated in the other turtle groups. The primitive skull is posteriorly short as a whole because of the short ear area, the nearly vertical quadrate and the absence of a *cavum tympani* and an *antrum postoticum*, which develop in Cryptodira as in Pleurodira (see below). Beyond the basioccipital condyle, the paroccipital processes of the opisthotics are strong and weakly united to the squamosals and quadrates. In the early Jurassic North-American *Kayentachelys*, considered to be the earliest cryptodiran (GAFFNEY *et al.,* 1987), the skull is postero-laterally elongated by the partly rolled up quadrate, the apparent constitution of a short *antrum postoticum* and the backward dorsally prolonged squamosal and parietal : it looks high for its length ; the paroccipital processes are reduced at the length of the condyle.

In Pleurodira (including Chelidae and Pelomedusoides s.l. in addition to the primitive forms *Platychelys*, *Notoemys laticentralis*, *Caribemys* and the Dortokidae, above mentioned in the introduction) different lineages tend to have a flattened skull after the elongation due to the acquisition of the *cavum tympani* and the *antrum postoticum* : this is known for the first time in *N. laticentralis* in Pleurodira, but is seems similar in the skull of *Platychelys* (KARL & TICHY in press). The Pelomedusoides s.l. include various primitive taxa and constituted groups : Bothremydidae, Pelomedusidae and Podocnemididae (LAPPARENT DE BROIN, 2000a). The lineages with a flattened skull are most of the Chelidae groups, the basal Pelomedusoides s.l. *Araripemys* PRICE (MEYLAN & GAFFNEY, 1991 ; MEYLAN, 1996) (Fig. 5, A-E) and all the Pelomedusidae (here, Fig. 5, H, I) : the flattening is variable according to the taxa (Tab. 1). Some of them have also an anterior elongation (in the pterygoideo-palato-masticatory part). However, some other lineages such as, in Bothremydidae, the *Bothremys* group and forms in the *Nigeremys* group, tend to independently have a shorter basicranium part (basioccipital principally), in relation to the much developed masticatory part, either in posterior width of the maxillary with a particular concavity (*Bothremys* group, GAFFNEY & ZANGERL, 1968) or in strength and crests (*Nigeremys* group).

An example of debatable homoplasy as well as

Table 1 :   Estimated height of the back skull in *Notoemys laticentralis*, compared to the more primitive taxa and to some Pleurodires : ratio posterior height, at the quadrate articulation with the lower jaw, on the length between the anterior border of the *cavum tympani* and the posterior extremity of the squamosal (Chelidae, sublined) or the opisthotic (others).

Tableau 1 : Hauteur estimée de la partie postérieure du crâne chez *Notoemys laticentralis*, comparé aux taxons les plus primitifs et à des Pleurodires : rapport hauteur postérieure, à l'articulation du carré avec la mandibule, sur la longueur entre le bord antérieur du *cavum tympani* et l'extrémité postérieure du squamosal (Chelidae, taxons soulignés) ou de l'opisthotique (les autres).

Taxon	Ratio posterior height / length %	Age, country
Proganochelys	124	Triassic, Germany
Palaeochersis	218 ; 159,37	Triassic, Argentine
Australochelys	ca 280	Early Jurassic, South Africa
Kayentachelys	ca 200	Early Jurassic, USA
Annemys levensis	87,67	Late Jurassic, Mongolia
Emydura macquarii	102,5	extant, Australia
Phrynops vanderhaegei	81,35	extant, South-America
Acanthochelys radiolata	68,42	extant, South-America
Platemys palatycephala	68,75	extant, South-America
Hydromedusa tectifera	55,17	extant, South-America
Yaminuechelys	ca 18-28	Late Cretaceous, South-America
Cearachelys (from authors's data)	ca 109	Early Cretaceous, Brasil
Brasilemys	96,42	Early Cretaceous, Brasil
Galianemys cf. *whitei*	112,5	late Early Cretaceous, Morocco
Galianemys cf. *emringeri*	98,21	late Early Cretaceous, Morocco
Aff. *Galianemys* sp.	104,54	late Early Cretaceous, Morocco
Araripemys	66,66 ; 77,41 and 88,88 (three more or less spoiled)	Early Cretaceous, Brasil
Teneremys	70 and 65,62	Early Cretaceous, Niger
Pelomedusa	68,18	extant, Africa
Pelusios castaneus	80,95	extant, Africa
Hamadachelys (from authors's data)	ca 105	late Early Cretaceous, Morocco
Podocnemis expansa	92,3	extant, South-America
Podocnemis vogli	86,36	extant, South-America
Podocnemis cayennensis	73,52	extant, South-America
Notoemys laticentralis	**ca 73**	**Late Jurassic, South-America**

debatable synapomorphy in Pleurodira is observed in Podocnemididae. Some genera of Podocnemididae tend to elevate the skull posteriorly by a secondary roofing, such as the extant *Peltocephalus* and *Erymnochelys* (figs in GAFFNEY, 1979a ; GAFFNEY, DEBLIEUX *et al.,* 2002 ; LAPPARENT DE BROIN & WERNER, 1998) : the globosity (best seen in lateral view) and the longitudinal and dorsal outlines are different in both genera (LAPPARENT DE BROIN, 2000a) indicating an independent elevation, not homologous (no homoplasy or synapomorphy either). Besides, the shell characters include the intergular proportion which can be considerably reduced so that the gulars meet behind : this character identify an Euro-African *Erymnochelys* group including forms with skulls differently roofed posteriorly than that of the extant *Erymnochelys madagascariensis* : there is no possibility to unite *Peltocephalus* and *Erymnochelys* in the same group when integrating all the fossils and after a careful observation of the way the roof is constituted.

In Cryptodira, approximately at the same time as in Pleurodira, the skull flattening is known as soon as during the late Jurassic in Asia (for example *Anemys levensis* SUKHANOV & NARMANDAKH, 2006 ; SUKHANOV, 2000), and probably during the late Jurassic in North America
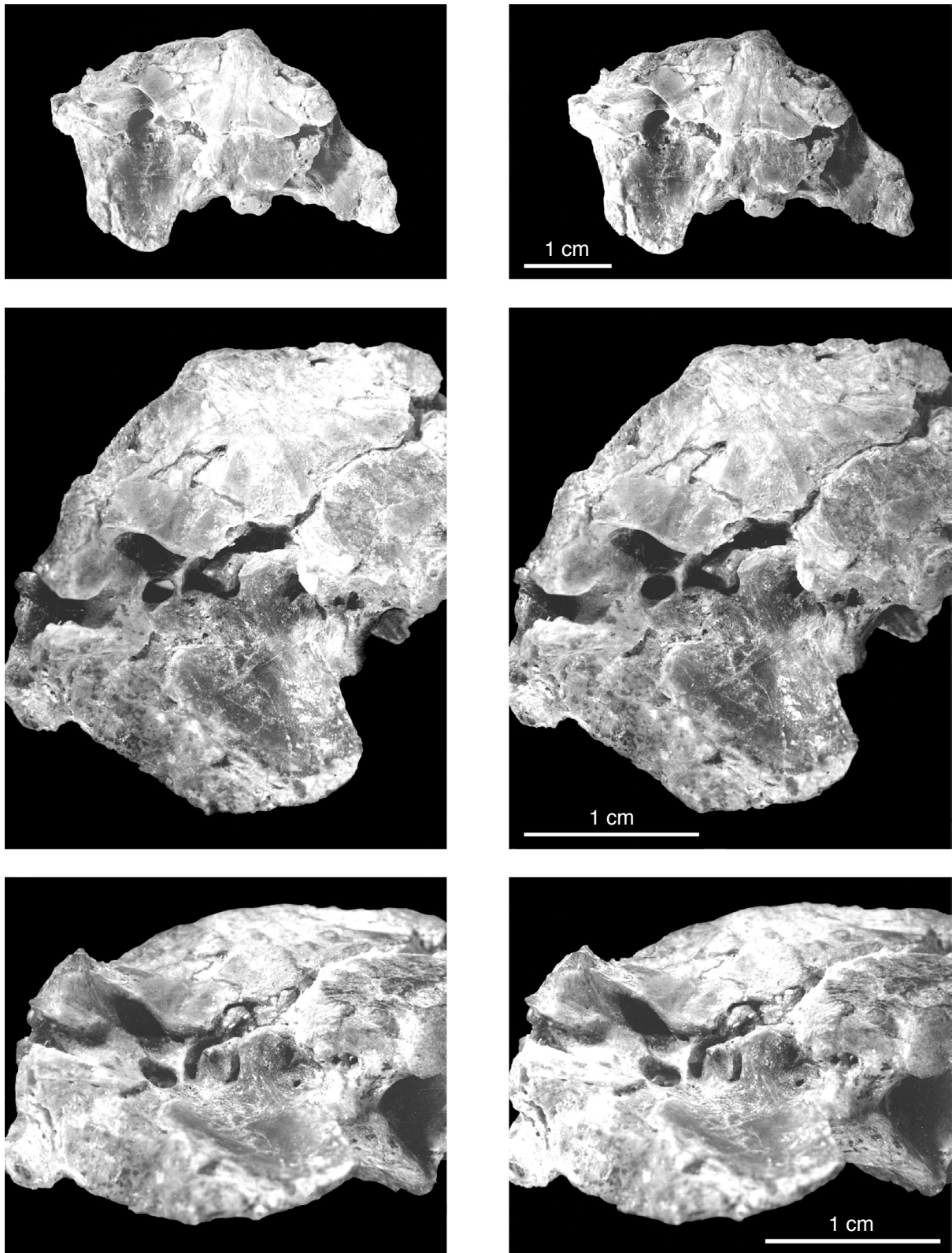
Fig. 4 : *Notoemys laticentralis* CATTOI & FREIBERG, 1961, MOZP 2487, Cerro Lotena, Neuquén province, Argentina. Formation Vaca Muerta, Late Jurassic. A-C, stereoscopic views of the skull, A, ventral ; B, ventro-latero-posterior view, from above ; C, ventro-latero-posterior view, from behind

Fig. 4 : *Notoemys laticentralis* CATTOI & FREIBERG, 1961, MOZP 2487, Cerro Lotena, province du Neuquén, Argentine. Formation Vaca Muerta, Jurassique supérieur. A-C, vues stéréoscopiques du crâne, A, ventrale ; B, ventro-latéro-postérieure, vue du dessus ; C, ventro-latéro-postérieure, vue de l'arrière.

(GAFFNEY, 1979b: unknown part of the posterior extremity of the skull of *Glytops*, medio-anteriorly flat). As in Pleurodira, some forms of Cryptodira elevate the skull, for example in Chelydridae and independently in two lineages: within the North American lineage, *Chelydra* and *Macroclemmys* present a hooked beak and the skull is elevated by a secondary roofing in *Macroclemmys*. In *Chelydropsis* s.l., constituting the European-Asiatic lineage which never presents a hooked beak, there is also a secondary roofing after the Oligocene forms, in Mio-Pliocene forms. This difference between the two lineages is correlated with the different plastral characters. The secondary roof might constitute a homoplasy, but here also the way the roof is elevated differs in both groups (LAPPARENT DE BROIN, 2000c) and is not strictly homologous.

Cavum tympani, incisura columellae auris, antrum postoticum, paroccipital process

Introduction to examination in N. laticentralis laticentralis:
The quadrate is bent over the stapes extremity in all turtles which is at best seen in lateral view (GAFFNEY 1990, 1979a, GAFFNEY & KITCHING, 1995, GAFFNEY *et al.*, 1987, ROUGIER *et al.*, 1995): few curved in Triassic turtles and more in *Palaeochersis* than in *Proganochelys*, it tends to completely enclose the stapes. In all the Chelidae and Pelomedusoides, as in most of but not all the Cryptodira, the quadrate is much rounded and bent over itself and either it remains more or less open, or it is nearly closed or closed (depending on the taxa and, by homoplasy, at various states of evolution within the monophyletic groups) behind the *incisura columellae auris* (see the introduction). In any case, connective tissue posteriorly closes the *incisura* and the Eustachian tube groove. Sometimes, the connective tissue is calcified (as observed in the cryptodire *Mauremys leprosa* and, as probably, in an inedited specimen of *Galianemys* from Morocco, MNHN coll.). In the rolling up process in Pleurodira, the lateral extremity of the Eustachian tube groove may be integrated posteriorly in the closed *incisura* (the derived Pleurodira, less most of the Bothremydidae) or in the nearly closed *incisura* (the primitive bothremydid *Cearachely*s). The *cavum tympani* may be few (more primitive condition) to more (more derived condition) elongated around the *columella* and particularly anteriorly to it, resulting less to more rounded. In any case, the *incisura* is short to long and, when closed, the suture (*commissura quadrati*) between the foramen and the Eustachian tube groove may also be as well short to long. The quadrate is often closed or nearly closed behind the *columella* alone in cryptodiran groups, unlike most of pleurodiran groups where the *incisura* also enclosed the Eustachian groove except in the Bothremydidae. Bothremydidae (*Cearachelys* excepted) present the most current condition observed in cryptodirans. However, the *incisura* remains more widely open in important cryptodiran groups, as seen above in the introduction: the differences traduce different states of quadrate closure, not exactly homologous by their different shape. When the quadrate is completely closed around the *columella* alone in turtles, there is no more *incisura* but a rounded *foramen columellae auris* situated either posteriorly in the *cavum tympani* (posteriorly in Cryptodira including most of terrestrial Testudinidae for example, as seen above in the introduction, and a little more medially in primitive Bothremydidae); or the foramen is well medially positioned (various diversified Bothremydidae, various Cryptodira including most of Trionychidae, Carettochelyidae, *Platysternon*, the Chelydridae and some terrestrial Testudinidae). The shape of the structure and more or less closure is characteristic of these taxa and of their constituents, without recorded individual variations. All the differences in the details show how the closure of the quadrate has independently developed, and ontogenetically, from an open state in the embryo, with its own rhythm in each group. The grade of evolution of these characters or the ontogenetic development quickness is variable within the groups, well established as monophyletic by other characters, such as within Testudinidae and Trionychoidea (in Cryptodira), or within Podocnemididae, Pelomedusidae and Bothremydidae (in Pelomedusoides).

After Triassic and early Jurassic forms, the quadrate part of the *antrum*, newly constituted, is posteriorly covered by the squamosal. This bone develops in length and in width, interiorly with the development of the *antrum postoticum* and ventro-posteriorly for the muscular attachment, and it may develop beyond the posterior extremity of the paroccipital process of the opisthotic for example in Chelidae with the formation of the latero-posterior *sulcus chelidianus* (see below).

Antrum postoticum (antrum squamosum): In *Notoemys laticentralis*, there is a true *antrum postoticum* in the quadrate, prolonged in the squamosal. It is not yet as much developed in length and volume as it can be in various Pelomedusoides and chelids. As it is posteriorly flattened, the inner air cavity must be thin and much reduced: the squamosal extremity ought to be without an air cavity.

The *antrum* is a cavity in the quadrate, posterior to the *cavum tympani*, opening in it, variable in depth and more or less covered by the squamosal. It is an air cavity for the middle ear; its external base, often protruding beyond the inner air cavity, is utilized for the masticatory muscle attachment. The realization of this *antrum postoticum* after the Triassic forms and its prolongation posteriorly elongates the skull in relation to the Triassic turtle skulls.

In Pleurodira (amphibious forms): The *cavum tympani* is few developed in Pelomedusoides basal forms (*Brasilemys*, *Araripemys*), variably developed within

each group and the most developed in some forms (the chelid *Platemys*, Pelomedusidae). Above and posteriorly to the *incisura*, the opening of the *antrum postoticum* (*apertura antri postotici*) of *N. laticentralis* in the *cavum tympani* is rather small as in primitive Pelomedusoides s.l. such as *Teneremys* (Fig. 5, H) and *Araripemys barretoi* (Fig. 5, B, C). In *N. laticentralis*, as in *Araripemys* (Fig. 5, A-E) and *Brasilemys,* the *antrum* is primitively slender dorsally and infero-laterally. It is a little larger in the other Pelomedusoides. In Pelomedusidae, the *antrum* is short but medio-dorsally inflated in *Teneremys* (Fig. 4, J) and together much larger and inflated dorsally and ventrally in extant Pelomedusidae (Figs in BOUR, 2000), with a wide opening in the *cavum*. It is more medio-ventrally developed in some Bothremydidae (from Araripe and Morocco at least) and in Podocnemididae than in primitive Pleurodira, but not inflated. The *antrum* is also more developed than in other groups, up to inflated, in some Chelidae (in particular in *Platemys*), but secondarily modified in flattened forms such as *Chelus* with an *antrum* only transversally developed, and variably according to the genera.

The development of the *antrum* observed as variable in various lines of chelids and Pelomedusoides is therefore independently acquired.

Relation of the squamosal length with the opisthotic process length: In *N. laticentralis* (Pl. I, C-F; Fig. 2, C-F; Fig. 3), the squamosal extremity posterior to the *antrum* is shorter than the posterior opisthotic process as basically in Pelomedusoides (Pl. II, G-J; BROIN, 1977, pl. III-1 and IV-3), which is a primitive condition in turtles, as observed in Triassic forms and *Australochelys*. **Secondarily in some Pelomedusoides, the** squamosal extremity develops medio-posteriorly: first, to be nearly at the same length as the opisthotic process, in the bothremydid *Cearachelys*; up to pass medially behind the opisthotic extremity (on the same ventral plane): 1) in Bothremydidae, with a rounded extremity (except in *Kurmademys* GAFFNEY, CHATTERJEE & RUDRA, 2001, from the Late Cretaceous of India, where the opisthotic is longer), and 2) in the podocnemidids *Schweboemys antiqua* (ANDREWS, 1903) from the late Eocene of the Fayum, Egypt (Figs in GAFFNEY, 1979a; GAFFNEY & TONG, 2000; GAFFNEY *et al.*, 2001; LAPPARENT DE BROIN & WERNER, 1998; specimen BM, NH R 11998, NHM, partly figured in ANDREWS, 1906, pl. 25, fig. 1), *Bairdemys venezuelensis* (WOOD & DIAZ DE GAMERO, 1971) with a pointed extremity, and in *B. harsteinei* GAFFNEY & WOOD, 2002, with a more rounded extremity. In other Bothremydidae, the squamosal may be longer than the paroccipital process. In all these forms, the air cavity is more or less prolonged within this squamosal extremity, and the squamosal external longitudinal crest for the muscle attachment is more or less developed.

In chelids, we have no preserved primitive stages. The known forms have the squamosal always clearly longer than the opisthotic (Pl. II, C, E, D; Fig. 4, F; GAFFNEY, 1977); but because of the presence of a latero-posterior chelid groove (*sulcus chelidianus*, see below) the squamosal extremity becomes a thin squamosal protuberance, beyond the *antrum* inner cavity, forming a crest disposed in an horizontal plane in *Chelus* (highly modified skull, flattened and transversally expanded) and in an obliquo-vertical ventral plane in the other groups (the crest is weakened by the inflated *antrum* in *Platemys*, Pl. II, figs C and D): the morphology of the bones is different from that of the Pelomedusoides and Cryptodira.

Nevertheless in turtles, the *antrum* cavity is prolonged up to the extremity of the squamosal only in the forms with an inflated *antrum* (*Platemys*, modern Pelomedusidae, Testudinidae and terrestrial forms in particular etc.): *N. laticentralis* is in the case of a primitive non inflated *antrum*, with a thin flat protruding squamosal extremity and squamosal shorter than the paroccipital process which is reduced, compared with the Triassic forms.

In Cryptodira: The *antrum,* when it is well developed and inflated, may also be prolonged up to the squamosal extremity; the squamosal is also primitively shorter than the paroccipital process, becomes as long and may become longer, while the paroccipital process is reduced (but the depth of the *antrum*, if developed, is undescribed in the primitive forms *Kayentachelys* and *Glyptops*). There are many conditions of development of the *antrum*. For example in Chelydridae and *Platysternon*, the upper extremity of the squamosal is much developed, curved and pointed, but the air cavity of the *antrum* is moderate posteriorly and more medially extended. While in Testudinoidea, the squamosal extremity is widened and the air cavity is inflated up to the extremity, overall in the terrestrial forms. In Cryptodira, the *antrum* is not as much developed when the quadrate is not much rolled up, such as in primitive fossil forms and it is few developed in marine Dermochelyoidea and more or less in marine Chelonioidea: the *incisura* is widely open and the squamosal and quadrate part of the air cavity is relatively weak and not medially prolonged (more or less according to the species). However in Cryptodira, the squamosal extremity posterior to the air cavity is already more or less upwards or posteriorly prolonged (such as in *Platysternon*, Chelydridae, Cheloniidae) for the muscle attachment, in relation with the masticatory system development, as well or even much more (when the air cavity is not much developed in marine forms), than in forms with a large air cavity (testudinids, particularly the terrestrial ones).

In any case, Cryptodira or Pleurodira, it is necessary to distinguish the development of the air cavity in the quadrate and in the squamosal (representing the complete volume of the *antrum* cavity) from the posterior extremity of the squamosal which may be longer (to support the stronger muscle attachment) or not longer than the air cavity.

The paroccipital process: suture with the lateral skull, relative proportions of the process:

N. laticentralis has posteriorly long paroccipital processes, well fused to the exoccipital and the quadrate, flattened and with a rounded posterior border. The morphology in *N. laticentralis* is present in most of Pelomedusoides s.l., while the other taxa (various Cryptodira, most Bothremydidae, Chelidae) have a derived development in length of the squamosal in relation to the opisthotic process, more or less strong (see above). But *N. laticentralis* is different from the basic state in Pelomedusoides s.l. and autapomorphic in the wider opisthotic process, dorsally and ventrally flat and with a rounded posterior outline.

The primitive Triassic and early Jurassic taxa: They lack an *antrum* and a squamosal posterior development: the paroccipital process is ventrally prominent, ridged, and very long and it is the most postero-laterally developed element in ventral view. Its extremity is ventral to the squamosal and, in ventral view, only the quadrate and the paroccipital process unite posteriorly. The paroccipital process is not firmly sutured all along to the quadrate in *Proganochely*s, with a space between them. Remaining ventrally prominent, the paroccipital process loosely contacts the quadrate in *Paleochersis* and *Australochelys,* ventrally and up to posteriorly. The quadrate is shorter and latero-anteriorly situated to the strong paroccipital process in *Proganochelys*. In *Palaeochersis*, the process is approximately as long as the quadrate extremity in the two known skulls, below the shorter squamosal not developed in an *antrum*, and the process is less developed than in *Proganochelys*. In *Australochelys* (badly preserved), also without an *antrum*, the process appears also slender and as long as the quadrate, approximately, but seeming (as figured) a little more slender than in

Palaeochersis although still prominent ventrally. We have seen above that in Cryptodira as in Pleurodira, the squamosal has become ventrally posteriorly developed. In *Kayentachelys*, with a complete roof not emarginated, the squamosal is dorso-laterally posteriorly protruding although it is short above and beside the paroccipital opisthotic process; but the contacts opisthotic-quadrate-squamosal are not clear in the figures (drawing only) of the authors. Anyway, in all these Triassic and early Jurassic forms, the quadrate is not enough rolled up and the antrum of the squamosal is not enough posteriorly developed, so that this bone does not unit the paroccipital process posteriorly to the quadrate, in ventral view.

In Pleurodira: In *N. laticentralis* (Pl. I, C, E, D; Figs 2, 4), the paroccipital process extremity is primitively longer than the squamosal and well sutured to the quadrate and squamosal; but it is wide and flat, with a rounded posterior outline. In return, it is pointed and, ventrally, it is medially ridged in most Pelomedusoides (most Bothremydidae excepted) including primitive ones such as *Araripemys* (Fig. 5, D, E), *Teneremys* (Fig. 5, K) and *Brasilemys* or other derived Pelomedusoides such as the extant *Podocnemis cayennensis* (*unifilis* auct.) or *Pelomedusa* (Pl. II, I.). In *Teneremys*, the paroccipital process is medio-ventrally ridged but short. In other Pelomedusoides, the posterior part of the opisthotic paroccipital processes may be medially narrowed and elongated, doing prominent points in relation to the squamosal (Pl. II, G, I), underlined by the ventro-medial crest: such as in *Araripemys*, *Pelomedusa*, some species of *Pelusios* and of Podocnemididae (Pl. II, I; Fig. 5, C; Figs in BOUR, 2000, GAFFNEY 1979a, GAFFNEY *et al.,* 2002, LAPPARENT DE BROIN, 2000a), recording the strong primitive paroccipital processes of the Triassic forms. The more the processes elongate and their border

Fig. 5: *Araripemys berretoi* PRICE, 1973, Chapada do Araripe, Ceará, Brazil, late Aptian-early Albian, A-E, skull; A, B, TUTg 1357, dorsal and right lateral views; C, D, E, AMNH 24454, skull with lower jaw and hyoids, right lateral, dorsal and ventral views. The *incisura columellae* is better shown in the Fig. 5C, the precolumellar fossa in the Fig. 5B. The quadratojugal arch and the anterior snout are broken in the Figs C and D but preserved in the Figs B and A. The Fig. B, without the lower jaw, better shows the flattening of the skull. *Hydromedusa tectifera* COPE, 1869, extant, Argentina-Uruguay, MNHN, AC, 1870-9, skull, dorsal view. G, *Pelusios castaneus* (SCHWEIGGER, 1812), extant, Congo, MNHN, H, 1887-0220, skull, dorsal view. H-K, *Teneremys lapparenti* BROIN, 1980, late Aptian, Gadoufaoua, Niger, MNHN, P, GDF 916, skull with lower jaw, right lateral, left lateral, dorsal and ventral views.

ar, parietosquamosal arch (arc pariéto-squamosal); at, atlas; boc, break in the basioccipital; bs, basisphenoid (basisphénoïde); c, *foramen posterius canalis carotici interni*; g, chelid groove or *sulcus chelidianus* (gouttière chélidienne); ico, *incisura columellae auris*; lj, lower jaw (mandibule); oc, occipital condyle (condyle occipital); pco, precolumellar fossa (fosse précolumellaire); ppo, paroccipital process of the opisthotic (processus paroccipital de l'opisthotique); pr, prootic (prootique); q, quadrate (carré) qj, quadratojugal; sq, squamosal; tr, *processus trochlearis pterygodeum.*.

Fig. 5: *Araripemys berretoi* PRICE, 1973, Chapada do Araripe, Ceará, Brazil, Aptien terminal-début de l'Albian, A-E, crâne; A, B, TUTg 1357, vues dorsale et latérale droite; C, D, E, AMNH 24454, crâne avec mandibule et hyoïde, vues latérale, dorsale et ventrale. La Fig. 5C montre mieux l'*incisura columellae* et la Fig. 5B la fosse précolumellaire. L'arc quadratojugal et le museau antérieur sont incomplets sur les Fig. C et D mais préservés sur les Fig. B et A. La Fig. B, sans mandibule, montre bien l'aplatissement du crâne. *Hydromedusa tectifera* COPE, 1869, actuel, Argentine-Uruguay, MNHN, AC, 1870-9, crâne, vue dorsale. G, *Pelusios castaneus* (SCHWEIGGER, 1812), actuel, Congo, MNHN, H, 1887-0220, crânel, vue dorsale. H-K, *Teneremys lapparenti* BROIN, 1980, Aptien terminal, Gadoufaoua, Niger, MNHN, P, GDF 916, crâne avec mandibule, vues latérales droite, gauche, dorsale et ventrale.
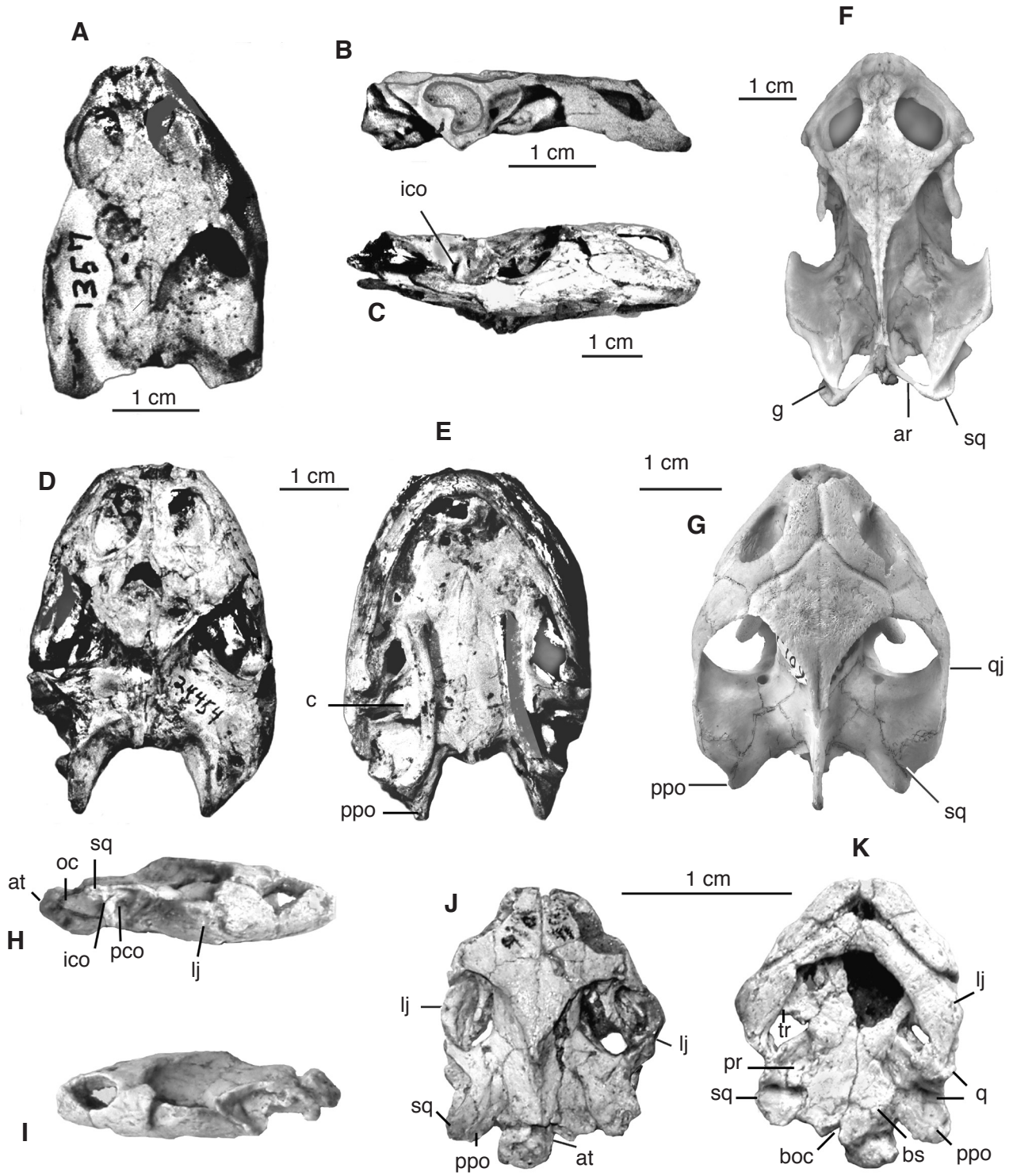
is protruding, the more the posterior inferior surface of the quadrate, squamosal and opisthotic is concave. The opisthotic process is well dorsally visible (Fig. 5, G).

In chelids, the paroccipital process is more reduced, more or less ventrally wide or/and rounded (Pl. II, C-E) and in any case dorsally covered by the prolonged squamosal, therefore dorsally hidden (Fig. 5, F) and it is well sutured to the skull as in other Pleurodira.

Relative proportions and surfaces: Ventrally, in *N. laticentralis* (Pl. I, C-E; Fig. 2, C; Fig. 4), the opisthotic surface is very slightly concave, with a slight elevation at the squamoso-quadrato-opisthotic suture laterally, doing just a slightly obtuse angle; it has a well rounded and wide opisthotic extremity not making a medial point but just slightly curved downward, few prominent. Ventro-posteriorly, the wide ventral exposition of the paroccipital process of the opisthotic, short exposition of the quadrate (behind the sulcus of the *columella* and of the Eustachian tube) and narrow lateral exposition of the squamosal are the more similar, in Pleurodira, to those of *Brasilemys* (LAPPARENT DE BROIN, 2000a: pl. 2, fig. 3; Fig. 3: quadrate-opisthotic ventral suture forgotten in the drawing), and more laterally developed than in *Teneremys*. This development of the flattened opisthotic process, forward and laterally, at the expense of the quadrate, with which it is well sutured (as well as with the squamosal), is derived in relation to *Proganochelys* and *Palaeochersis*. The ventral exposition of the squamosal is derived in relation to the Triassic forms but its short surface is primitive in relation to most of the Eupleurodira.

This widening of the process is also present in eupleurodires, although variably in proportion, and more in Pelomedusoides than in Chelidae. In *Brasilemys*, as in *N. laticentralis*, the posterior ventral part of the quadrate is particulalry medially shorter behind the *columella* than in other Pelomedusoides, phylogenetically more derived. But in *Brasilemys*, the opisthotic process extremity is more pointed, as in Podocnemidoidea and several species of Pelomedusidae, instead of slightly rounded as in several other species of Pelomedusidae (see BOUR, 2000) or well rounded as in *N. laticentralis*. The ventro-lateral surface of the slender *antrum*, few developed, is therefore narrower than the wide ventral surface of the opisthotic, posteriorly rounded as seen above, without the clear curve observed in Podocnemididae. Variable in proportion within the groups, the lateral development of the opisthotic process must have been independently acquired in *N. laticentralis* and Pelomedusoides. In Chelidae, the paroccipital process is flattened, its extremity is rounded or triangular and its superficy enlarges with the development of the chelid groove (see below, *sulcus chelidianus*).

In Cryptodira: The paroccipital process is reduced, as in Pleurodira; it may be ventrally as long as the squamosal in some forms (*Plesiochelys*, *Chisternon*, *Sternotherus*..: GAFFNEY, 1979a) as in the pleurodiran *Cearachelys*, but most Cryptodira have the squamosal varying from longer (*Chelydra*, Pl. II, A, as in some Bothremydidae and as in chelids, but without any chelid groove, see below) to much longer than the reduced opisthotic process, and eventually passing medially behind the paroccipital process as in some Bothremydidae (as seen above). The paroccipital process elongates more or less with the strong development of the squamosal extremity in Trionychidae and Carettochelyidae. There is a variable development of the squamosal, and different possibilities of modification of the paroccipital process in the two "infraorders" (Cryptodira and Pleurodira).

The flattening of the skull:
The posterior part of the skull is flattened in *Notoemys*. This can be estimated by the height at the *condylus mandibularis quadrati* level (the top slightly incomplete, with up to 2 mm more maximum) in relation to the length, from the quadrate (at the middle-upper anterior part of the *cavum* or *meatus quadrati*, slightly incomplete but easy to reconstruct with up to 2 or 3 mm more maximum) up to the posterior opisthotic extremity: the approximative ratio was ca 73, which enters in the approximate ratio of *Araripemys* as well as other Pleurodira including the Pelomedusidae, all of them only more or less moderately posteriorly elongated and moderately anteriorly elongated and flattened (Tab. 1).

In Pleurodira: Among Pleurodira, after *N. laticentralis*, the older known skull is from the pelomedusid *Teneremys lapparenti* (Fig. 5, H-K), up to now the earliest derived lineage in relation to *Araripemys* (see LAPPARENT DE BROIN, 2000a). It is a form with a flattened back skull as in *N. laticentralis* and *Araripemys*. Its shell is similar to that of *Pelomedusa* by the plastron; the dorsal part is more primitive by the not anteriorly expanded border (anterior peripherals and nuchal) and the first neural hexagonal with short sides behind. However, *T. lapparenti* has at least some cervical vertebrae with postzygapophyses united in a collerette, as in *Araripemys* and in some *Podocnemis*, and its skull is more specialized than that of the extant members of the family by the marked posterior emargination: this is present as in the extant pelomedusids but stronger, here prolonged up to meet the lateral emargination; the basisphenoid is latero-posteriorly elongated around the basioccipital up to meet the posterior process of the opisthotic and the exoccipital, hiding the *vestibulum*, the *processus interfenestralis* and the *recessus scalae tympani*, but only medio-posteriorly closing the *fenestra postotica*. With *Teneremys*, *Araripemys* was already present at Gadoufaoua (BROIN, 1980) (although without preserved skull) as shown by the typical ornamented plates with pits, flattened and much elongated procoelous cervical vertebrae with linked postzygapophyses in collerette, longer and more flattened than those of *Teneremys*. The oldest skull of this genus is that from the slightly more recent *A. barretoi* (Chapada do Araripe, Brasil), as seen above. We notice that the

posterior elongation of the squamosal of *N. laticentralis* and *Teneremys* is moderate beyond the occipital condyle and the air cavity had to be relatively short. In *Araripemys* there is a posterior elongation together of the squamosal with the air cavity, the most posterior opisthotic process (the paroccipital process) and the exoccipitals, the skull seeming therefore relatively more elongated in dorsal and complete lateral view (MEYLAN 1996) (Fig. 5, D, C) than in *N. laticentralis* and *Teneremys*. From the same locality as the first skull of *Araripemys*, from Brasil, and from the late-early Cretaceous (late Albian-early Cenomanian boundary) from Morocco, forms known by their skull belong to two diversified lines of Podocnemidoidea : *Cearachelys* (Brasil) and *Galianemys* (Morocco) (bothremydids), and *Brasilemys* (Brasil) and *Hamadachelys* TONG & BUFFETAUT, 1996 (Morocco) (pre-podocnemidids). Although more recent, their skull is moderately posteriorly flattened and a little less flattened as a whole than in *N. laticentralis*, *Araripemys* and *Teneremys*. Their skull is approximately high as in the extant chelid *Emydura* wich has the less flattened extant chelid skull and which belongs to the most primitive lineage of chelids from Australia, while in *N. laticentralis*, *Araripemys* and *Teneremys*, the flattening is closer to that of the derived chelid groups of *Phrynops*, *Hydromedusa* and *Chelodina* (Tab. 1). This flattening, variable in proportions, has clearly independently developed in each line.

In Chelidae, the oldest known skull is that of *Yaminuechelys* DE LA FUENTE *et al.,* 2001, Upper Cretaceous of Argentina, but it is a member of one of the more derived line in chelids by the amount of modifications, the *Hydromedusa* lineage (Fig. 5, F), and it is already very flattened and elongated (anteriorly and posteriorly). Other extant South-American groups were also present in Patagonia during the Cretaceous, known by fragments of carapaces and neck vertebrae as soon as the lower Albian (BROIN & DE LA FUENTE, 1993 ; LAPPARENT DE BROIN & DE LA FUENTE, 2001 ; LAPPARENT DE BROIN *et al.,* 1997), including members of the *Phrynops* group (extant *Phrynops* s.l. and *Acanthochelys*) such as *Prochelidella argentinae* and *Palaeophrynops patagonicus* LAPPARENT DE BROIN & DE LA FUENTE, 2001 : the extant representatives of the group have a less posteriorly flattened skull than in *Hydromedusa* (more or less according to the genera) but more or less than in *N. laticentralis* (Tab. 1) and always with a chelid groove (see below) unlike the Pelomedusoides and *N. laticentralis*. Finally, *Chelus*, the extant representative of the *Chelus* group, has (see above) a particularly flat much modified skull together shortened, because strongly widened, and flattened and with a well transversally positioned *antrum* and an elongated occipital condyle ; the relative length of the extremity of the squamosal is therefore modified, although this one is longer than the opisthotic as in other chelids.

The flattening of the skull, which appears as well in chelids as in Pelomedusoides in various diversified lineages, is therefore homoplastic and, as shown by other characters (see below), *N. laticentralis* is not engaged in one of these eupleurodiran lineages, although its *antrum* has the development of that of the primitive Pelomedusoides and less derived than that of the Chelidae. Actually, as soon as their apparition, the first Pelomedusoides s.l. show various derived forms with a flattening of the skull, by comparison with posteriorly emerged podocnemidoid lines (stratigraphically and in a phylogenetic point of view) which retain a higher skull or sometimes elevate it by a secondary roofing. Although older and primitive by many characters, *N. laticentralis* was also early derived on that point. All the body is flattened : the flattening of the skull seems in relation with the flattened carapace in *N. laticentralis* as well as in *Araripemys*, *Teneremys, Yaminuechelys, Hydromedusa* and other pleurodires. However, some littoral cryptodires, such as the late Jurassic Eurysternidae, present a flattened shell with a domed roofed skull.

Lateral and posterior emarginations, dorsal roof, depressor mandibulae area, presence or absence of a chelid groove (sulcus chelidianus) :

It is not possible to estimate the degree of lateral and posterior emarginations in *N. laticentralis*, but a minimum of lateral emargination was possible as in *Platychelys*, *Araripemys*, Pelomedusoides s.s. and in the ancestor of chelids, before the progression backward of the lateral emargination known in the family. The posterior emargination of *N. laticentralis* seems to have been constituted as in *Platychelys* and the primitive Pelomedusoides s.l., surely not as in the Chelidae. There was a posterior emargination of the parietal of *N. laticentralis*, at least weak as in Chelidae and probably as in *Platychelys* and as in the most primitive Pelomedusoides. The ventral posterior surface for the *depressor mandibulae* attachment is gently concave and weakly longitudinally crested at the squamosal-paroccipital process of the opisthotic suture. Not any chelid groove is present.

In Chelidae : The lateral emargination is much pronounced, nearly up to the back or up to it. There is a weak posterior emargination of the parietals on each side of the supraoccipital (except in *Pseudemydura*, secondarily dorsally completely covered backward), more or less developed according to the taxa (Figs in BOULENGER, 1889 ; GAFFNEY, 1977, 1979a ; WERMUTH & MERTENS, 1961). Chelids keep the squamoso-parietal contact in front of this emargination, except *Chelodina* where the lateral emargination is prolonged up to the back. In most extant chelids (*Emydura, Acanthochelys, Platemys, Chelus, Chelodina*), a part of the primitive complete dorsal roof remains posteriorly present : the latero-dorsal border of the *antrum*, constituted by the lateral squamosal roof, is flat (more or less narrow) ; this flat roof part is followed in an acute angle by the medial

flat and narrow squamosal roof part, going forward to contact the parietal (except in *Chelodina* where this squamoso-parietal arch is broken). In some other extant forms, where the anterior roof emargination is more laterally developed (*Phrynops* s.l. and *Hydromedusa*), this latero-dorsal border of the *antrum* is very thinned, doing a very acute angle at the contact with the chelid groove situated below (Fig. 5, F); the only flat roof part remains the medial squamosal roof part (Fig. 5, F, ar). In these two forms, the squamoso-parietal arch is particularly posteriorly prolonged beyond the supraoccipital extremity and the posterior roof emargination is minimal. While in others (*Emydura, Acanthochelys, Platemys, Chelus*) the posterior emargination is more or less marked in front of the supraoccipital extremity, and up to link the lateral emargination in *Chelodina*. In this last case, the lateral emargination has linked the posterior emargination, but in the precedent, it is not much extended postero-laterally so that the flat squamosal roof part, between the posterior extremity of the *antrum* and the *cavum tympani*, remains present. This different, not homologous, process of development of the anterior emargination in *Chelodina* is one of the anatomical arguments to phylogenetically separate the *Chelodina* group from the *Hydromedusa* group, partly strengthening the hypothesis of GEORGES *et al.,* 1999. The lateral emargination being much prolonged backward in chelids, the quadratojugal is absent. As a result, the latero-posterior dorsal borders of the skull do not bear any more mark, antero-superiorly to the *cavum tympani*, of the suture of a quadratojugal elevating to meet the postorbitary and the jugal. Instead, the anterior and upper border of the quadrate on the *cavum tympani* is free, thin and acute (Fig. 5, F). Behind, the *antrum* border bears the flat or acute remaining lateral part of the squamosal and it is medially followed (except in *Chelodina* where the contact is broken) by the squamosal medial part going forward to contact the parietal medially. Dorsally, the latero-posterior extremity of the paroccipital process is hidden by the prolonged *antrum* and squamoso-parietal arch. In chelids, the squamosal elongates behind the posterior border of the posterior opisthotic process or paroccipital process; it elongates with the *antrum postoticum*, and its posterior extremity is developed beyond the *condylus occipitalis* in all forms except in the much modified skull of *Chelus* which has a not much posteriorly elongated squamosal and *antrum*, laterally developed instead (see above) and an elongated occipital condyle base. The squamosal becomes particularly developed backward in *Phrynops* s.l. (i.e. *Acanthochelys* and *Platemys* not included; all the sub-divisions of MCCORD *et al.,* 2001, included) and overall in the *Hydromedusa* lineage, accompanying a posterior elongation of the squamoso-parietal arch. In all chelids, the lateral squamosal surface does a typical chelid groove (Pl. II, E, F; Fig. 5, F): it is an oblique deep sulcus downward directed laterally and below the *antrum*, from the posterior dorsal squamosal extremity up to the lateral border of the *cavum tympani,* at the *incisura columellae auris*, that we name *sulcus chelidianus*. This groove is well delimited in relation to the corresponding part in other turtles including the Pelomedusoides s.l. In all turtles, this area supports the *depressor mandibulae* muscle (SCHUMACHER, 1973, in GAFFNEY, 1979a). The chelid groove is constituted by the quadrate (anteriorly-ventrally) and the ventrally expanded and posteriorly elongated squamosal passing beyond the opisthotic posterior process, laterally up to dorsomedially (*Hydromedusa*) to this process. The squamosal crest medially bording the groove is well marked (Pl. II, E, F) and not in the same place as the crest for the *depressor mandibulae* in Pelomedusoides (Pl. II, I, J) because it abruptly limits the medial flatter surface of the shorter paroccipital process, the lateral limit of which is protruding, and it is prolonged posteriorly to the latter. Ventrally, the crest becomes particularly more protruding and vertical in *Hydromedusa*, medially supporting the ventrally expanded surface of the opisthotic. The chelid groove is weakened in *Platemys* because of the particular inflation of the *antrum postoticum*, not only dorsomedially (and more than in *Acanthochelys*) but also latero-inferiorly (Pl. II, C, D) (unlike *Acanthochelys*): however, it remains perceptible.

In Pelomedusoides: The lateral emargination is few developed, variable and extended up to the height of the top of the *meatus quadratri*, except in *Teneremys*: the complete primitive dorsal roof is more preserved, at least anteriorly, and the lateral emargination is limited to the lateral wall part of the skull. The posterior emargination is generally more accentuated than the lateral. It is most prolonged in Pelomedusidae and, within them and alone in Pelomedusoides, *Teneremys* has a very prolonged posterior emargination up to link the lateral one (Fig. 5, H-K). In some podocnemidoid forms, the skull is roofed laterally (Bothremydidae, *Erymnochelys* and *Peltocephalus*), secondarily and independently because of the variable construction of the cheek (LAPPARENT DE BROIN & WERNER, 1998) and/or it is more or less roofed posteriorly (Podocnemididae *Erymnochelys*, *Dacquemys* and *Peltocephalus*), secondarily because of the exclusion of the postorbitary from the posterior roofing by a quadratojugal-parietal contact. Except in the erymnochelyine *Dacquemys* (secondarily much porsteriorly roofed by analogy with the Australian *Pseudemydura* and without posterior elevation), the posterior emargination of Pelomedusoides is at least sufficient to break the contact squamosal-parietal and there is no more lateral or/and posterior roof part of squamosal between the parietal and the *antrum* border, unlike chelids, even with *Chelodina*. In Pelomedusoides, the squamosal is shorter than the opisthotic process, as seen above and there is no chelid groove. Above the anterior part of the *cavum cranii*, the quadratojugal advances and elevates to link the jugal and postorbitary (Fig. 5, A, B and G) except in *Teneremys* (Fig. 5, H to J).

As in many cryptodiran turtles, there is a kind of wide groove between the exoccipital-opisthotic limit and the lateral border of the squamosal, where the *depressor mandibulae* is inserted inside. This groove is different in Pelomedusoides from that of Chelidae because it medially includes the opisthotic ventral surface. It is more or less weakly concave, according to the taxa and it remains longer than the squamosal. There is a crest (apparently supporting the muscle insertion) situated within the surface of the groove (Pl. II, I, J) and not at its medial border. It is marked in the middle of the squamosal ventral surface, either all along the surface or just at the border, either weakly in most forms or strongly (Aff. *Roxochelys vilavilensis*: see BROIN, 1991; *Dacquemys*: see the figure of DACQUÉ, 1912 in GAFFNEY, 1979a, better than the figures in GAFFNEY, DEBLIEUX *et al.*, 2002), with individual variations according to the age of the specimen. There is eventually a transversal angle or a slight elevation at the quadrato-squamosal suture (*Galianemys* group, GAFFNEY, TONG & MEYLAN, 2002; MNHN coll.).

In *N. laticentralis* (Pl. I, E; Fig. 2, E): The chelid structures are not present: chelid groove, prolonged squamosal arch beyond the paroccipital opisthotic process and thinned *antrum* dorsal roof part lack. As seen above, the *antrum postoticum*, although posteriorly developed in length, does not pass the posterior opisthotic process. Dorsally, this process is well visible, rounded at its extremity (right better preserved side) as seen above. A small part of squamosal is dorsally preserved, laterally in front of the opisthotic, with a thin lateral border without any mark of a possible broken arch to contact the parietal and without chelid groove below. Then, still in front on the right, the quadrate is laterally broken before the suture for the quadratojugal. But the absence of remains of squamosal dorsal roofing, latero-ventral groove and prolonged squamosal beyond the postotic posterior process are parts of the basic morphology of the Pelomedusoides. They are sufficient to allow us to deduce that *N. laticentralis* had a posterior emargination of the Pelomedusoides type. It may be acquired independently in the two taxa but it is opposite to the derived chelid condition. Such a posterior emargination of the Pelomedusoides type is also found in *Platychelys*, as observed in the photograph of the new recently found skeleton (KARL & TICHY, in press).

In Cryptodira: Lateral and posterior skull emarginations also independently develop in Cryptodira, variable in height (laterally) and progression forward (posteriorly) and in limiting bones according to the taxa (see Figs in GAFFNEY, 1979a) so that they are not homologous in all the taxa. The squamosal posterior ventral surface may be depressed. The ventral muscular crest may be present, or a small protuberance (various Testudinidae, *Carettochelys*, etc.), variably situated, according to the taxa (taxonomic value) at the limit of the quadrate, squamosal and opisthotic or between two of them or at the posterior ventral squamosal extremity. In modern Cheloniidae,

the crest is squamosal, longitudinal and strong, typically delimiting two parallel grooves in the squamosal surface, for two heads of the powerful *depressor mandibulae*. *Hyoid*: In turtles, the anterior, lateral and larger hyoid horn runs below the medial part of this area (Fig. 5, E).

The area of the cavum tympani, antrum postoticum, incisura columellae auris and precolumellar fossa :

N. laticentralis has a small *cavum tympani*, infero-posteriorly open by a thin *incisura columellae auris*, downwards directed, and no precolumellar fossa (*fossa precolumellaris*) is present.

Although already rolled up, the *cavum tympani* of *N. laticentralis*, slightly anteriory incomplete, is however primitively short (Pl. I, F; Fig. 2, F), anteriorly as ventrally. The *cavum* is well open, postero-inferiorly, in a moderately wide split, a rather thin *incisura columellae auris* for the passage of the *columella*, dorsally, and of the Eustachian tube, ventrally-posteriorly (see above). The *incisura* is nearly equally wide from the center of the *cavum* up to its extremity, as in *Brasilemys*, contrarily to other forms where it widens toward the posterior extremity (particularly in Cryptodira). In front of the *incisura*, all the surface of the *cavum tympani* is slightly depressed which does not correspond to a delimited precolumellar fossa, as present in Pelomedusoides and chelids.

The incisura columellae auris in Pleurodira : As seen in the introduction, the *incisura columellae auris* is open in all the primitive members of each branch of Pelomedusoides s.l. and in primitive chelids (ontogenetic and homoplastic development of the closure in both groups) (LAPPARENT DE BROIN & MOLNAR, 2001; LAPPARENT DE BROIN 2000a; GAFFNEY et al., 2001), being more or less inferiorly inclined but rather moderately wide. Sometimes, it is crushed or partly damaged in fossils. In *Araripemys*, the *incisura* is not well visible in the photographs of the two observed specimens, TUT 1907 and TUT 1357 (Fig. 5B), better exposed in another one, AMNH, 24454 (Fig. 5, C). From this specimen and the specimen AMNH 24453, it is represented as open and thin by MEYLAN (1996) and downwards directed, as in *N. laticentralis*. In *Teneremys*, the *incisura* is more posteriorly directed (Fig. 5, H; inferior border of the *incisura* lacking on the left side, Fig. 5, I). In Podocnemidoids, after the more primitive open state represented in *Brasilemys*, the *incisura* is closed behind the *columella* and the Eustachian tube, as in modern Pelomedusidae and modern Chelidae, with various shapes according to the taxa or groups of taxa and various degrees of closure (simple junction of the two quadrate borders, to a still visible suture and up to a solid suture). In Pelomedusidae, the *incisura* is more posteriorly directed, while in podocnemidoids and most chelids it is more downwards directed. *Cearachelys*, the oldest described bothremydid skull (Upper Aptian, Albian boundary) has an open and dilated *incisura*, including the Eustachian tube as in Podocnemididae, and

the two borders of the rolled quadrate are approximated behind but not united, unlike Podocnemididae. In bothremydids, stratigraphically later, as soon as Albian-Cenomanian boundary, a *commissura* closes the *incisura* between the *columella* foramen and the Eustachian tube groove; the quadrate borders may also approximate (one side of a *Galianemys* specimen from Morocco, MNHN MRS 3106) or, even, join behind this Eustachian groove (another specimen of the *Galianemys* group, MNHN MRS 3105). The bothremydid *commissura* is more or less short in these specimens of *Galianemys* and in the specimen *affinis* of *Galianemys* from Erfoud area, figured in LAPPARENT DE BROIN & WERNER, 1998, and particularly short in the Oman Miocene form. The closure may be not complete and a slit may remain between the foramen and the Eustachian tube groove, although the junction place is already elongated, as in *Polysternon provinciale* (crushed posterior dorsal part of the quadrate applied to the *cavum*) and *Foxemys mechinorum* (BUFFETAUT *et al.*, 1996; GAFFNEY & TONG, 2000; TONG *et al.*, 1998) (a *Polysternon* for us: anyway both species are sister-taxa), both from the Upper Cretaceous of Europe and essentially similar by their shell morphology. All the other bothremydids have a long sutured *commissura quadrati* between the *foramen columellae auris* and the Eustachian tube groove, in a well rounded *cavum tympani*.

The precolumellar fossa in Pleurodira: In *N. laticentralis*, the anterior border of the *cavum tympani* is broken but the preserved part, shortly and flatly directed transversally in front of the *incisura*, is sufficient to indicate that there was no precolumellar fossa.

A precolumellar fossa is variably present in turtles (see below) and variably shaped, deep and large. In Pleurodira, it is constituted by an ovoid depression, well delimited in front of the *incisura*, ventrally in the *cavum tympani*. It is more or less open, large and deep. Its presence or absence is characteristic of the taxa, but at different levels: either at the group level (family, subfamily), or genus or species, with few individual variations within a given taxon (for example in *Podocnemis expansa*: present or absent). We do not know its significance; it is not dependent of the strength of the *antrum*.

The absence of precolumellar fossa in *N. laticentralis* is a primitive character as shown by comparison with the Triassic taxa. In more derived pleurodires, it may be absent by regression or primitively. When present, it is variably shaped and large, characteristic of taxa at different levels and with occasionnal individual variations.

In Bothremydidae, the precolumellar fossa is absent except in *Kurmademys*. A weak, small and rounded depression is present in the three specimens of the *Galianemys* group of the MNHN collection, below the crested *commissura* and the rounded columellar foramen.

In Pelomedusidae, it is present in *Teneremys* (Fig. 5 H, MNHN GDF 916, new prepared skull in relation to LAPPARENT DE BROIN, 2000) and strong in *Pelomedusa* and *Pelusios*. It is present in all the preserved skulls of

fossil pre-Podocnemididae and Podocnemididae (as soon as *Araripemys*, *Brasilemys* and *Hamadachelys*) and in the extant forms, more or less important, and being weak to absent in *Podocnemis expansa*.

In Chelidae, it is more or less important, but very weak to nearly absent in *Chelus* and absent in *Phrynops* s.l., except: hardly esquissed in one observed *P. tuberculatus*, differently esquissed by a weak wide concavity anterior to all the *incisura* in the holotype skull of *P. rufipes* and by a weak small concavity anterior to the upper part of the *incisura* in one *P. gibbus* specimen but not in two other observed specimens. It is well present in *Acanthochelys radiolata* and *A. pallidipectoris* (the other species of the genus having not being observed) and *Platemys*; it is also present in *Pseudemydura* and the *Emydura*, *Hydromedusa* and *Chelodina* groups. We can therefore suppose that the absence in chelids is secondary (ontogenetic undevelopment in the embryo) as in *Podocnemis expansa*. Anyhow, its presence cannot be employed to qualify the Chelidae or the Pelomedusoides (or subgroups in the latter) as a whole in a cladisic analysis.

The precolumellar fossa in Cryptodira: In observed Cryptodira, a precolumellar fossa is possibly present only in *Sinemys gamera* BRINKMAN & PENG, 1993b (Fig. 10: a drawing), but it is not anteriorly well delimited. In cryptodiran taxa, either those having a closed *incisura columellae auris* or those with an open *incisura*, it may happen a depression area in front of the posterior border of the quadrate posteriorly supporting the Eustachian tube groove: it is a concavity which is part of the deepening of the tympanic wall of the quadrate, more (*Centrochelys, Astrochelys*) or less (freshwater Testudinidae and Emydidae) pronounced around the foramen of the *columella*; it is situated, with the entrance of the *antrum*, in a more depressed area in relation to the anterior part of the *cavum tympani*, gently inclined; it is separated (or not) from the *antrum* entrance by a more (*Centrochelys*) or less (*Astrochelys*, freshwater Testudinidae and Emydidae) strong transversal crest beginning at the *foramen columellae auris* and forwards. In other cases, the *cavum* surface gently depresses from the anterior border of the *cavum* toward the foramen of the *columella* and there is only a depression below the foramen of the *columella* in front of the widely open *incisura* (*Kinosternon, Ordosemys*, Chelydridae, *Platysternon*) varying from small (*Chelydra, Platysternon*) to wide (*Macroclemmys*, inedite *Chelydropsis* specimen from the Miocene of Tavers, France): this depression is not as well delimited and with an ovoid shape as the precolumellar fossa in Pleurodira, such as in extant Pelomedusidae and Podocnemididae. The fossa in *Sinemys* (specimen not observed by us) possibly belongs to this kind of depression, limited to the ventral anterior part of the *cavum*. The character of the precolumellar fossa is difficult to define in a cladistic analysis mixing Cryptodira

and Cryptodira, because of the frequent dissimilarity in shape and development of the depression within groups.

The trochlear process and the dorsal foramen stapedio-temporale position :

N. laticentralis logically had a pleurodiran pterygoid trochlear process but it is not preserved. The *foramen stapedio-temporale* is relatively posterior compared with other Pleurodira.

The pterygoids are not preserved, therefore the pleurodiran pterygoid trochlear process for the mandibular muscles is not present, contrarily to MEYLAN's 1996 data in the matrix of characters. But if not preserved, it can be considered that it was present. There is no trochlear process on the otic part of the skull, as present in Cryptodira. However, the muscles might have gone to the coronoid process by this way as in primitive turtles even when a trochlear process with a *cartilago transiliens* is not yet well defined on the external surface of the prootic chamber. But the forward much inclined surface of the quadrate and prootic, in this area, from the back at the *foramen stapediotemporale* level (which is dorsally positioned at the transversal of the rear of the *columella auris*) to forward (Fig. 2, E, F) is exactly similar to that of the flattened Pleurodiran skulls. This inclination of the anterior inner ear surface is linked to the flattening of the skull, as in chelids such as *Acanthochelys*, *Chelodina*, *Hydromedusa*, *Yaminuechelys* and *Chelus*. What we know of the pleurodiran lateral retraction of the neck (see below the opisthocoelous vertebrae 2 to 4 as in chelids) implicates the presence of trochlear processes as in Pleurodira.

The primitiveness of the posterior position of the *foramen stapedio-temporale* is corroborated by its posterior position in the primitive Triassic *Proganochelys* and its evolution in Cryptodira and Pleurodira. In *Proganochelys*, the foramen is posterior, situated between the quadrate and the opisthotic (GAFFNEY, 1990) and the prootic is relatively narrow, medially situated beside the quadrate. The prootic is dorsally undescribed in *Australochelys*, *Palaeochersis*, primitive Cryptodira such as *Kayentachelys* (earky Jurassic of North America), *Glytops* (late Jurassic of North America) and *Dorsetochelys* (early Cretaceous from England) (see GAFFNEY, 1979b).

In known Cryptodira, with the closure of the cranio-quadrate passage, the foramen becomes firstly situated between the opisthotic and the prootic, for example in *Trinitichelys* (early Cretaceous from North America, see GAFFNEY, 1972b, 1979b) and *Mesochelys* EVANS & KEMP, 1975 (early Cretaceous from England). The prootic either tends to anteriorly and/or posteriorly widen or to narrow, particularly anteriorly and eventually all along, up to be concealed by the quadrate (some Testudininei ; Shachemydinae in LAPPARENT DE BROIN, 2004). The foramen tends to migrate from the back of the prootic at the suture with the opisthotic to its lateral part at the prootic-parietal suture and then anteriorly on the same lateral border, except in some Baenidae where it may migrate medially towards the parietal (GAFFNEY, 1972b).

In Pleurodira, *N. laticentralis* presents the older known skull : the prootic is moderately wide and the foramen is already lateral and not posterior on the prootic border or between the quadrate and the opisthotic. It is already advanced at a time it is still posterior in Jurassic Crytodira of Asia (SUKHANOV, 2000). The prootic remains moderately wide in Pleurodira or it is sometimes a little narrowed ; but the *foramen stapedio-temporale* tends to progress forward between the quadrate and the prootic as in Cryptodira. The position of the *foramen stapediotemporale* in *Notoemys*, relatively posterior, is rather primitive by comparison with all the other pleurodires and particularly with the primitive *Teneremys*, *Brasilemys* and *Araripemys*. In *N. laticentralis*, the *foramen nervi trigemini* is therefore primitively well anterior to the *foramen stapedio-temporale* (Fig. 2, A, F) and in a lower position. The outline of the *foramen nervi trigemini* is not completely preserved because the skull is slightly distorted in the area of the anterior *cavum cranii* opening. The tendency to the antero-medial progression of the foramen is more marked in Pleurodira than in Cryptodira and is particularly more achieved in *Shweboemys* and Bothremydidae in Pleurodira. Here also, *N. laticentralis* has the most primitive known condition in Pleurodira but not in relation to Cryptodira.

The closure of the cranio-quadrate passage and of the fenestra postotica, the posterior carotid foramen :

In *Notoemys laticentralis*, the cranio-quadrate passage is only closed by a ventral expansion of the prootic, exceptionally widened up to the *area articularis quadrati*, and not by a medial expansion of the quadrate (anterior or posterior to the prootic, or covering it) or a posterior extension of the pterygoid, and the ventral opening of the canal of the stapedio-temporal artery is not covered. The *fenestra postotica* is widely open laterally and posteriorly : the *vestibulum* is ventrally incompletely hidden ; the ventral border of the *processus interfenestralis opisthotici* is nearly completely free ; the posterior exoccipital process is not enough developed to close the *recessus scalae tympani* behind the *processus interfenestralis*, no other posterior opisthotic process is either developed, and the *foramen jugulare posterius* is not constituted. The medial border of the *columella* is thick. The carotid runs much obliquely on the ventral prootic surface and enters into the basisphenoid close to the antero-medial angle of the prootic and the postero-medial angle of the pterygoid.

In *N. laticentralis*, posteriorly to the pterygoid, the cranio-quadrate passage is ventrally closed by a ventral expansion of the prootic, between the basisphenoid and the quadrate (Fig. 2, C, D ; Fig. 4 ; Pl. I, C, D), as basically in pleurodiran forms except Podocnemidoidea, although it is more extended latero-ventraly in *N. laticentralis* :

most primitive chelids (*Pseudemydura*; *Emydura,* Pl. II, E), most primitive Pelomedusoides s.l. (*Araripemys*, MEYLAN, 1996; *Teneremys,* Fig. 5, K; some specimens of *Pelomedusa*). The closure makes possible the existence of a *canalis cavernosus* (principally between the quadrate, dorsolaterally, and the prootic, ventrally), where principally runs the lateral head vein (the *vena capitis lateralis*) and which is anteriorly followed by the *sulcus cavernosus* upon the pterygoid-basisphenoid limit (see GAFFNEY, 1979a). The base of the articular process of the quadrate does not send a medial expansion, even short, to contribute to the cranio-quadrate passage closure, in addition to the prootic.

The prootic and the quadrate and basiphenoid extensions: In Triassic forms, i.e. *Proganochelys* and *Palaeochersis*, the prootic is primarily exposed beside and "below" (in ventral view, but anatomically above) the basisphenoid, and much "below" (above) the pterygoid extension toward the quadrate. The prootic covers the inner ear with the help of an opisthotic anterior process fused to it. In *Kayentachelys*, the condition is unclear and the original drawing is not understandable in view of the observation of photographs of the skull of *Kayentachelys* made by one of us (M. de la F.) in New-York. It is difficult to recognize the structures of this area principally because of the texture of the fossil, very dark and full of cracks, as confirmed by W. JOYCE (pers. comm.). Laterally in *Kayentachelys*, the medium ear looks open because of the open cranio-quadrate passage medially to the quadrate articulation, and there is no evident *canalis cavernosus* between the basicranium and the quadrate, the pterygoid being not elongated behind as in the true Cryptodira: in Cryptodira posterior to *Kayentachelys* in the diversification scheme (Selmacryptodira of GAFFNEY *et al.*, 1987), the pterygoid extends between the quadrate and the basisphenoid-basioccipital to close the cranio-quadrate passage ventrally. But in *Kayentachelys,* according to the original figure, the prootic ought to be lowered (in anatomical sense) in relation to the Triassic forms, so that to be at least medially at the level of the basisphenoid ventral surface: perhaps the prootic is not lowered, as in *Palaeochersis*.

In Pleurodira, besides in *N. laticentralis*, the prootic is completely lowered medially and laterally between the quadrate and the basisphenoid in primitive forms of Pelomedusoides (as seen above). In pleurodires other than *N. laticentralis*, the quadrate is developed, at the expanse of the prootic, postero-medially to the articular process. Moreover, in modern Pelomedusidae and Chelidae (Pl. II, D to J) other than the primitive forms (above cited), the quadrate tends also to cover the prootic anteriorly, sending an arm which separates the pterygoid and the prootic and links the basisphenoid; but instead of the quadrate, the basisphenoid may laterally extends anteriorly to the prootic towards and up to the quadrate; or both bones extend an arm to join at mid width. In Podocnemidoidea, the quadrate posteriorly covers the prootic, sending an arm toward the basisphenoid and the basioccipital posteriorly to the prootic. In Podocnemididae and some Bothremydidae, the prootic is most of times not lowered at the ventral level of the basisphenoid and basioccipital as it is in the other pleurodires. Indeed, in Podocnemidoidea, with the development of the podocnemidoid fossa (LAPPARENT DE BROIN, 2000, corresponding in Podocnemididae to the enlarged "carotid" or pterygoideus channel of GAFFNEY, 1979a), either the prootic is completely progressively covered by the quadrate or the pterygoid (more or less complete ventral reduction in Bothremydidae) or it is present but concealed in the fossa of the enlarged carotid canal in Podocnemididae: the prootic ventral surface is hollowed and often much reduced ventrally and anyway ventrally out of sight, hidden by the developed pterygoid wings, extended anatomically below the fossa (above in ventral view). In *N. laticentralis*, instead of the quadrate, the lateral expansion of the prootic is particularly developed, descending along the medial border of the *processus articularis quadrati* nearly up to the *area articularis* (well evident on the right side, Pl. I, C; Fig. 2, C, D; Fig. 5). This is an autapomorphy of *N. laticentralis*, up to now.

The inner carotid entrance (foramen basisphenoidale or posterior foramen canalis carotici interni): In *N. laticentralis*, the inner carotid enters the basisphenoid, close to the junction of the pterygoid, basisphenoid and prootic, possibly as in *Palaeochersis*. But in the latter the prootic is differently positioned, not lowered at the level of the basisphenoid surface, and the foramina, concealed in ventral view, are difficult to precisely situate in the angle, where they have to be because both carotid foramens are not visible in the ventral basisphenoid surface, toward the medial line and far from the prootic border, as they do (primitively in our opinion) in *Proganochelys* (see GAFFNEY, 1990), *Kayentachelys* (fide GAFFNEY *et al.*, 1987) and some Mesozoic Cryptodira such as *Anemys* SUKHANOV & NARMANDAKH, 2006 (SUKHANOV, 2000), *Dracochelys* GAFFNEY & YE, 1992 and *Ordosemys* BRINKMAN & PENG, 1993a. In the Eupleurodira, the carotid enters the basisphenoid into its latero-anterior corner or close to it, and close to the prootic in the more primitive state in Pelomedusoides: it is visible in ventral view in *Brasilemys* and *Hamadachelys* at the medial border in the small podocnemoid depression or fossa. The carotid also enters into the basisphenoid close to the peterygoid or at the limit basisphenoid-pterygoid in rare Bothremydidae (*Kurmademys*) and in Podocnemididae but is is concealed in the fossa podocnemidoidea by the pterygoid podocnemidid wing. In *Araripemys*, seemingly *Teneremys*, extant Pelomedusidae and Chelidae (Fig. 5 K; Pl. II, B to J) with a well ventral prootic exposure, the carotid enters the inner skull either at the suture prootic-basisphenoid or either close to the quadrate or close to the

basisphenoid (possibly differently in both sides, Pl. II, G), by the migration of the foramen in the bone surface and, depending on the posterior extension of the pterygoid or the lateral expansion of the basisphenoid producing the reduction of the ventral prootic exposure; there are various points of bone junction with the foramen: prootic - basiphenoid; prootic - quadrate; basisphenoid - prootic - pterygoid; or basisphenoid - prootic - quadrate. The position is also much variable in Bothremydidae depending on the posterior extension of the pterygoid and reduction of the prootic exposure: at the sutures basisphenoid - pterygoid (most often, and the primitive *Cearachelys* included); prootic - pterygoid; basisphenoid - quadrate - pterygoid; or quadrate - pterygoid.

In *N. laticentralis*, before entering in the skull in the basishenoid (Fig. 2, C and D, c; Fig. 4B; Pl. I, C and D) close to the prootic, the carotid lets its mark in the prootic ventral surface as an oblique sulcus coming from latero-posteriorly, above the *foramen posterior canalis cavernosi*. A similar sulcus is seen in Pelomedusidae (Pl. II, I) and Chelidae (Pl. II, C) which always have a ventral prootic exposure, but the sulcus is more longitudinal, the prootic not being laterally expanded toward the quadrate as it is in *N. laticentralis*. The foramen for the carotid is small in relation to modern Pelomedusidae and Chelidae. In the sulcus, at the basisphenoid-prootic boundary on the right side, there is a minute foramen (well visible Fig. 4B, and Pl. I, C) probably for a branch of the facial nerve, according to GAFFNEY (1979a). There is no "Chelyd foramen" of MC DOWELL or *foramen retropterygoideum* for a vein and /or a possible artery in the posterior border of the pterygoid, as present in chelids according to BOUR & PAULER (1987), foramen seeming present also in Pelomedusidae (Pl. II, G).

In Cryptodira: The carotid also primitively enters the basisphenoid at ventral view, but medially and far from the border of the bone as in *Proganochelys*, as seen above. The closure of the canal for the inner carotid is variably leaded (see examples in BRINKMAN & PENG, 1993b; GAFFNEY, 1979a, 1983, 1990; GAFFNEY & YE, 1992; LAPPARENT DE BROIN, 2004; SUKHANOV, 2000; TONG *et al.,* 2004). The carotid canal accompanies the posterior progression of the pterygoid between the quadrate and the basicranium in more modern cryptodires, and its entrance foramen is visible posteriorly at the boundary basisphenoid - pterygoid. The canal may be enclosed in the pterygoid or between pterygoid and basisphenoid more or less completely, a window remaining sometimes at the boundary of the basisphenoid (in *Sinemys* and *Meiolania* for example). And, when the canal completely runs in the pterygoid, the foramen opens more or less posteriorly in the pterygoid or at its posterior extremity: it does not run on the prootic surface and it does not enter in that bone, which is covered by the pterygoid in Cryptodira, as it does in pleurodires with a prootic ventral exposure, *N. laticentralis* included.

The foramen posterior canalis stapedio-temporalis and the fenestra postotica: In *N. laticentralis* (Fig. 2, C), between the *processus articularis* of the quadrate and the prootic, is the slit in which longitudinally runs the *canalis cavernosus,* posteriorly and nearly vertically opening by the *foramen posterior canalis cavernosi*. Postero-laterally, in the top (anatomically) of the quadrate articular process is the transversal *incisura columellae auris* housing the *columella* and, posteriorly, the Eustachian tube groove. Posteriorly to the foramen of the longitudinal *canalis cavernosus*, is the ventral opening (the *foramen posterior canalis stapedio-temporalis*) of the vertical canal for the stapedial artery (which has just separated from the inner carotid), canal vertically perforating the skull: the ventral opening of the canal is situated between the quadrate and the prootic, dorsally in relation to the posterior border of the ventral face of this bone: according to the posterior position of the *foramen stapedio-temporale* in dorsal view and the not medially prolonged quadrate (Fig. 2, E), the *foramen posterior canalis stapedio-temporalis* is well posterior to the ventral prootic border and ventrally well visible: in Eupleurodira, the stapedio-temporal canal opens inside the *canalis cavernosus* which runs longitudinally and which opens at the expanded quadrate posterior border level, so that the *foramen posterior canalis stapedio-temporalis* is not ventrally visible. In *N. laticentralis*, the posterior limit of the ventral prootic is relatively anterior and oblique, instead of transversal in eupleurodires; it constitutes the ventral border of the lateral part of the *fenestra postotica*. As seen above, the inner carotid has its groove in the ventral prootic surface, obliquely from the lateral point of separation from the stapedial artery outside the skull.

In the primitive forms: in *Proganochelys,* the stapedial artery runs well posteriorly between the quadrate and the paroccipital opisthotic process, not yet anteriorly firmly sutured to the quadrate, and the foramen of the *canalis stapedio-temporalis* is not yet exactly defined; it is represented by a slit, posterior to the *fenestra ovalis* (GAFFNEY, 1990, fig. 27). In the *Palaeochersis* original description, the stapedio-temporal canal is indicated as anterior to the *fenestra ovalis* in the list of characters: the ventral foramen interpreted as the foramen of this canal is positioned anteriorly to the *fenestra ovalis*, against the *processus articularis quadrati*, similarly to *N. laticentralis*, which is much more derived than in *Proganochelys* and implicates that the *canalis stapedio-temporalis* is more anteriorly positioned. This interpretation is not asserted. The *foramen posterior canalis cavernosi* and the *foramen posterior canalis stapedio-temporalis* are not identifed in *Kayentachelys*. In these primitive forms, the paroccipital process is not solidly fused and the foramen of the cranio-quadrate passage is not well delimited. It appears that in the two Triassic forms, in *Australochelys* and possibly in *Kayentachelys*, there is not yet a delimited *canalis cavernosus* and a partly constituted *fenestra postotica* as present in *Notoemys laticentralis*. This latter is therefore more derived than the primitive forms on that

point. However, *N. laticentralis* is more primitive than the Eupleurodira known by their skull because of the not prolonged *fenestra postotica* laterally, therefore not hiding the *foramen posterior canalis stapedio-temporalis* of the corresponding canal, itself posteriorly positioned. The same occurs in Cryptodira of the late Jurassic of North America (GAFFNEY, 1979b) with *Glytops*, where the foramen is apparent medially to the quadrate articular process, just a little more advanced forward than in *N. laticentralis.*

The cavum labyrinthicum (vestibulum) area: In *N. laticentralis* as in Eupleurodira, the foramen of the hyomandibular branch of the facial nerve (VII) is visible in the prootic wall, between the *canalis cavernosus* (cranio-quadrate passage) and the *vestibulum* (*cavum labyrinticum*) and just below the *foramen posterior canalis stapedio-temporalis*. Medial to the *foramen posterior canalis stapedio-temporalis*, is the *fenestra ovalis* which laterally opens the *cavum labyrinthicum*: in *N. laticentralis*, the *fenestra* is filled by a thick cylinder (Fig. 2, D; Fig. 4, C) which constitutes the medial extremity of the *columella*, instead of a thin circle: it is supposed that it is a remains of the primitive stronger stapes, if not a secondary thickening. Immediately behind the *columella* extremity, the posterior border of the *cavum labyrinthicum* (*vestibulum*) is constituted by a rather wide, moderately thin and laterally curved process, ventrally free, vertically issued from the opisthotic and which is perforated in its posterior top by a foramen for the glossopharyngeal nerve, the *foramen externum nervi glossopharyngei* (nerve IX), just dorso-lateral relative to the *foramen jugulare anterius*: the process constitutes the *processus interfenestralis opisthotici* (Fig. 2, C, D; Fig. 4; Pl. I, C and D). This process is rather vertical and its ventral extremity does a slightly rounded free border posterior to the prootic in ventral view, as in the Chelidae and the more primitive Pelomedusoides, including the extant Pelomedusidae (Pl. II, C-J). In turtles, the surrounding bones (basisphenoid, basioccipital, exoccipital, opisthotic) may ventrally cover it in part with various different ways according to the taxa (see GAFFNEY, 1979a; LAPPARENT DE BROIN & WERNER, 1998). Secondarily also, the pterygoid (Cryptodira), or the quadrate (Podocnemidoidea), or the basisphenoid (*Teneremys*) extend below the *processus interfenestralis*, completely hiding it in ventral view, although it remains ventrally free inside.

The recessus scalae tympani: In *Notoemys laticentralis*, posteriorly to the *processus interfenestralis*, there is no other opisthotic process behind it: there is just a narrow exoccipital descending process linking the posterior lateral corner of the basioccipital and widely separated from the *processus interfenestralis*: there is no posterior opisthotic process, linking the exoccipital ventral process at the corner of the basioccipital, to constitute a complete posterior wall to the *recessus scalae tympani*.

In *N. laticentralis,* this wide space between the *processus interfenestralis* and the posterior extremity of the paroccipital process of the opisthotic is not closed by bone, ventrally and posteriorly. Between the medial border of the *processus interfenestralis* and the antero-lateral wall of the exoccipital, the *foramen jugulare anterius* opens for the *vena cerebralis posterior* and the nerves X, *vagus*, and XI, accessory, therefore joining the nerve IX, glossopharyngeal, in the same exit: the *fenestra postotica* is widely open latero-posteriorly. Ventro-posteriorly, as seen above, the *cavum labyrinthicum* is also open below the *processus interfenestralis*. The posterior wall of the exoccipital process is only pierced by the two nerves XII, the nervi hypoglossi. In *N. laticentralis*, the ventral exoccipital posterior process extends just along the ventro-lateral border of the basioccipital up to link the medial base of the *processus interfenestralis* (preserved on the left side, Fig. 2, C).

In the Eupleurodira, the *recessus scalae tympani* is covered ventrally and partly posteriorly but differently, i.e. independently, according to the taxa. In Chelidae, Pelomedusidae and Podocnemididae, there is a posterior descending process of the opisthotic, antero-medially expanded, and joining a posterior exoccipital process, medially expanded: the *foramen jugulare posterius* opens between them or completely in the exoccipital process (see the different details in the closure of the *fenestra postotica* described in LAPPARENT DE BROIN & WERNER, 1998). In the two first groups, the lateral part of the *fenestra postotica* is not ventrally covered at the level of the *vestibulum*, or just partly, in some exceptions in Chelidae such as *Emydura macquarii*, by a small quadrate expansion, and in *Teneremys* by the basisphenoid medio-posterior expansion up to the posterior descending opisthotic process of the paroccipital process and up to the exoccipital (Fig. 5, K, bs). But the *recessus scalae tympani* is well ventrally and posteriorly covered by these posterior opisthotic and exoccipital expansions. While in Podocnemididae, all the *fenestra postotica* and *recessus scalae tympani* are covered, ventrally and posteriorly, by the podocnemidoid quadrate expansion toward the quadrate and the posterior opisthotic and exoccipital expansions. In Bothremydidae, however, the opisthotic posterior process is not always completely developed ventrally and a slit remains between the opisthotic and the quadrate (this, in other regards, expanded toward the basioccipital as in Podocnemididae): in this case, the *foramen jugulare posterius* is partly well defined but incompletely separated from the most lateral part of the *fenestra postotica*. Therefore at least, in the Podocnemidoidea, all the *fenestra postotica* including the *recessus scalae tympani* is well ventrally covered by this quadrate-basioccipital union. *N. laticentralis* is therefore primitive and completely distinct from the Eupleurodira by this weak posterior and ventral bony closure of the *recessus scalae tympani* and absence of a bony wall for a constituted *foramen jugulare posterius*.

In evolved Cryptodira, the *recessus scalae tympani* is more or less posteriorly closed. In many forms, the exoccipital descending process (pierced by the nerves XII) is generally laterally expanded, much wider posteriorly, and it much better posteriorly closes the *recessus scalae tympani*, at the rear of the skull instead of anteriorly to the rear in Pleurodira, for example in Cheloniidae, *Dermatemys, Carettochelys*. But there is a trend in Cryptodira such as the opisthotic posterior border also descends to join the exoccipital expansion and contribute to enclose the *foramen jugulare posterius* (Kinosternidae, *Platysternon*, Testudinidae, etc.) (Figs in GAFFNEY, 1979a ; MNHN coll.). In small terrestrial testudinids such as *Testudo graeca*, the posterior bony process does not ontogenetically develop much, unlike in the larger ones : only the top of this posterior process is ossified, formed by the opisthotic and the exoccipital. In Trionychidae and Chelydridae, both situations are present : in *Chelydra* and *Chelydropsis* sp. (from the inedite skull from the Miocene of France), the *recessus* is partly posteriorly limited by a lateral expansion of the exoccipital process enclosing the *foramen jugulare posterius* (Pl. II, A, B) while in *Macroclemys* the *foramen jugulare posterius* is also partly enclosed by the opisthotic. In the primitive *Glytops* (fig. 17 in GAFFNEY, 1979b), the *processus interfenestralis* is well posteriorly visible, as in *N. laticentralis* (although infero-anteriorly covered by the posterior expansion of the pterygoid) but it seems there is a posterior thin medial opisthotic process joining the posterior exoccipital process to separate the *foramen jugulare posterius* from the *fenestra postotica*. It seems to be the same in *Dorsetochelys* EVANS & KEMP, 1976, from the early Cretaceous of England. However, a very similar situation to that of *N. laticentralis,* as far as the posterior unclosure of the *recessus scalae tympani* is concerned, exists in *Mesochelys durlstonensis* EVANS & KEMP, 1975, from the early Cretaceous of England. *Mesochelys* is evidently a true cryptodire by the backward prolongation of the pterygoid, hiding the inner ear. Although not indicated as pierced by the nerve IX, the figured posterior vertical opisthotic process (see EVANS & KEMP, 1975) seems to be, by its shape, a true *processus interfenestralis* and no other opisthotic is posteriorly developed so that to separate the *foramen jugulare posterius* from the *fenestra postotica*. The same occurs in *Plesiobaena antiqua*, a Campanian Canadian cryptodiran baenid (BRINKMAN, pers. comm. and BRINKMAN, 2003). It likely occurs in all the beaenids although no precise indication is given on this subject (BRINKMAN & NICHOLLS, 1993 ; GAFFNEY, 1972b), and with the difference, in all baenids, that the pterygoid is apomorphically much posteriorly prolonged, just infero-medially, to cover the *cavum acustico-jugulare*. As a whole, in Cryptodira posteriorly in grade (but not always in stratigraphical time) to *Kayentachelys, Mesochelys* and *Plesiobaena* at least (and probably all the baenids), a

posterior process expansion is at least partly present and the *foramen jugulare posterius* is at least partly delimited by bone, as in Eupleurodira but differently, and while not in *N. laticentralis*. In Cryptodira, the laterally developed posterior process (isolating or not a *foramen jugulare posterius*) is mainly constituted by the exoccipital and it is very posterior at the border of the skull. As ventrally in Cryptodira, anteriorly to the posterior descending opisthotic and exoccipital processes, the *fenestra postotica* is more or less hidden by the typically cryptodiran pterygoid posterior expansion.

In *Proganochelys*, the area posterior to the inner ear is very short. The paroccipital opisthotic process constitutes the *"processus interfenestralis"* (its equivalent) ; it elevates (in ventral view) from the medial border of the long paroccipital process of the opisthotic and, linked to the prootic, the basioccipital and the exoccipital, comes to ventrally cover the inner ear. There is no posterior process to posteriorly close a *recessus scalae tympani*, not yet constituted. The exit of the nerve IX in the process strengthens its homology with the *processus interfenestralis* but it is not shortly elevating (in ventral view), anteriorly and vertically. In *Palaeochersis* there is an identical opisthotic process coming from the back and covering the inner ear, close to the posterior border, although no nerve IX exit is visible because of the preservation. The same morphology is indicated in the drawing of *Kayentachelys* (no photographs) but the limits of the bones are unclear.

Conclusion to the fenestra postotica-recessus scalae tympani area : The closure of the *fenestra postotica-recessus scalae tympani* is not homologous in both "infraorders" or "suborders" (Cryptodira and Pleurodira) and there are different degrees for each closure type within the groups.The *recessus scalae tympani* is posteriorly independently completely closed in Pleurodira and Cryptodira. The *recessus* is completely closed in Pleurodira as soon as the first known Chelidae and Pelomedusoides s. l, but *Notoemys laticentralis* has a more primitive known condition of closure, being however more derived than in Triassic forms.

It is actually probable that, in the same way, many other skull characters, supposed as characters of Casichelydia, may have been independently acquired, besides the fact that some of them are actually not exactly homologous characters in the way they are constructed.

Exoccipital dorsal and posterior exposure, foramina externa nervi hypoglossi :

The exoccipitals are dorsally exposed as in most Pelomedusoides (primitively). The posterior foramens of the nerve XII are enclosed in the exoccipital, the only foramina posteriorly closed.

Posteriorly, in *Notoemys laticentralis*, the supraoccipital crest (possibly partly broken) separates the two exoccipitals. These surround nearly all the posterior

opening of the *cavum cranii* which is rather triangular in shape (Fig. 2, B): the exoccipitals are well exposed dorsally on each part of the crest (Fig. 2, B, E; Pl. I, B, E), in a strip disposed in width and which is softly inclined and slightly concave. The exoccipital exposure is variable in Pleurodira (more or less reduced in length or width, or enlarged). In *Notoemys* it is conformed as in *Pelomedusa* and more similar to that of Pelomedusoides (although the exoccipitals are often dorsally reduced in length) than to that of Chelidae where the exoccipitals are more medially verticalized against the *cavum cranii* wall and where the *antrum* posterior inflation produces a bombing on each side of the exoccipitals. This configuration is congruent with the dorsal posterior emargination of a Pelomedusoides type and is part of the similitude of the back skull of Pelomedusoides, *Platychelys* and *N. laticentralis* (Figs 2E, 3) in dorsal view.

The two foramina externa nervi hypoglossi (XII) are situated in a concavity in the posterior face of the exoccipital. There is a crest, made by the exoccipital descending and posterior process, between their concavity and that of the *foramen jugulare anterius* (more anterior and opening laterally) (Fig.2, B; Pl. I B). A distinctive feature of *Notoemys laticentralis* in relation to the other Pleurodira, on account of the absence of process between the opisthotic and the basioccipital to close the *recessus scale tympani*, is that the hypoglossal nerves are the only elements to be situated in a separated area from the *fenestra postotica*, where all the other posterior vessels and nerves run.

Neck (Pl. I, H to K; FERNANDEZ & DE LA FUENTE, 1994: fig. 3.)

The preserved cervical vertebrae of *Notoemys laticentralis* are the 1st to 4th (Pl. I, G-K), i.e.: the atlas, the axis and the vertebrae 3 and 4. They are low and elongated (centrum and neural arch). They are opisthocoelous. The 2d to 4th vertebrae bear anterior triangular transverse apophyses with a transversal anterior border. The prezygapophyses are horizontal. There are no neural spines. The prezygapophyses and postzygapophyses of each side are widely separated.

The Triassic and early Jurassic forms: The vertebrae are unknown in *Proterochersis*, *Kayentachelys* and *Australochelys*. *Proganochelys* has cervical vertebrae with a high and short centrum with concave anterior and posterior faces (amphicoelous vertebrae) and bicipital rib attachments, a low central ventral crest, more or less medially complete in the intermediate cervicals, an elevated neural arch with a very high neural spine (its top horizontal in lateral view), prominent between the postzygapophyses above the neural arch and ascending from the 1st to the 8th, and well separated zygapophyses approximately at the same horizontal level (see GAFFNEY, 1990). From a preliminary observation, *Palaeochersis* has nearly all these straights, but the neural crest is less

prominent and rounded in lateral view, and the ventral crest is missing. The neural spine is slightly posteriorly inclined, the base of the postzygapopyses is slightly elevated above the base of the prezygapophyses but, as in *Glytops* (see below), they are not elevated above the medullar canal. Nearly each of these elements may be modified in the turtles following in time the oldest ones. Some changes affect one or all the vertebrae of the neck (according to the character). The possible changes are (not exclusive): loss of ribs and formation of wing shaped transverse apophyses (with various possibilities of position on the centrum from anterior to medio-posterior and variable curve of its borders), formation of articulated joints, concave or convexe, with all the possibilities of assemblage along the neck (procoelous, opisthocoelous, biconcave and biconvexe vertebrae), simple or double joints, absence or enlargment of the ventral crest of the centrum, modification of the shape of the cotyles and condyles (more or less ovoid rounded or rectangular), elongation of the vertebrae (centrum and neural arch), formation of tubercles anteriorly or posteriorly below the centrum, formation of saddle shaped joints, diminution to loss of the neural crest, complete lowering of the neural arch up to an horizontal plane or variable inclination towards the back (from the anterior to the posterior vertebra) and approximation of the postzygapophyses up to their junction in a flat collerette or in a bi-facet pad, loss of the neural spine (generally except the axis long horizontal spine) or its enlargement, modification of the position of the articular facets (overall at the atlas axis junction), inclination of the last vertebra in relation to the first thoracic vertebra and rolling of the postzygapophyses etc. The modern forms of vertebrae are particularly described in WILLIAMS (1950) and HOFFSTETTER & GASC (1969).

Compared to the most known turtles, the vertebrae of *Notoemys laticentralis* are derived principally because:

- They are low (vertebra 4, height: 1,25 cm from the posterior base of the centrum to the roof of the postzygapophyses, 0,9 cm from the anterior base of the centrum to the anterior roof of the neural arch medially; length: 2,3 cm maximum between the zygapophyses; h/l = 54,34 per cent);
- With lowered centra (wider than high, Pl. I, K; 0,6 on 0,8 cm, posterior 4th centrum face);
- With reduced neural arch up to the horizontal plane and reduction of the neural spine; are present (in the preserved four vertebrae): a low and long spine on the axis, anteriorly prominent, no more spine and just a fine straight line on the third vertebra and just a slight median and rounded elevation on the fourth (Pl. I, H, J);
- The centrum is elongated (a little more than two times longer than wide, Pl. H, K);
- The centrum is narrow behind the transverse apophysis;
- The vertebrae lack cervical ribs with two heads and they

just present transverse apophyses which are completely anteriorly situated at the position of the dorsal insertion of the primitive bicipital rib (Pl. I and H-J).

- The transverse apophyses are developed in wing, with a transverse anterior border and an oblique and straight posterior border (with a external short but consequent and oblique border between them); the transverse apophyses increase in width from the 2d to the 4th; the smaller first transverse apophyses of the axis are not much different from those of modern cryptodires (see WILLIAMS, 1950) but the following apophyses of 3d and 4th cervicals are distinct by their lateral development in trapezoid wing, more conform to pleurodires; but they differ from those of the pleurodires, being not posteriorly directed (Pl. I, N, O) and more anteriorly situated;

- They have formed articulations (LAPPARENT DE BROIN & MURELAGA, 1999; DE LA FUENTE & ITURRALDE-VINENT, 2001); after the biconcave atlas, as usual, the following 2 to 4 are opisthocoelous, with anteriorly a convexe face (a condyle, Pl. I, G: con), and posteriorly a concave face (a cotyle, Pl. I, K: ca);

- They have low pre- and postzygapohyses, well separated (Pl. I and J).

The derived characters of lowering, elongation, neural spine reduction, modification of the ventral crest, formation of articulated joints and of transverse apophyses may be as well seen in cryptodires as in pleurodires, with particularities. Some features of *N. laticentralis* are compared below with Cryptodira and Pleurodira.

Position of the prezygapophyses of the axis: The cervical vertebrae of *N. laticentralis* have a thin and not prominent ventral crest below the centrum (reduced crest); the prezygapophyses of the axis have an horizontal position, as in the primitive forms in the constituted groups of pleurodires such as *Emydura* in Chelidae and *Brasilemys* in Pelomedusoides s.l., and of Cryptodira, such as *Puppigerus* in Cheloniidae (see MOODY, 1974) or *Meiolania* (see GAFFNEY, 1985), but also as in the long necked chelids *Hydromedusa* and *Chelodina*. In *Notoemys*, the pre- and post-zygapophyses of each side are strongly separated from each other at their root (Pl. I, J), both couples at the same height, and their dorsal faces are nearly flat, hardly inclined and not curved (Pl. I, H), as it appears in the dorsally visible 3d vertebras of the new skeleton of *Platychelys* (H.-V. KARL comm.).

Modification of the neural arch: The vertebrae of *N. laticentralis* (as well as *Platychelys*, *Caribemys* and various Cryptodira) have a lowered neural arch nearly without a neural spine. It is not derived in the same way as the pleurodire Dortokidae, Chelidae and Pelomedusoides which have developed the primitive neural arch in a pleurodiran common pedicel of the postzygapophyses. This is a posterior elevation of the neural arch part bearing the postzygapophyses, behind and above the

posterior foramen of the medullar canal and above the base of the prezygapophyses, with a posterior inclination and reduction of the neural spine crest between and above the postzygapophyses, and with approximation of both postzygapophyses up to their complete junction (at least in the last vertebra). The postzygapophyses are united in a flattened collerette in *Araripemys*, the known anterior vertebra of *Teneremys* (MNHN GAD 918), in the South-American *Podocnemis* and some related podocnemidine forms such as Aff. *Roxochelys vilavilensis*, and in *Hydromedusa* and *Chelodina* in Chelidae. In Eupleurodira, the elevation of the pedicel increases from forwards to backwards in the cervical column; it is variably high and inclined in forms (according to the flatness or elevation of the column); the neural crest becomes a tubercle above the postzygapophyses on the 7th and overall the 8th vertebra. When the postzygapophyses are united in a collerette, the union is variable according to the taxa; it may vary in the neck, from more or less united in the anterior vertebrae to completely united in the following ones.

Comparisons with primitive cryptodires: three preserved vertebrae from the Early Cretaceous of Griman Creek, Lightning Ridge Formation, Australia, have been observed in Sydney (Australian Museum, AM collection). The specimen F 72276 is opisthocoelous, with bicipital rib attachment, short and high centrum (well crested below) and what we can consider as a postzygapophyses pedicel because the base of the postzygapophyses is higher than the base of the prezygapophyses (broken) and higher than the top of the medullar canal; the pedicel is few inclined (the vertebra is very short) and the postzygapophyses are well separated, downward inclinated. The specimen F 68245 is similar (high, short, ventral crest, bicipital rib attachment; broken prezygapophyses at the base) and it also has a pedicel higher than the medullar canal; it is amphicoelous and has preserved a broken base of the high neural spine found in *Proganochelys* or *Meiolania* between the postzygapophyses. The last vertebra F 68254, biconvexe, is different: without pedicel, lowered neural arch and low neural crest above the postzygapoplyses, well separated zygapophyses, transverse apophyses medially positioned on the centrum, well transversally directed and their extremity rounded.

A Lightning Ridge vertebra similar to the two first ones has been attributed to turtles by GAFFNEY (1981) by comparison with the Jurassic *Glytops*. These (Yale coll., YPM 5963 and 5986, photographs from GAFFNEY, pers. comm.) seem to present a pedicel bearing the postzygapophyses above the prezygapophyses in lateral view; but in posterior view, it appears that there is no elevation of the pedicel above the medullar canal, unlike in pleurodires and in the Australian vertebrae. Anyway: if the Australian vertebrae are cryptodiran, as hypothetized by the other parameters (ventral crest, bicipital ribs, neural spine between and above the postzygapophyses), the first ones show that Cryptodira may also have a

pedicel, as in pleurodires. The last vertebra is not much different from a vertebra of *Notomemys* by the lowering and the separation of the zygapophyses; it differs by the presence of the strong ventral crest, the remaining neural crest and the transverse apophyses shape.

Development of transverse apophyses: The loss of bicipital ribs and the consecutive presence of developed transverse apophyses occur in *Notoemys*: the transverse apophyses are anterior instead of central in Pleurodira. The presence of laterally developed transverse apophyses is a pleurodire feature, although also present in Cryptodira, but most of time they are more reduced, and differently shaped and positioned. In Pleurodira, the transverse apophyses were present in the notoemydid *Caribemys* (8th cervical only known, apophyses broken at the basis); similar well developed and anteriorly positioned transverse apophyses are present in the 8th cervical of *Platychelys*. In *Dortoka*, the known vertebrae have transverse apophyses (laterally broken) more centrally positioned and posteriorly directed as in Chelids such as *Emydura macquarii*: the 2d to 4th vertebra shorter at the basis, and the presumed 5th longer as in these chelids. All the Eupleurodira have apophyses well developed and centrally positioned on the centrum; the apophyses have the anterior border posteriorly directed, convexe, while the posterior border is more or less straight or incurved according to taxa, as well as they are more or less wide: more in Pelomedusoides with a longer transverso-concave posterior border in Pelomedusoides than in Chelidae. The basis of the pleurodire transverse apophyses is rather thin. In Cryptodira, Mesozoic Jurassic taxa such as *Xinjiangchelys* have diapophyses on the middle of the centrum, besides the parapophyses (situated on the anterior base; both present for cervical bicipital ribs) (PENG & BRINKMAN, 1993) instead of anterior as in *Proganochelys* and *Meiolania* (GAFFNEY, 1985, 1990). Transverse apophyses are also present in Cryptodira on all the vertebrae in modern taxa or, in rather primitive fossil taxa, on the vertebrae lacking cervical ribs of a neck also still including some cervical bicipital ribs. But they are slightly different from those of the known Pleurodira in position and morphology: - In some Mesozoic taxa, they are present in some vertebrae of the column (the other still having bicipital ribs), generally short with a stout lateral border and, as in *Xinjiangchelys* for the dorsal diapophyses, they are not completely anterior on the centrum: *Ordosemys*, on the 4th and 5th (BRINKMAN & PENG, 1993a), *Dracochelys*, on the 3d to 6th (BRINKMAN, 2001), *Sinemys* and *Solnhofia* on the 2d to 8th (BRINKMAN & PENG, 1993b; JOYCE, 2000), and *Thalassemys* on several known isolated vertebrae (three mentioned in BRÄM, 1965, and others unpublished, preserved in the Museum of Solothurn). All these forms have still more or less high neural spines (partly reduced in *Thalassemys*) and they already have one, some, or all formed articulations instead of being primitively

amphicoelous. In the middle Campanian baenid *Boremys pulchra*, transverse apophyses, present in all the vertebrae (BRINKMAN & NICHOLLS, 1991), have approximately the same development in width as in pleurodires including *Notoemys*. But the anterior border of the 4th is more posteriorly curved: the vertebrae 3 to 8 are more primitive by their height and the difference is increased by the neural spine, being present, and the different articulations, being biconcave with intermediate cartilage. - Later in time, the late Cretaceous *Plesiobaena antiqua* has transverse apophyses in median position, rather round in section (BRINKMAN, 2003), formed joints and reduced neural spines. - In modern cryptodiran groups, lacking cervical ribs, with formed joints and reduced neural spine, the transverse apophyses are always anterior and thicker at their basis than in pleurodires and very small. They are particularly thick in marine extant Cheloniidae s.s. (see WILLIAMS, 1950). They are also particularly thick in marine fossil Cheloniidae s.l. (see *Puppigerus* and *Argillochelys* in MOODY, 1974) which preserve the presence of high neural spines. But sometimes, when the neural crest is completely reduced, the neural arch completely reduced and the zygapophyses well separated, some cryptodires have apparently rather similar vertebrae to those of *Notoemys,* except for the slightly thicker base of the anterior transverse apophysis: as a whole, the vertebra 2 of *N. laticentralis* is not much different from the vertebrae 2 and 3 of the cryptodire *Chelydra*, just a little shorter for the same width (more elongated neck in *Chelydra*). But the 3d of *N. laticentralis* is clearly different by the better development of the transverse apophysis than in all the vertebrae of *Chelydra*; and the next 4d of *Chelydra* is biconvexe and the following are procoelous with double articulation between vertebrae 6, 7 and 8: the 8th is very similar to the 8th of *Platychelys*, except for the larger laterally transverse apophyses of the latter.

The articulated joints: In pleurodires, the opisthocoelous vertebrae only occur in cervicals 2 to 4 of Chelidae and presumably of the Dortokidae (one preserved, 2d to 4th). In *Platychelys* (preserved biconcave 7th and biconvexe 8th, with double articulation; the neck is not prepared in the new specimen, H.-V. KARL comm.), *Caribemys* (biconvexe 8th) and the other one known of *Dortoka* (a biconvexe, possible 5th), the known vertebrae are posterior in the neck in relation to those known from *Notoemys*, but here also they are of the chelid type. The formula of each of the two "modern" groups ("Eupleurodira") is fixed. That of Chelidae is that rather primitive type present in the Jurassic forms and presumably in *Dortoka*: opisthocoelous 2 to 4, biconvexe 5, procoelous 6, biconcave 7 and biconvexe 8, without double joints. Whereas Pelomedusoides s.l. have the 2d biconvexe and the following procoelous, which is a more derived condition (in agreement with the formation of procoelous joints in the tail) and unique in turtles. Up to now, the

double joints occur only in the Jurassic *Platychelys* in pleurodires. In Cryptodira, the acquisition of joints from a primitive stage with platycoelous vertebrae as seen in *Proganochelys*, occurred several times with a much larger possibility of differences along the neck than in Pleurodires (see WILLIAMS, 1950 and the references of fossil taxa above given), often including double (as in *Platychelys* but variably situated) or single joints on a single neck and variations within a single family. The presence of opisthocoelous vertebrae 2 to 4 is known in modern cryptodires (some Testudinoidea, the Trionychia, *Eretmochelys*: see WILLIAMS, 1950) but the following vertebrae articulations (6-8) are different from those of Chelidae.

Reduction of the neural spine: In the primitive forms, there is a high neural spine between the postzygapophyses, as seen above, elevating from the axis or behind up to the last, between the zygapophyses, separating them on each side, with a rather straight horizontal upper border (in lateral view) in *Proganochelys*, *Otwayemys* or *Meiloania* which have particularly high neural spines (as a whole).The reduction of the neural spine occurred several times in Cryptodira. In Pleurodira, there is not protuberant neural spine in the known Jurassic forms and the neural arch is flat between the zygapophyses. The lowering of the neural arch and centrum in relation to the centrum length in *N. laticentralis* is approximately as in *Platychelys* (but vertebrae 7 and 8 only known in three dimensions and 1th to 3d only known in dorsal view) and probably in the anterior unknown vertebrae of *Caribemys* (by extrapolation from the preserved posterior one). In the Eupleurodira and Dortokidae (both groups with a common pedicel for the postzygapophyses), there is a crest on the upper border of the common pedicel of the neural spine. It is a fine straight line, present from the base of the common pedicel up to the separation of the postzygapophyses, from the axis up to the 8th vertebra, unlike *Notoemys*, devoid of common pedicel of the postzygapophyses and devoid of a dorsal line line as soon as the 4th. The wide separation of the zygapophyses and absence of high neural spine is derived in *Notoemys*, by comparison with *Proganochelys* and *Palaeochersis*. The common pedicel of the Dortokidae and Eupleurodira may be directly issued from a *Palaeochersis* grade with still a high neural arch but a weak neural spine crest, and with a slight elevation of the postzygapophyses toward the neural spine summit. It seems unlikely that it derived from the flat neural arch of the Jurassic forms. And, therefore, it is unlikely that Dortokidae and Eupleurodira derived from one of them and, more probably they may have been sister-groups of the Jurasssic forms which may constitute a clade Platychelyidae-Notoemydidae (LAPPARENT DE BROIN *et al.,* 2004; CADENA RUEDA & GAFFNEY, 2005) (see below). Postzygapophyses pedicel, transverse apophyses and articulated joints presence in Cryptodira as in Pleurodira are some given examples

showing the necessity to add all the elements of each vertebra as different characters to well differentiate the taxa, because of the evident possible homoplastic and heterochronic evolution of the parameters, and one element is not sufficient to state the evolutionary degree of the neck.

Remarks on the atlas and axis:
In the atlas of *Notoemys laticentralis*, the ventral spine is a ventral ridge of the short intercentrum prolonged on the longer centrum where it posteriorly dies in a triangular area, from forward toward backward, laterally limited by two processes, posteriorly prominent. In the axis and the two following vertebrae, the centrum is longer; the ventral ridge is sharper and the triangular area is relatively longer, the processes being not posteriorly prominent. The triangular posterior part is absent in *Proganochelys*; it is present in Cryptodira and Pleurodira, variable in shape.

The *N. laticentralis* neck has derived with characters found in various pleurodires as well as in cryptodires, by homoplasy owing to the moment of apparition of the character in the radiations. As far as pleurodires are concerned, the *N. laticentralis* atlas better conforms by its shape to the primitive chelids (when in those, the atlas is not transformed in a true vertebra as it is in the long necked forms) than to Pelomedusoides; it is similar to that in *Emydura*; but the centrum is rather long (derived condition) (the width on length proportion is between those of *Phrynops* s.l. and *Chelus*) and the intercentrum has two posterior processes as in the pelomedusoides *Pelusios* but more protruding.

The axis has present the primitive anteriorly prominent dorsal process of the neural arch, as preserved in most turtles and as it appears in *Platychelys* (new skeleton). This process is lost in the chelid *Hydromedusa*, but not in its primitive related form *Yaminuechelys* DE LA FUENTE *et al.,* 2001, and neither in *Chelodina expansa* and *C. longicollis*, other long necked chelids. In these two species of *Chelodina* s.l., belonging to two lineages separated from a long time (LAPPARENT DE BROIN & MOLNAR, 2001), the process is slightly reduced, thin instead of rod-like as it is in the South-American forms, pointed or rounded which indicates an independent reduction of that of *Hydromedusa*. This independent reduction conforms the independent acquisition of other anatomical characters in the two groups of long necked chelids, such as the different pattern of skull emargination (see above) and the different pattern of carapace (although elongated in both groups, in relation with the elongated neck, at the end of the evolution of each group). All that supports the hypothesis of an independent radiation of the two long necked lineages in South America and Australia (GEORGES *et al.,* 1999: PRITCHARD, 1984). However, BONA (2004), examining the phylogenetic position of *Yaminuechelys* DE LA FUENTE *et al.,* 2001, confirms the point of view of GAFFNEY (1977), supporting the clade

Chelodina/Hydromedusa-Yaminuechelys because her work does not introduce all these necessary characters in the analysis. The posterior processes of the preserved centra 2 to 4 of *N. laticentralis* are not as posteriorly protruding as in corresponding opisthocoelous vertebrae in chelids.

Conclusion to the neck : At the late Jurassic, there is in *Notoemys* a pleurodiran formula of cervical joints united to a pleurodiran ventral exposition of the prootic, a relatively modern pleurodiran plastron (intergular, lateral mesoplastra shape, absence of axillary and inguinal scutes) and a pleurodiran suture of the pelvis and sacral vertebrae to the carapace. But the neural arch and zygapophyse system of this cervical vertebrae formula are different from that of the Eupleurodira. The definitive derived formula of each of the two modern pleurodiran groups is known as soon as the early Cretaceous and had to derive in Jurassic times (probably at least at the middle-late Jurassic as in Platychelyidae-Notemydidae). Modern formulae are supposed also present in Cryptodira as soon as the middle-late Jurassic. Indeed, the differentiation of the Trionychidae and Carettochelyidae, the oldest still living families, implicating the acquisition of the trionychoid vertebral formula, is realized as soon as the late Jurassic. This is shown by the existence during the late Jurassic of China of one of the oldest known Trionychoidea, the carettochelyid *Sinaspideretes wimani* YOUNG & CHOW, 1953 (BROIN, 1977 ; MEYLAN & GAFFNEY, 1992), which implicates the separation of the Carettochelyidae from the Trionychidae, although the latter are known only from the early Cretaceous of Asia (Mongolia, China, Thailand, Japan and Laos) : Trionychidae are present in Laos at the late Aptian-early Albian, with Carettochelyidae and with another trionychoid group, the Adocidae Shachemydinae (HIRAYAMA, 2000 ; LAPPARENT DE BROIN, 2004 ; TONG *et al.,* 2003). The group including the Adocidae was also considered as present as soon as the late Jurassic of China with *"Plesiochelys" tatsuensis* YEH, 1963. Therefore, the separation of all these trionychoid families is realized at the late Jurassic. Unfortunately, the cervical vertebrae of these Jurassic forms are unknown. A vertebra from an Adocid of the early Cretaceous from Japan (HIRAYAMA *et al.*, 2000) conforms to the trionychoid formula. It should be interesting to also know the cervical vertebrae of the Jurassic possible protostegids, the Argentine *Neusticemys* FERNANDEZ & DE LA FUENTE, 1993 (and 1988) and the undefined form from Bavaria (LAPPARENT DE BROIN, 2001), to see if they differ or are similar to those of the Dermochelyidae, considered as the sister taxon of the Protostegidae. Anyway, primitive and already derived vertebrae formulae coexisted for a longer time in cryptodires (much more diversified in groups) than in pleurodires.

It is evident that most of shared characters of the neck of Cryptodires and Pleurodires are acquired by homoplasy after a grade of primitive forms represented by the *Proganochelys* or the *Palaeochersis* types and do not represent a casichelydian shared acquisition. As far as *Palaeochersis* is concerned, it is more derived than *Proganochelys* at the same approximate stratigraphic age, as *Proterochersis* for the shell. As far as the pleurodire Jurassic forms are concerned, they may then have a common ancestor with Dortokidae and Eupleurodira (modern pleurodires), posterior to the *Palaeochersis* radiation by the realization of the chelid type of joints. But, having lost the neural spine and well separated and low zygapophyses, these Jurassic forms have an ancestor not shared by the modern pleurodires. As far as the latter are concerned, it is possible to conceive that the specialized formula of the Pelomedusoides with most procoelous vertebrae is acquired from an ancestor of the dortokid-chelid type (LAPPARENT DE BROIN & MURELAGA BEREIKUA, 2003 ; LAPPARENT DE BROIN *et al.,* 2004). However, the homoplasy of many characters does that the acquisition of the postzygapophyses pedicel in only one time in Pleurodira is not sure.

CONCLUSION

With multiple homoplasies up to inside the groups, becoming aquatic, the turtles have lost many thick primitive terrestrial features. They have become alleviated, acquired body and head mobility including a better ear and a better ability to catch their preys and to protect themselves in new environments, by few possible ways from a single basic pattern. After the examination of the evolutionary grade of the posterior skull of *Notoemys laticentralis*, it appears that many of the common "rhaptochelydian" and "casichelydian" characters of "Eupleurodira" and Cryptodira, that have been estimated as possible synapomorphies in each of these nodes of the analysis of ROUGIER *et al.*, 1995, may have evolved by homoplasy (same evolutionary process leading to the same result) or only by analogy (different progressive process and not exactly similar result). In the same way, possible "synapomorphic" pleurodiran characters developed several times. The development of the rolling up of the quadrate and the closure of the *incisura columellae auris* with the thinning of the stapes, the development of the *antrum postoticum*, the ventral closure of the ear, *canalis cavernosus* and *fenestra postotica*, the posterior reduction of the paroccipital process and consecutive size of the bones, the modifications due to the neck retraction and the emplacement for the neck and jaw muscles, leaded in parallel, have produced some globally identical structures with some identical modifications around two types, the pleurodiran and the cryptodiran modes.

Several computer-generated cladograms of Pleurodira including *Notoemys laticentralis* have been presented, but these include few taxa (at the genus or at the family level) and with characters focalized on a precise subject. MEYLAN, 1996, is principally based on the skull characters

of some genera of the hyperfamily Pelomedusoides (a taxon established on hand-made cladograms, see BROIN, 1988a, b), from the pre-Pelomedusoides (basal Pelomedusoides s.l.) *Araripemys*. LAPPARENT DE BROIN & MURELAGA, 1999, is nearly exclusively based on the carapace of *Dortoka* with few pleurodiran genera of each pleurodiran group in comparison. DE LA FUENTE, 2003, is focused on the position of a podocnemidoid turtle within the Pleurodira. DE LA FUENTE & ITURRALDE-VINENT, 2001, is mostly focused on the postcranial of *Caribemys* compared to *N. laticentralis* and *Platychelys*, the basic taxa *Proganochelys* and *Proterochersis* and both Pelomedusoides and Chelidae (each group only being taken as a whole and not integrating the differences present in their primitive fossil taxa), and the work not including *Dortoka*. CADENA RUEDA & GAFFNEY, 2005 is focused on a new definition of *Notoemys*, including *Caribemys* and a new species *N. zapatocaensis,* compared with the same taxa as in the previous work and an insufficient definition of the characters resulting in the assimilation of the family Notoemydidae to the Platychelyidae. Overall in the first work, there are many of these characters, the states of which are reduced ("present, absent"; "yes, no") and established on a too much wide definition. It is true that it is not easy to exactly define the characters in appropriate terms for a cladistic analysis with a computer program: the resulting proposed cladograms depend on the subjective definition and homology of the characters. But, actually, the detail of the characters in the different taxa has never been sufficiently studied, although some of these pleurodiran characters are more or less better defined in some works such as GAFFNEY, TONG & MEYLAN, 2002, LAPPARENT DE BROIN & MURELAGA, 1999, LAPPARENT DE BROIN & WERNER, 1998 and GAFFNEY *et al.* (in prep, pers. comm.). Another uncomputorized analysis integrates the position of *N. laticentralis* in relation to the other Pleurodira (LAPPARENT DE BROIN, 2000a) (but before the publication of *Caribemys* and *N. zapatocaensis),* and another work (LAPPARENT DE BROIN *et al.*, 2003, 2004) examines the evolutionary grade of the Dortokidae, but not the phyletic relationships. According to the state of knowledge of most of the pleurodiran primitive taxa (absence of skull and vertebrae in *Proterochersis*, incomplete skull and neck in *Notoemys laticentralis* and *Platychelys*, absence of skull and incomplete neck in *Caribemys* and *Dortoka,* absence of skull and neck in *N. zapatocaensis),* the new interpretation of the skull and neck morphology of *N. laticentralis* given here does not change much its relative position: *N. laticentralis* remains positioned independently from the diversification of the Chelidae and Pelomedusoides. Only its position in relation to *Caribemys* and *Platychelys* may be changed, with the help of the examination of *N. zapatocaensis*, and the clade Patychelyidae - Notoemydidae be supported.

Notoemys laticentralis is a form characterized by autapomorphies such as the ventrally widened prootic descending up to the *area articularis quadrati*, the flattened, shortened and posteriorly rounded opisthotic paroccipital process and the long plastral fontanelle; it is particularly primitive by the thickened medial extremity of the *columella*, the ventral exposure of the stapedial canal and the absence of posterior closure of the *recessus scalae tympani*. In the light of the new observation of its structures, the present study indicates that its evolutionary grade was correctly positioned in the previous works. *Notoemys zapatocaensis* CADENA RUEDA & GAFFNEY, 2005, appears to us as included in the family Notoemydidae with *N. laticentralis* and *Caribemys oxfordiensis* and the family is not included in the Platychelydidae as proposed by these authors. As seen above, for us, *N. zapatocaensis* is a member of a monophyletic para-Tethysian group (GASPARINI *et al.,* 1999), the Notoemydidae. This is principally based on the shared hydrodynamic flattened shape of the cordiform carapace without the protuberances and denticulations present in *Platychelys*, which is a more lagunar form still with the pattern of a continental form (KARL & TICHY, in press). *Notemys laticentralis* and *N. zapatoccaensis* are a little more progressive than *Caribemys* (at least as far as the anatomy of the carapace is concerned, in view of the known presence of the skull only in the first one) by the longer and narrower iliac scar in *Caribemys*, still contacting the peripheral. *N. laticentralis* differs from *Caribemys* and *N. zapatoccaensis* (as well as in relation to *Platychelys*) by the wider and longer fontanelle. *N. zapatoccaensis* is more primitive (or autapomorphic) by the slightly serrated carapace border but more progressive by the narrower vertebrals; the supposed reduction of the 3d peripheral in *N. zapatoccaensis*, remaining dubious (particularly in view of the ventral face), is not considered here.

The Notoemydidae are clearly more derived than *Platychelys*, by characters such as the anterior plastral lobe configuration (more quadratic, wider intergular and wider humerals: at least for *Caribemys* and *Notoemys laticentralis*, the anterior lobe not being described from *Notoemys zapatocaensis*), the more regular and short neurals, the fixation of the posterior suprapygal-pygal schema (8 neurals, 2 suprapygals, 1 pygal) with the shape of the two suprapygals (as often found in Cryptodira) and the absence of supplementary scutes (supramarginals, pygal scute).

We agree with the position of Notoemydidae and Platychelyidae in a same clade. The cervical vertebrae of *Platychelys* and Notoemydidae are still insufficiently known, the posterior ones of *Notoemys* being unknown; but there is similarity between the 8th vertebra kown in *Platychelys* and *Caribemys* (DE LA FUENTE & ITURRALDE-VINENT, 2001), in the shape of the curved and separated posterior zygapophyses as it occurs in Cryptodira. Overall, both *Platychelys* and Notoemydidae have flattened known vertebrae, with constituted articular joints, according to the chelid formula from what we know and showing a

lateral neck retraction, which is progressive in relation to *Proganochelys* and *Palaeochersis* (unknown vertebrae in *Proterochersis*); they share widely separated pre- and postzygapophyses and completely lowered neural spine, which is unique in Pleurodira. Both Platychelyidae and Notoemydidae have a derived prominence on the anterior border of the thoracic rib 1 medially (CADENA RUEDA & GAFFNEY, 2005). But *Platychelys* is derived with by the presence of double joints (7th and 8th) not present in the 8th of *Caribemys* and the four anterior of *N. laticentralis*. The particular morphological type of cervical vertebrae with widely separated zygapophyses in both *Platychelys* and Notoemydidae is differently constituted in relation to the other Pleurodira (Dortokidae, Chelidae, Pelomedusoides) with the elevated and close postzygapophyses beared on a transformed neural spine, in a particular pedicel of the postzygapophyses above the medullar canal, which cannot be issued from the morphological type of *Notoemys laticentralis*. In view of the multiple homoplasies, nobody can assure that the common pedicel is appeared one or several times, which cannot be tested by comparison of other useful characters, in the absence of skull of *Platychelys* and Dortokidae. In any case, the morphology of the preserved posterior skull and neck of *Notoemys laticentralis* implicates an independent radiation from that of the Chelidae, the Dortokidae and the Pelomedusoides.

Abbreviations
AMNH: American Museum of Natural History, New York, USA. MACN: Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina. MNHN: Muséum national d'histoire naturelle, Paris, France; AC, Anatomie Comparée; P, Paléontologie; H, Reptiles et Amphibiens. MOZP: Museo "Prof. Dr. Juan A. Olsacher", Zapala, Argentina. NHM: Natural History Museum, London, UK. TUT Teikyo Heisei University, Chiba, Japan.

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Plate I

Notoemys laticentralis CATTOI & FREIBERG, 1961, MOZP 2487, Cerro Lotena, Neuquén province, Argentina. Formation Vaca Muerta, Late Jurassic. A-F: skull, anterior, posterior, ventral, ventro-latero-posterior from above, dorsal and right lateral views. G-J: anterior part of the neck, vertebrae 1-4, ventro-posterior, left lateral, ventral and dorsal views. K: vertebra 4, posterior face. *Emydura macquarii* (GRAY, 1831), L-O: vertebra 4, posterior, left lateral, ventral and dorsal views; ca, cotyle (posterior concavity); con, condyle (anterior convexity).

Planche I

Notoemys laticentralis CATTOI & FREIBERG, 1961, MOZP 2487, Cerro Lotena, province du Neuquén, Argentine. Formation Vaca Muerta, Jurassique supérieur. A-F : crâne, vues antérieure, postérieure, ventrale, ventro-latéro-postérieure vue du dessus, dorsale et latérale droite. G-J: partie antérieure du cou, vertèbres 1-4, vues ventro-postérieure, latérale gauche, ventrale et dorsale. K: vertèbre 4, face postérieure. *Emydura macquarii* (GRAY, 1831), L-O: vertèbre 4, vues postérieure, latérale gauche, ventrale et dorsale; ca, cotyle (concavité postérieure); con, condyle (convexité antérieure).
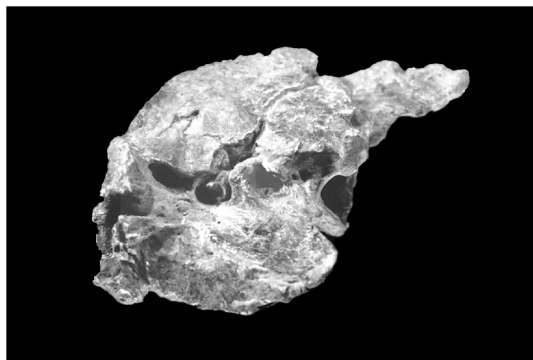
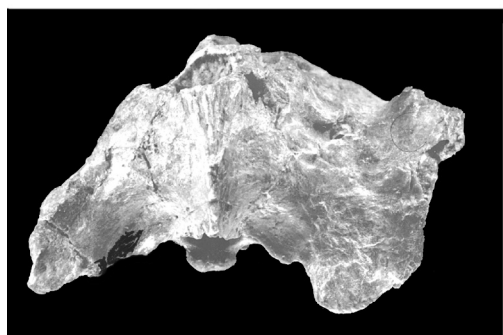**Plate I**
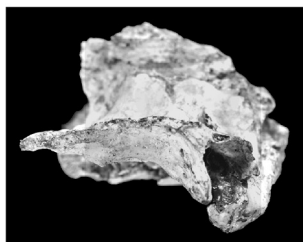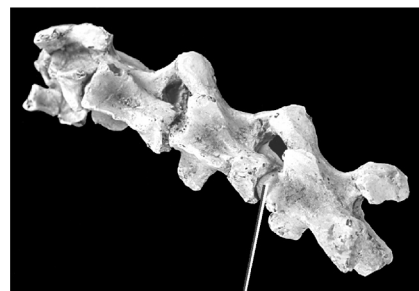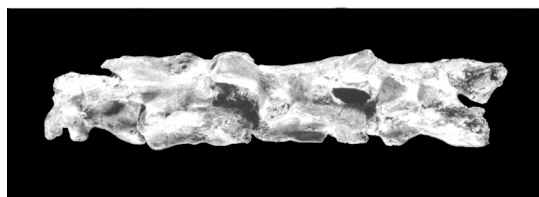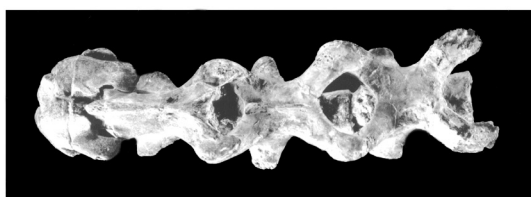

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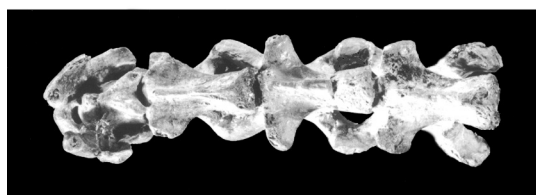
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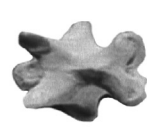
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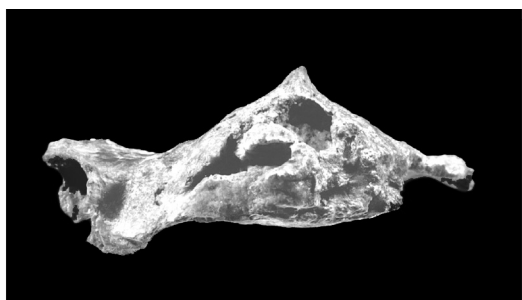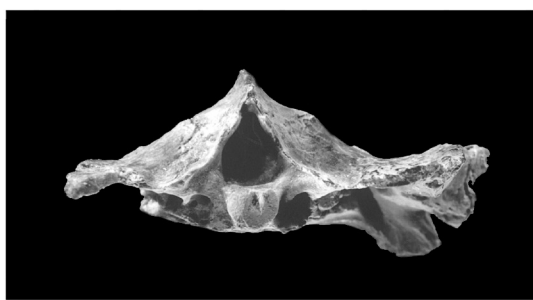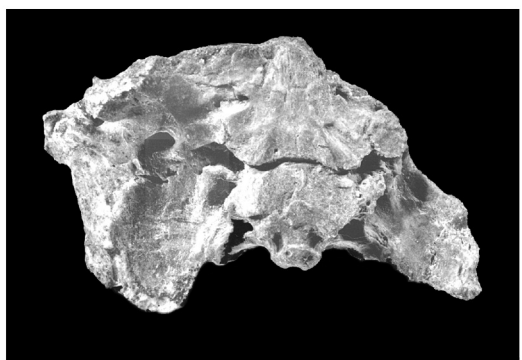
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Plate II

Extant skulls, ventral and ventro-latero-posterior views. A, B: *Chelydra serpentina*, USA, MNHN, AC, 1870-465. C, D: *Platemys platycephala* (SCHNEIDER, 1792), Amazonia. E, F: *Emydura macquarii* (GRAY, 1831). G, H: *Pelusios castaneus* (SCHWEIGGER, 1812). I, J: *Pelomedusa subrufa* (LACÉPÈDE, 1788).

Planche II

Crânes actuels, vues ventrale et ventro-latéro-postérieure. A, B: *Chelydra serpentina*, USA, MNHN, AC, 1870-465. C, D: *Platemys platycephala* (SCHNEIDER, 1792), Amazonie. E, F: *Emydura macquarii* (GRAY, 1831). G, H: *Pelusios castaneus* (SCHWEIGGER, 1812). I, J: *Pelomedusa subrufa* (LACEPÈDE, 1788).

ant, *antrum postoticum*; ante, *antrum* extremity (extrémité de l'*antrum*); cr, squamosal crest (crête squamosale); fg, *foramen externum nervi glossopharyngei* (IX); fh, *foramen externum nervi hypoglossi* (XII); fj, *foramen jugulare*; g, chelid groove or *sulcus chelidianus* (gouttière chélidienne); op, opisthotic; pi, *processus interfenestralis opisthotici*; pop, posterior opisthotic process (processus postérieur de l'opisthothique); ppo, paroccipital process of the opisthotic (processus paroccipital de l'opisthotique); sq, squamosal.
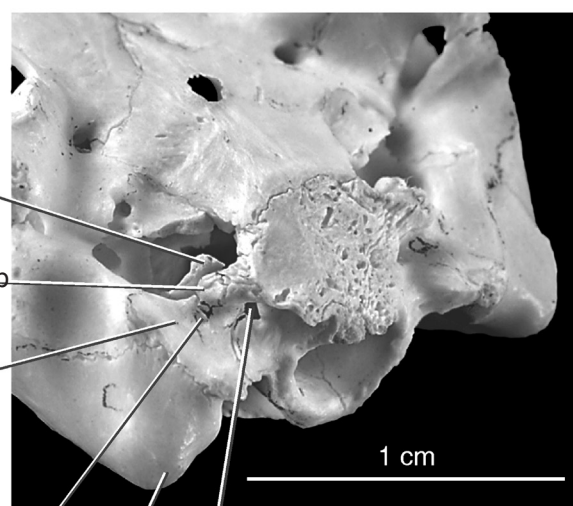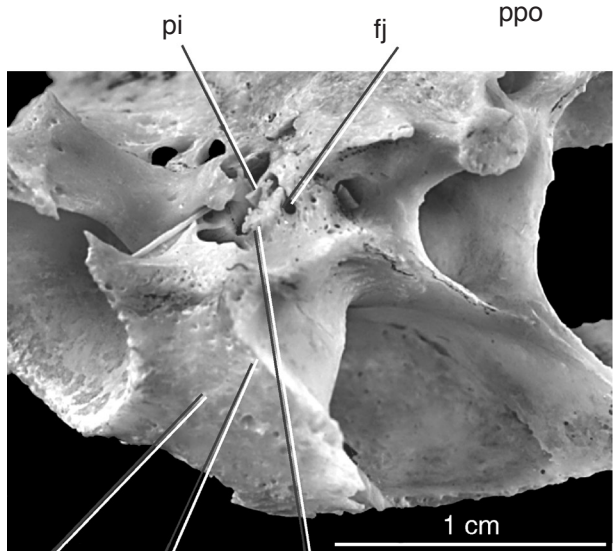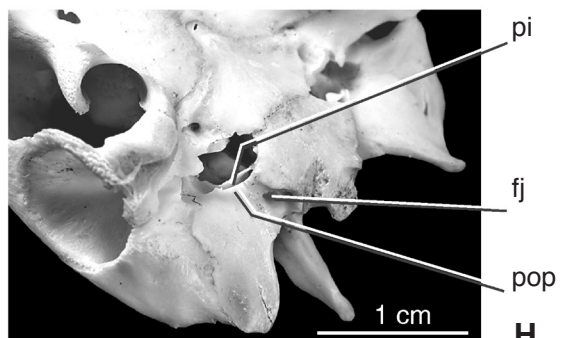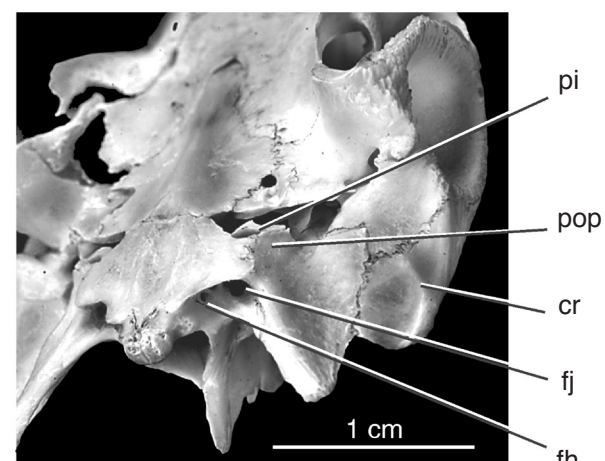
Plate II
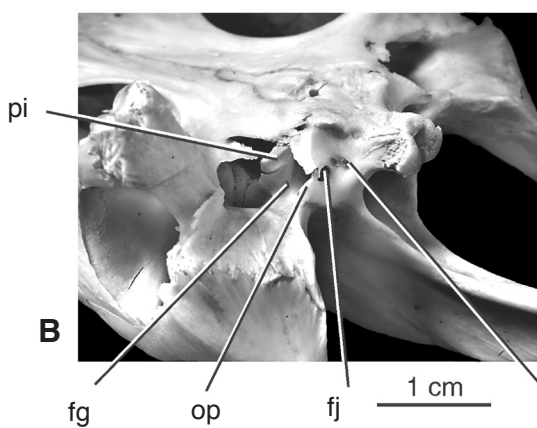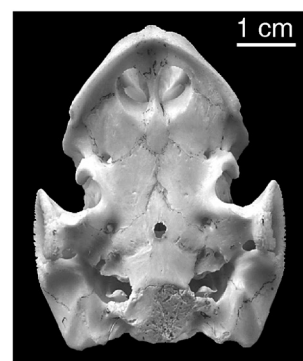
nouvelle faune de Chéloniens dans le Crétacé supérieur européen. *Comptes Rendus de l'Académie des Sciences, Paris*, sér. IIa, 323, (8), a : 729-735.

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