

Palaeontology / Paléontologie
(Vertebrate Palaeontology / Paléontologie des Vertébrés)

Oldest world Chelidae (Chelonii, Pleurodira), from the Cretaceous of Patagonia, Argentina

France de Lapparent de Broin^{a,*}, Marcelo S. de la Fuente^b

^a Laboratoire de paléontologie, UMR 8569 du CNRS, Muséum national d'histoire naturelle, 8, rue Buffon, 75005 Paris, France

^b Facultad de Ciencias y Museo de La Plata, Departamento Palaeontología Vertebrados, Paseo del Bosque S/N, 1900 La Plata, Argentina

Received 9 May 2001; accepted 21 August 2001

Communicated by Philippe Taquet

Abstract – Four new taxa are described. Three of them are attributed to the extant *Phrynops* group: a primitive member, unidentified within the group or related to the large extant *Phrynops* forms; a primitive member of the *Acanthochelys* subgroup, small extant members of the group; a more evolved member, although still primitive, of the large extant *Phrynops*. The fourth is either a representative of an extinct group or a form related to the extant *Chelus* group. The presence of the second taxon in older Patagonian localities, as early as Lower Albian, indicates that the diversification of the extant groups was achieved as early as the Lower Cretaceous. © 2001 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Chelonians / new taxa / Cretaceous / Patagonia / Argentina

Résumé – Les plus anciens Chelidae (Chelonii, Pleurodira) du monde, Crétacé de Patagonie, Argentine. Quatre nouveaux taxons sont créés. Trois sont attribués au groupe *Phrynops* : un membre primitif ou apparenté aux grands *Phrynops* actuels ; un membre primitif du sous-groupe des petits *Acanthochelys* ; un plus récent, plus évolué vers les grands *Phrynops* actuels. Le quatrième est, soit un représentant d'une lignée indépendante éteinte, soit un membre apparenté au groupe *Chelus*. La présence du second, *Prochelidella* n. g., dans d'autres localités de Patagonie, dès l'Albien inférieur notamment, atteste que la diversification des groupes actuels est réalisée à cette date et remonte probablement au moins à la base du Crétacé. © 2001 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

tortues / nouveaux taxons / Crétacé / Patagonie / Argentine

Version abrégée

1. Introduction

Les plus anciennes formes chélidées connues jusqu'à présent proviennent du Nord de la Patagonie. *Yaminuechelys* Fuente et al., 2001 [9], groupe *Hydromedusa–Chelodina*, Campanien–Maastrichtien, fut la première nommée. La description des plus anciennes formes définissables à ce jour dans la famille (données générales) est

donnée dans les références [6, 7, 10, 12, 13, 16, 21]. Les nouveaux taxons (examen préliminaire in [7, 14, 15]) sont d'âge plus ancien que *Yaminuechelys* pour trois d'entre eux ; le dernier est d'âge équivalent.

2. Systématique

O. Chelonii Brongniart (Latreille) 1800, I.O. Pleurodira Cope, 1864, F. Chelidae Gray, 1830.

* Correspondence and reprints.

E-mail addresses: fdelap@cimrs1.mnhn.fr (F. de Lapparent de Broin), mdelafu@museo.fcnym.unlp.edu.ar (M.S. de la Fuente).

Groupe *Phrynops* primitif, ***Bonapartemys* n. g., *B. bajorrealis* n. sp.**, holotype MACN-CH-1469 (figures 1 et 2). Carapace moins une partie à droite, plastron, restes des ceintures, des membres et de la queue. Découverte du Dr Bonaparte à l'«Estancia Ocho Hermanos», Chubut, Argentine, Turonien–Campanien [1, 7–17, 20]. Diagnoses de l'espèce et du genre confondues : grande forme ovale à décoration atténuée, ressemblant à un grand *Phrynops* actuel, mais plus primitif (voir ci-dessous). Apomorphique par le bord postérieur de la carapace, allongé progressivement médialement par les périphériques 8–11 ; à marginales 12 sur la suprapygale, leur longueur augmentant vers le milieu ; vertébrales (V) 2 à 4 bien étrencies et de manière égale, dès l'arrière de la première jusqu'à la cinquième (largeur $V2 = V3 = V4$) ; intergulaire antérieurement étrencie, pont allongé. La crête qui prolonge (plus ou moins longuement) les bords des lobes plastraux à la limite des ponts chez les Chelidae est très marquée, l'antérieure jusqu'aux mésoplastrons.

Groupe *Phrynops*, sous-groupe *Acanthochelys*, ***Prochelidella* n. g., *P. argentinae* n. sp.**, holotype MACN-CH-1680 (figure 3). Partie antérieure de carapace dorsale. Découverte du Dr Bonaparte à l'«Estancia Ocho Hermanos», Chubut, Argentine, Turonien–Campanien [1, 7–17, 20]. Diagnoses de l'espèce et du genre confondues : petite forme basse et large à faible encoche à la cervicale. Engagée dans la voie d'*Acanthochelys*, du groupe *Phrynops*, par la taille petite et la décoration ; relativement évolué par la neurale 1, quadrangulaire, la cervicale relativement (mais modérément) étrencie. Primitif par l'allongement faible de la bordure périphérique antérieure, la nucale courte et large en avant et en arrière, la cervicale moins allongée et étrencie, la présence de neurales, les processus axillaires avancés.

Groupe *Phrynops*, section *Phrynops* s.l., ***Palaeophrynops* n. g., *P. patagonicus* n. sp.**, holotype MACN-RN 906 (figure 4). Parties antérieure et latérale de carapace, du plastron, restes de vertèbres cervicales, fémur et humérus gauches d'un individu. Découverte du Dr Bonaparte à l'«Estancia Los Alamitos», Río Negro, Argentine, Campanien supérieur–Maastrichtien inférieur [2, 4, 5, 7–17, 19]. Diagnoses de l'espèce et du genre confondues : état relativement évolué dans le groupe *Phrynops* par : le bord antérieur de la carapace en arrondi, nettement allongé progressivement depuis les périphériques 3 et au maximum à la nucale, celle-ci étrencie surtout antérieurement, à bord antérieur rectiligne, longue pour sa largeur et par rapport à la carapace ; les vertèbres cervicales allongées modérément et à centrum abaissé, avec postzygapophyses ovales et proches au bout de leur pédicelle commun ; la dilatation de l'intergulaire. Apomorphique par les vertébrales étrencies dès la première, puis la seconde ; l'intergulaire très grande s'évasant depuis l'arrière, à bords latéropostérieurs légèrement concaves et à bords latéroantérieurs arrondis s'étrencissant antérieurement, encadrée par les gulaires très élargies antérieurement.

Groupe *Chelus*?, ***Lomalatachelys* n. g., *L. neuquina* n. sp.**, holotype MOZ 5117P (figure 5). Carapace et plastron avec restes du pelvis. Zone de Loma de La Lata, Neuquén, Argentine, Santonien [3, 7, 15, 19]. Diagnoses de l'espèce et du genre confondues : grande carapace quadrangulaire légèrement étrencie, à partie antérieure allongée (périphériques 4 à 1, pleurales 1, nucale), bord antérieur nucale étrenci, cervicale allongée et étrencie. Spécificité : petite encoche aux marginales 1 et à la nucale, vertébrale 1 de la largeur arrière de la nucale (large) et s'étrencissant postérieurement, vertébrales 2, 3 et 4 bien étrencies progressivement, longues marginales 13 sur la suprapygale, s'allongeant depuis la suture suprapygale–périphérique vers le milieu ; processus axillaires à la mi-largeur postérieure de la périphériques 3 ; lobe antérieur arrondi-quadratique à symphyse épiplastrale un peu allongée, à intergulaire ni étrencie ni élargie en avant. $LP > LA > P$. Caractères primitifs, dont le large bord postérieur nucale.

3. Conclusion

Tous les taxons décrits ici et précédemment [9] présentent, lorsque le caractère est préservé : le bassin suturé à la carapace (pleurodires) ; la relation lâche carapace–plastron, des fontanelles ou sutures lâches pleuro–périphériques, des vertébrales 2 à 4 étrencies (chélidés). Plusieurs ont un rebord latéral périphérique ourlé ou/et deux bombements longitudinaux et une dépression médiane (caractères dérivés de chélidés). Ils ont des caractères chélidés primitifs détaillés ci-dessous (version anglaise), soit pour tous, soit pour quelques-uns d'entre eux seulement. L'évolution homoplasique de ces caractères se fait lignée par lignée. Les processus axillaires s'étendent à la limite des périphériques 2–3 dans le groupe *Phrynops* primitif. La microvermiculation (caractère chélonien) est toujours présente.

Les Chelidae doivent être séparés des Pelomedusoides, nord-gondwaniens, au Jurassique supérieur [6, 7, 13]. Le groupe *Phrynops* est bien représenté au Crétacé supérieur avec *Bonapartemys* n. g., *Palaeophrynops* n. g. et *Prochelidella* n. g. (ou aff.) ; la diversification de ce dernier dès l'Albien inférieur dans d'autres localités de Patagonie [8, 15, 17–19] implique celle des autres *Phrynops* s.l. et aussi celle des autres groupes d'actuels dès cet âge. Le groupe *Hydromedusa–Chelodina* n'est attesté qu'à partir du Turonien–Coniacien [9]. *Lomalatachelys* n. g., santonien, peut, soit être allié au groupe *Chelus* (attesté au Campanien–Maastrichtien [7] de façon sûre), soit représenter une branche latérale de Chelidae, reliée ou non à d'autres grandes formes inédites du Campanien–Maastrichtien patagonien [7, 11, 14]. L'absence de représentants fossiles des taxons australiens actuels et la présence en Patagonie de taxons (non décrits ici), soit encore plus primitifs, soit diversifiés suivant d'autres voies que les actuels [7], montre que la diversification a dû commencer au moins à la base du Crétacé inférieur et que la séparation avec l'Australie a été très ancienne.

1. Introduction

Chelidae are freshwater pleurodire turtles, extant in South America and Australasia [12, 16, 21], that diversified in South-Gondwana [6, 7]. Their phylogeny has been studied only on skull characters of extant forms [10]. Their place in the pleurodire phylogeny has been briefly re-examined [13]. The oldest forms are known from northern Patagonia, including *Yaminuechelys* Fuente et al., 2001 [9], *Hydromedusa-Chelodina* group, Campanian–Maastrichtian. Other chelid forms are described here (preliminary data in [7, 14, 15]). Three new taxa are older in age than *Yaminuechelys* and another one is as old as the latter. When characters are preserved, all the taxa described here and formerly [9] have: pelvis sutured to shell (pleurodires); loose carapace–plastron and pleuro-peripheral contact: fontanelles, hence or loose sutures, narrowed vertebrals 2–4 (chelids). They have peculiar chelid characters, detailed below in the *Bonapartemys* section. Some are derived and present in some chelids (1, 2). Others are primitive chelid characters retained by the four taxa (a to h) or retained by some of them (A to I). Axillary processes at peripherals 2–3 limit (P) characterize the primitive *Phrynops* group. Microvermiculation, a chelonian character that had never been evidenced before in chelids, is always present but variable in morphology.

2. Systematics

Order Chelonii Brongniart (Latreille), 1800

Infra-order Pleurodira Cope, 1864

Family Chelidae Gray, 1830

Primitive *Phrynops* group, *Bonapartemys* n. g.
Bonapartemys bajobarrealis n. sp.

Etymology. Genus, dedicated to Dr Bonaparte and from Greek *ἐμύς*, freshwater turtle; species, from the Bajo Barreal Formation, to which belongs the locality.

Holotype. MACN-CH-1469, carapace, a right posterolateral part lacking, plastron less a right longitudinal part, part of girdles, limbs and tail. Discovered by Dr Bonaparte.

Locality and age. 6 km north to ‘Estancia Ocho Hermanos’, west to Musters Lake, Sierra de San Bernardo, Sarmiento Department, Chubut, Argentina. Upper part of the lower member of Bajo Barreal Formation, Upper Cretaceous, Turonian–Campanian [1, 7–17, 20].

Diagnosis. Same for the genus and species. Large ovale carapace, with an attenuated decoration, similar to large extant *Phrynops*, but with more primitive characters, given below. Apomorphic: posterior border of the carapace medially progressively elongated at peripherals 8–11; marginals 12 on the suprapygal, progressively medially elongated; vertebrals (V) 2 to 4 clearly narrowed, anteriorly as wide as posteriorly (V2 = V3 = V4); anteriorly narrowed intergular, elongated bridge. Plastral lobes are prolonged by a ridge at the bridge limit: the anterior lobe ridge particularly marked, up to the mesoplastra. B > PL > AL.

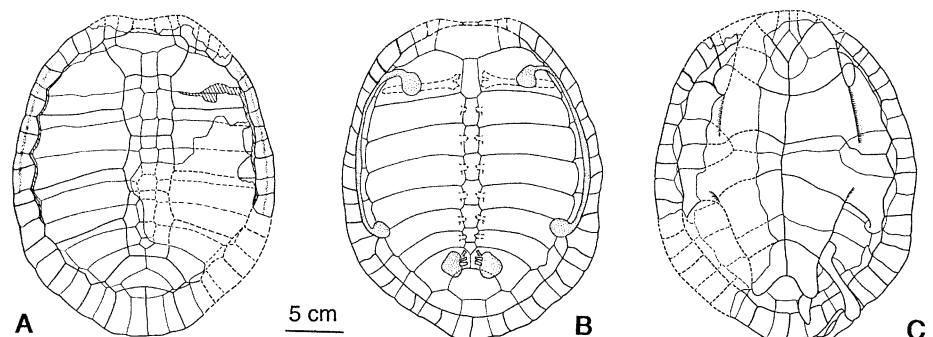
Description. See figures 1 and 2.

Measurements (in mm). Carapace maximal length (L) × width (w): ca 351 (on 341 preserved) × 289. Carapace width: 69. Plastral L: ca 309. L × w, nuchal: ca 40 × 67; of pleural 1: 103.2 × 51.8; of cervical: ca 31 × 58. Lateral and medial L, peripheral 2: 22.7 × 30.9; of peripheral 1: 30.9 × 33. L × w, anterior plastral lobe (AL): ca 93 × 139; of posterior plastral lobe (PL): 104 × 130; of entoplastron: 51 × 49; of left mesoplastron: 51 × 63; of intergular: 42 × 23; of left gular: 22 × 19. Epiplastral medial L: 15. Bridge (B) L: 105.

Additional characters and discussion. Apparent smooth decoration, striations, granulations, localized dichotomic sulci. Microvermiculation. Lateral longitudinal bulgings and medial depression (1). Upwards curled lateral border (2) as anteriorly as from peripheral 3. Primitive by the low form (a), large (A), not

Figure 1. *Bonapartemys bajobarrealis* n. g., n. sp., MACN-CH-1469, ‘Estancia Ocho Hermanos’, Chubut, Argentina, Turonian–Campanian. Carapace. **A**, dorsal view. **B**, inner part reconstruction. **C**, ventral view with plastron.

Figure 1. *Bonapartemys bajobarrealis* n. g., n. sp., MACN-CH-1469, «Estancia Ocho Hermanos», Chubut, Argentine, Turonien–Campanien. Carapace. **A**, face dorsale. **B**, face ventrale de la dossière, reconstitution. **C**, face ventrale avec plastron.



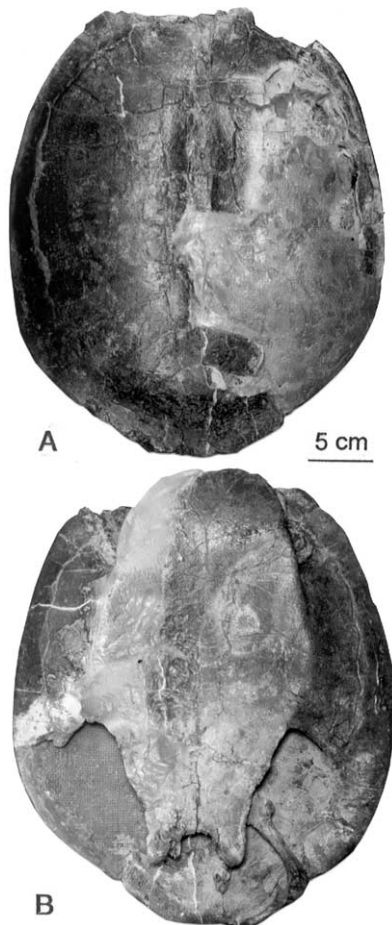


Figure 2. *Bonapartemys bajobarrealis* n. g., n. sp., MACN-CH-1469, 'Estancia Ocho Hermanos', Chubut, Argentina, Turonian–Campanian. Carapace. **A, B**, dorsal and ventral views.

Figure 2. *Bonapartemys bajobarrealis* n. g., n. sp., MACN-CH-1469, «Estancia Ocho Hermanos», Chubut, Argentina, Turonian–Campanian. Carapace. **A, B**, faces dorsale et ventrale.

narrowed (B), anteriorly a little elongated (by the medially and progressively elongated peripherals 3, 2 and 1), moderately (C1), but not elongated pleural 1 and neural 1 (C2); short (D1) anteriorly (D2) and posteriorly (D3) wide nuchal (anteriorly slightly incomplete, notched or not?) with regard to the carapace, short (E1) anteriorly (E2) (probably) and posteriorly (E3) wide cervical, long neural series (b) posteriorly interrupted (reduced 8th not contacting pygal), with anteriorly inversed neurals (F) (hexagonal inverse neural 1, pentagonal neurals 2 and 3), lateral inguinal processes extremity at pleurals 5–6 limit (G), axillary processes prolonged up to mid-thoracic rib 2 (H), anterior plastral lobe (LA) not enlarged (c) with a primitive scute pattern (acquired early in Pleurodira [13]), including a humeropectoral sulcus well posterior to entoplastron (d), long entoplastron (e), lateral mesoplastra relatively long (compared to *Yaminuechelys* [8]) (I) crossed by the

pectoroabdominal sulci (f), converging plastral lateral lobes (g), ischia prolonged in xiphiplastral points (h1), extroverted (h2). Anal notch U shaped, rounded-trapezoidal iliac sutures below pleurals 8 and a small suprapygal part. Stout femur, little curved. *Bonapartemys* n. g. is like large extant *Phrynops* with neurals (such as *P. williamsi*, *P. geoffroanus*, *P. hilarii*) being primitive by the characters given above (lacking particularly the anterior dorsal and ventral strong elongation and the dilated intergular) and with axillary processes at peripherals 2–3 limit (P) (primitive *Phrynops* group). Long and narrow pygal and/or long marginals 12 are present (specific characters), with small variations in shape, in some other chelids, including *Lomalatachelys* n. g. (marginals). *Bonapartemys* n. g. is either a basic member of the group or of a part of the group including large *Phrynops*.

Phrynops group, *Acanthochelys* subgroup,
***Prochelidella* n. g.**
***Prochelidella argentinae* n. sp.**

Etymology. Genus, from Latin 'pro', before, and 'ella', referring to a small form of Chelidae; species, from Argentina, the country.

Holotype. MACN-CH-1680, anterior part of a dorsal carapace, mostly in imprint, showing the anterior border and the three first pleurals and neurals. Preserved bony part of peripherals 1 to 3 (left or right), half nuchal and lateral pleurals 1 and 2. Discovered by Dr Bonaparte.

Locality and age. As for *Bonapartemys bajobarrealis* n. g., n. sp.

Diagnosis. Same for the genus and species. Carapace low (a) and wide (B), with a slight cervical notch. Part of the *Acanthochelys* subgroup of the *Phrynops* group as shown by the small size and decoration; relatively derived within the *Phrynops* group by the quadrangular neural 1 and moderately

narrowed cervical. Primitive with respect to *Acanthochelys* by the moderate elongation of the anterior border of the carapace (C1), the nuchal anteriorly and posteriorly wide (D2–3), the cervical less elongated and narrowed (E-), the presence of neurals (b) and the more anteriorly placed axillary processes (P).

Description. See figure 3.

Measurements (mm). Length (*L*) and width (*w*), of the carapace: ca 20 × 17 (estimated); of the nuchal: 23 × 44; of the pleural 1: 30 × 60. Lateral and medial *L*: peripheral 1: 21 and 19.5; peripheral 2: 18 et 21; cervical *L* × *w*: 11 × 7.

Additional characters and discussion. Apparent smooth decoration. Dense microvermiculation with

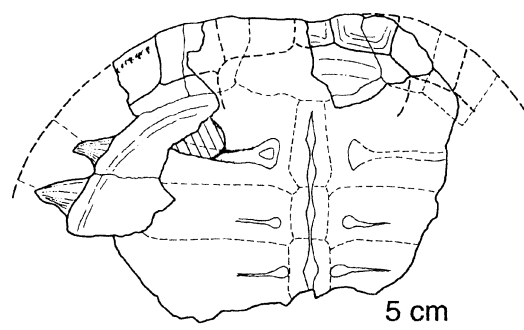


Figure 3. *Prochelidella argentinae* n. g., n. sp., MACN-CH-1680, 'Estancia Ocho Hermanos', Chubut, Argentina, Turonian–Campanian. Dorsal anterior part of carapace, imprint with some preserved plates.

Figure 3. *Prochelidella argentinae* n. g., n. sp., MACN-CH-1680, «Estancia Ocho Hermanos», Chubut, Argentine, Turonien–Campanien. Partie antérieure dorsale de carapace, empreinte avec quelques plaques.

rounded ridges, locally fine sulci delimiting irregular polygons around microvermiculations, as in observed extant *Acanthochelys macrocephala*, *A. radiolata* and *A. pallidipectoris*. Upwards curled and rounded lateral border (2) from peripheral 2. Carapace low (a), transversal contour dorsally rounded; slightly medially elongated peripheral 2 and peripheral 1 (C1) as much elongated medially as laterally; neurals: 1 quadrangular then hexagonal, short sides before; pleural 1 not elongated (C2); strong free rib extremities of the pleural 1 and 2 in the peripherals 3–4 and 4–5; primitive axillary processes (H) at peripherals 2–3 limit (P); moderately wide cervical (E2–3) rather short on the nuchal (E1); costals and vertebral 1 clearly overlapping the peripherals (on 1/3) more than in other taxa studied here; anteriorly wide vertebral 1, up to the midwidth posterior border of the peripheral 1 and narrowing posteriorly. Marked growth annuli. Unpreserved d to h, G and I characters.

Remains of small forms belonging or very close to *Prochelidella argentinae* n. g., n. sp. proceed from: Cerro Los Leones, Cullín Grande upper member, Lohan Cura Formation, Lower Albian [16, 18] (collected by Dr Bonaparte; Museo de Plaza Huincul), El Chocón, Candeleros Formation, Late Albian [8] or Early Cenomanian [17] (Museo de la Universidad del Comahue, Museo de El Chocón), Sierra del Portezuelo, Portezuelo Formation, Neuquén subgroup, Turonian–Coniacian (Museo de Plaza Huincul), Neuquén; such forms were also found in the Río Negro, at Los Alamitos (Los Alamitos Formation), El Abra and El Palomar, localities equivalent in age to the Allen Formation, Upper Campanian–Lower Maastrichtian, which is also the age of the earliest ascertained occurrence in the world of the cryptodire Meiolaniidae and of the first Podocnemididae in Patagonia [3, 7, 9, 11, 14, 15, 19]. The specimens

(most of them isolated plates) indicate the presence of several forms of this *Acanthochelys* subgroup, especially based on the short pygals (rectangular, or posteriorly widened trapeze) well overlapped by the vertebral 5, with a straight posterior border (as *A. radiolata*) or a slightly notched border, rounded (as *A. spixii* and *A. pallidipectoris*), with individual and specific variations: relative measurements and morphology of nuchal (more or less long and notched), cervical, marginals 1 and anterior border; 8th neural prolonged or not up to the pygal; neural 1 quadrangular or hexagonal, short sides behind; upwards curled border beginning more or less anteriorly or not present. Axillary processes at peripherals 2–3 limit. Similar to *Acanthochelys*, on the whole, by the primitive plastral scute pattern, but the intergular is less dilated and there are other primitive characters (c, e, h, I). Apparent decoration may consist of fine dichotomic sulci, locally united in small polygons as in all the *Phrynops* group members, but not strongly marked and salient as in *Yaminuechelys* [9] and its group. The more recent forms (El Palomar, El Abra) are more derived (narrowed cervical, posteriorly shortened entoplastron). *P. argentinae* n. g., n. sp. looks more similar to the oldest forms from Albian. The cervical vertebrae, partly known (El Chocón, biconcave 7ths; El Abra, 7th or 8th [7 (p. 1, figure 3)]) are moderately elongated and depressed, the ventral crest being less notched than in *Palaeophrynops* n. g. and mainly in the extant *Phrynops* group, the monophyletic *Acanthochelys-Platemys* subgroup included [7].

Phrynops group, *Phrynops* s.l. section,

***Palaeophrynops* n. g.**

***Palaeophrynops patagonicus* n. sp.**

Etymology. Genus from Greek *παλαός*, old, and from the genus name *Phrynops*; species from 'Patagonia', region of the fossil discovery.

Holotype. MACN-RN 906. Anterior part of a carapace, morphology mostly seen in imprint, with the anterior border (partial peripherals 1 to 5, left and right), the nuchal, pleurals 1 and 2, neural 1 and 2 (partly); right lateral fragment with lateral part of pleurals 4 to 6 and peripherals 7 and 8; partial plastral anterior lobe, remains of 5 cervicals (only the 4th sufficiently preserved); left humerus and femur. Discovered by Dr Bonaparte.

Locality and age. West Cerro Colorado, northwestern angle of 'Estancia Los Alamitos', close to Arroyo Verde, Valcheta Department, Río Negro, Patagonia, Argentina. Middle part of the Los Alamitos Formation, Upper Cretaceous, Campanian–Maastrichtian [2, 4, 5, 7–17] or more precisely Upper Campanian–Lower Maastrichtian [19].

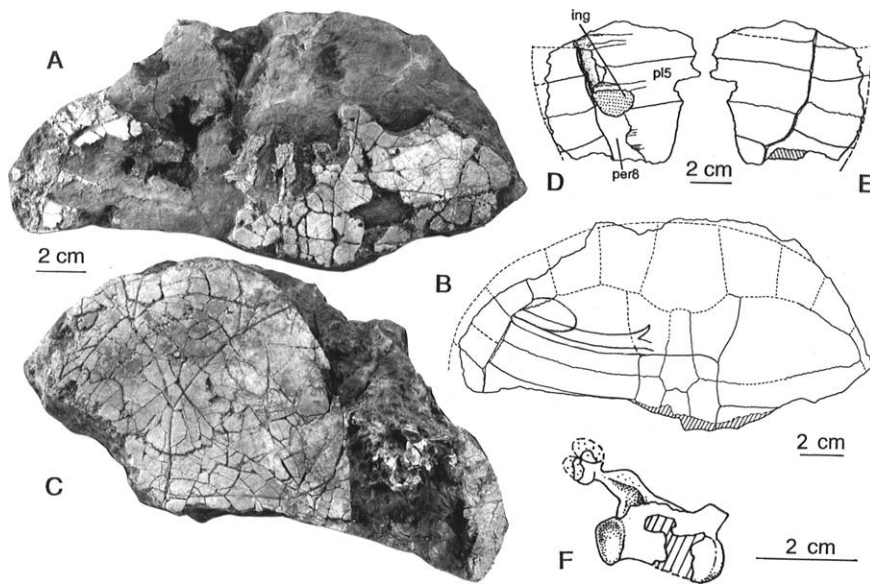


Figure 4. *Palaeophrynopis patagonicus* n. g., n. sp., MACN-RN 906, Los Alamitos, Río Negro, Argentina, Campanian–Lower Maastrichtian. Anterior part of carapace. **A**, dorsal view. **B**, drawing of the dorsal view. **C**, ventral view on the anterior lobe and cervical vertebrae. **D**, **E**, part of the carapace border, ventral and dorsal views. **F**, drawing of the cervical 4, posterior face on the left. **ing**, inguinal process scar, **per8**, peripheral 8, **pl5**, pleural 5.

Figure 4. *Palaeophrynopis patagonicus* n. g., n. sp., MACN-RN 906, Los Alamitos, Río Negro, Argentine, Campanien–Maastrichtien inférieur. Partie antérieure de carapace. **A**, vue dorsale. **B**, dessin de la vue dorsale. **C**, vue ventrale sur le lobe antérieur et les vertèbres cervicales. **D**, **E**, portion du bord de la carapace, faces ventrale et dorsale. **F**, Dessin de la vertèbre cervicale 4, face postérieure à gauche. **ing**, cicatrice du processus inguinal, **per8**, périphérique 8, **pl5**, pleurale 5.

Diagnosis. Same for the genus and species. Relatively derived state in the *Phrynopis* group by the anterior border of the carapace, rounded, clearly progressively elongated (although not as much as possible in chelids) from peripherals 3 up to nuchal; the nuchal narrowed, especially anteriorly (straight anterior border), long with regard to its width and to the carapace; the vertebrals narrowed from anterior part of vertebral 1, and more at vertebral 2; the dilated intergular; the moderately elongated and depressed cervical vertebra 4, with oval and close postzygapophyses facets on a not depressed common process. Apomorphic by its intergular very large, with lateroposterior border slightly concave, widening much anteriorly with rounded convex borders and then more anteriorly much narrowing, the gulars (not contacting entoplastron) much anteriorly widened.

Description. See figure 4.

Measurements (mm). Length (*L*) × width (*w*), carapace (estimated): ca 310 × 230–250. *L* × *w* of nuchal: 48 × 44; of right pleural 1: 44 × 82. Lateral and medial *L* of peripheral 2: ca 26 and 32; of peripheral 1: ca 32 and 40. *L* × *w* of anterior plastral lobe: 105 (preserved) on ca 126 × ca 153; of entoplastron: 56 × 52; of intergular: 62 × 42; of left gular: 28.4 × 33.3. Medial *L* of epiplastra: 25.5. Centrum *L* cervical vertebra 4 25; height, anterior condyle and posterior cotyle: ca 8 and 8.5; full posterior height from base of the crest to top of postzygapophyses: 20.

Additional characters and discussion. Apparent smooth decoration; small dichotomic sulci and some

polygons on the pleuroperipheral fragment. Microvermiculation. Primitive scute pattern (d) but the enlarged intergular is nearly as wide as the entoplastron. Gulars not contacting the entoplastron. Narrowed vertebrals 1 and 2 (V1 at the medial 1/3 of the peripheral 1). Primitive with regard to extant chelids (a, c, d, e, f, B, C2, F, G, H) and to extant *Phrynopis* spp. (P), absence of marked anterior ventral crest and weak ventral notch on the centrum of the cervical 4 (opisthocoealous) with high and narrow posterior cotyle and no inferolateral tuberosities as in *P. tuberculatus*. Characters g, h, E and I not preserved. First modern representative of the group, as demonstrated by the clear anterior elongation of the carapace (C1⁺), but not of the pleurals 1 (C2), the narrowed elongated nuchal and the dilated intergular. Based on its size, appears to be related to large extant *Phrynopis* spp. included in the subgenus *Phrynopis* [12, 21], but these species might form a paraphyletic group. Fragments attributable to *Palaeophrynopis* or affinis have been attested at El Abra [7 (vertebra, p. 1, figure 4)], Los Alamitos and El Palomar (carapace fragments) [7], Campanian–Maastrichtian.

Chelus group?, **Lomalatachelys** n. g.
Lomalatachelys neuquina n. sp.

Etymology. Genus name from the locality, Loma de La Lata, and from Greek χέλυσ, turtle; species from the province of Neuquén.

Holotype. MOZ 5117P, carapace and plastron, remains of pubis and ischia.

Locality and age. Loma de La Lata zone (75 km northwest from Neuquén City), Confluencia Department, Neuquén, NW Patagonia, Argentina. Bajo de la

Figure 5. *Lomalatachelys neuquina* n. g., n. sp., MOZ 5117P, Loma de La Lata, Neuquén, Argentina, Santonian. Carapace with plastron. **A, B**, dorsal and ventral views. **C**, inner posterior part of the carapace showing the inguinal processes and the iliac scars. **D**, dorsal part of the posterior plastral lobe showing some remains of the pubis and ischia and their scars on the xiphiplastron.

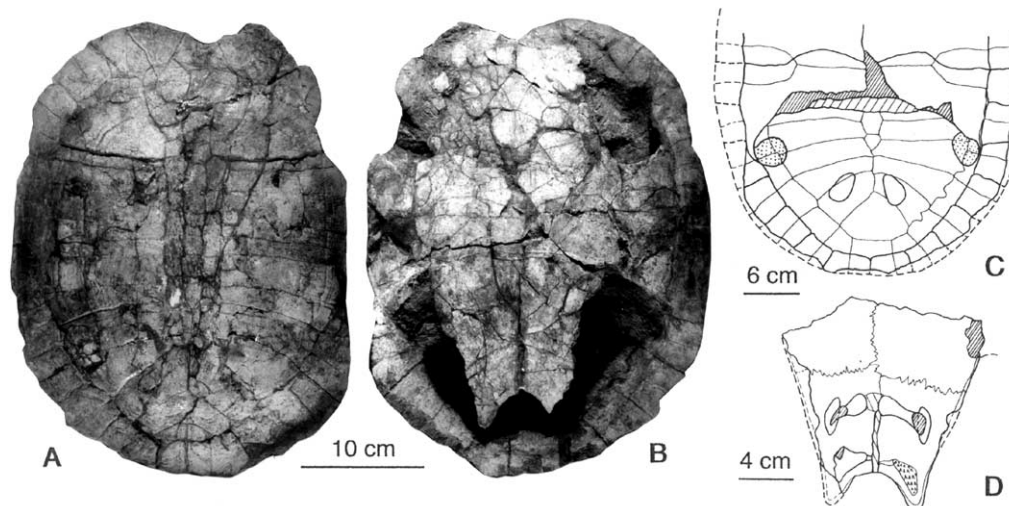


Figure 5. *Lomalatachelys neuquina* n. g., n. sp., MOZ 5117P, Loma de La Lata, Neuquén, Argentine, Santonien. Carapace avec plastron. **A**, vue dorsale. **B**, vue ventrale avec plastron. **C**, vue postérieure interne montrant les cicatrices des processus inguinaux et des ilions ; **D**, partie dorsale du lobe postérieur plastral, avec les restes des pubis et des ischions et de leurs cicatrices sur le xiphiplastron.

Carpa Formation, Río Colorado sub-group, Neuquén group, Upper Cretaceous, Santonian [3, 7–15, 19].

Diagnosis. Same for the genus and species. Large quadrangular carapace slightly narrowed, with elongated anterior border (peripherals 4 to 1, pleurals 1, nuchal narrowed anterior nuchal border, elongated and narrowed cervical). Specific characters: slight notch at mid-peripherals 1 (from marginals 1) and nuchal; vertebral 1 narrowed at the nuchal width and vertebrae 2, 3 and 4 clearly but progressively narrowed; long marginals 13 on the suprapygal, progressively elongated from their lateral border at suprapygal-peripheral suture; axillary processes at mid-length of peripherals 3; rather quadrate anterior lobe with slightly elongated epiplastral symphysis and neither widened nor narrowed intergular. $PL > AL > B$. Primitive posterior wide nuchal border and other characters (see below).

Description. See figure 5.

Measurements (mm). Maximal length (L) \times width (w) of the carapace: $385 \times 290?$ Plastral L : 323. Nuchal $L \times w$: $?67 \times 85$; of the pleural 1: 58.1×104.3 ; of the cervical: 2.8×1.7 . Lateral L and medial L , peripheral 2: 48.5×52 ; peripheral 1: 52×62 . $L \times w$, anterior plastral lobe (AL): 116×166 ; of plastral posterior lobe (PL): 130×150 ; of entoplastron: 66×48 ; of left mesoplastron: 39×61 ; of intergular: 60×33 ; of left gular: 32×29 . Medial L of epiplastron: 25; of bridge (B): ca 88–95.

Additional characters and discussion. Presence of occasional derived chelid characters (1, 2) and primitive chelid characters (a, b, d, e, f, g, A, D3, F, G,

I). Anomalous specimen (9 pairs of pleurals, 13 of marginals, 12 of peripherals; vertebral 5 seeming wide because of supplementary elements, dissymmetric sutures of the ilia, left one below pleural 9 and suprapygal short part, right below short part of 7th and 8th). Seven neurals. Apparent smooth decoration with localized polygons, granulations and short dichotomic sulci; some radiating striations preserved below some vertebrae and costals; marked dorsal wide growth annuli. Microvermiculation with rounded ridges and pits. Elongation of the peripherals 8 to 12, maximum at 10–11th (in extant chelids: peripherals 7 or 8 to 11, maximum at 9th, or 9–10th in *Chelus*). Similar to *Chelus* by the large preserved size and by: quadrangular carapace shape, similarly elongated anterior elements, scute radiations and plastral shape (synapomorphies?); absent dentations and protuberances of *Chelus*. The *Chelus* group is attested at Los Alamitos, Campanian–Maastrichtian [7]. There are other large forms unidentified below family level, related or not with *Lomalatachelys*, in Patagonia at Ranquilco, Los Alamitos, Trapal-có and La Colonia [7, 11, 14], Campanian–Maastrichtian.

3. Conclusion

The three oldest studied taxa have the greatest number of primitive characters: *Bonapartemys* n.g., a basic member of the *Phrynops* group or of large *Phrynops*, *Prochelidella* n. g., part of the subgroup of small *Acanthochelys*, Turonian–Campanian, and *Lomalatachelys* n. g., Santonian. The latter belongs either to the *Chelus* group (which is already attested in the Campanian–Maastrichtian [7]), or to a lateral che-

lid branch related or not with other large unidentified chelid forms [7, 11, 14]. The younger *Palaeophrynops* n. g., Campanian–Maastrichtian as *Yaminuechelys* Fuente et al., 2001 [9], is a member of the more evolved large extant *Phrynops*. The *Hydromedusa–Chelodina* group, not present among the new taxa, is known during the Turonian–Coniacian [9], anterior to the *Yaminuechelys* described specimen. Forms belonging or close to *Prochelidella* n. g. represent the oldest Chelidae (Early Albian). The early diversification of the *Phrynops* group, as early as the Lower Al-

bian, entails that the other groups were also diversified at that time. Our knowledge shows that Chelidae separated from Pelomedusoides during the Late Jurassic at least [6, 7, 13]. There are no Patagonian fossil representatives of the Australian taxa in the named material. Other Patagonian taxa, not yet identified and poorly preserved are either primitive or diversified otherwise than in the extant lines [7], which means that diversification began very early, during the Earliest Cretaceous or before, and separation from Australia is very old [16].

Acknowledgements. We thank J.-C. Rage (report and English correction), M.-C. Groessens Van Dyck (report). We thank also, for their welcome and for the material, J. Bonaparte (Buenos Aires), R. Pascual (La Plata), S. Cocca (Zapala), R. Coria (Plaza Huincul), J.O. Calvo and L. Salgado (Neuquén), R.D. Carolini (El Chocón), P. Vanzolini, A.M. Malva Ramos and M. Trefaut Rodrigues (USP); F. Castets (La Plata) and D. Serrette (MNHN, Paris) (photographs), O. Molina and J. Moly (La Plata) (material preparation), J. Gonzalez (La Plata) and F. Pilard (MNHN, Paris) (drawings).

References

- [1] Barcat C., Cortiñas J.S., Nevistic V.A., Zucchi H.E., Cuenca Golfo San Jorge, in: Chebli G., Spalletti L.A. (Eds.), Cuenca Sedimentarias Argentinas, Serie Correlación Geológica n 6, Trabajos X Congreso Argentino, San Miguel de Tucumán 1987, Instituto Superior Correlación Geológica, Univ. Nac. Tucumán, San Miguel de Tucumán, pub. 1430, 1989, pp. 319–345.
- [2] Bonaparte J.F., New Late Cretaceous Mammals from the Los Alamitos Formation, Northern Patagonia, *Nat. Geog. Res.* 6 (1) (1990) 63–93.
- [3] Bonaparte J.F., Los vertebrados fósiles de la Formación Río Colorado, de la ciudad Neuquén y cercanías, Cretácico superior, Argentina, *Rev. Mus. Argent. Cienc. Nat. “Bernardino Rivadavia”*, *Paleont.* 4 (3) (1991) 15–123.
- [4] Bonaparte J.F., Franchi M.R., Powell J.E., Sepulveda E., La Formación Los Alamitos (Campaniano–Maastrichtiano) del sudeste de Río Negro, con descripción de *Kritosaurus australis* n. sp. (Hadrosauridae). Significado paleogeográfico de los vertebrados, *Rev. Asoc. Geol. Argent.* 39 (3–4) (1984) 284–299.
- [5] Broin F. de, The Late Cretaceous Fauna of Los Alamitos, Patagonia, Argentina. Part IV. Chelonia, *Rev. Mus. Argent. Cienc. Nat. “Bernardino Rivadavia”*, *Paleont.* 3 (3) (1987) 131–139.
- [6] Broin F. de, Les Tortues et le Gondwana. Examen des rapports entre le fractionnement du Gondwana et la dispersion géographique des Tortues pleurodires à partir du Crétacé, *Stud. Geol. Salm., Studia Palaeocheloniologica II* (5) (1988) 103–142.
- [7] Broin F. de, De la Fuente M.S., Les tortues fossiles d’Argentine, *Ann. Paléontol.* 79 (3) (1993) 169–231.
- [8] Calvo J.O., Dinosaurs and other vertebrates of the Lake Ezequiel Ramos Mexia Area, Neuquén–Patagonia, Argentina, in: Tomida Y., Rich T.H., Vickers-Rich P. (Eds.), *Proc. 2nd Gondwanan Dinosaur Symposium, National Science Museum Monographs*, Vol. 15, Tokyo, 1999, pp. 13–14.
- [9] De la Fuente M., Lapparent de Broin F. de, Manera de Bianco T., The oldest and first nearly complete skeleton of a chelid, of the *Hydromedusa* sub-group (Chelidae, Pleurodira), from the Upper Cretaceous of Patagonia, *Bull. Soc. géol. France* 172 (2) (2001) 105–112.
- [10] Gaffney E.S., The side-necked turtle family Chelidae: a theory of relationships using shared derived characters, *Amer. Mus. Nov.* 2620 (1977) 1–28.
- [11] Gasparini Z., De la Fuente M.S., Tortugas y plesiosaurios de la Formación La Colonia (Cretácico Superior) de Patagonia, Argentina, *Rev. Esp. Paleont.* 15 (1) (2000) 23–35.
- [12] Iverson J.B., A Revised Checklist with Distribution Maps of the Turtles of the World, Privately Print, Richmond, IN, 1992, 363 p.
- [13] Lapparent de Broin F. de, The oldest Podocnemidoid turtle (Chelonii, Pleurodira), from the Early Cretaceous, Ceará state, Brasil, and its environment, *Treballs Mus. Geol. Barcelona*, in press.
- [14] Lapparent de Broin F. de, De la Fuente M.S., Particularidades de la fauna continental de tortugas del Cretácico de Argentina, in: XIV Jornadas Argentinas de Paleontología de Vertebrados, 18–20 Mayo 1998, Neuquén, Ameghiniana, 36, 1, 1999, 104 p.
- [15] Lapparent de Broin F. de, De la Fuente M.S., Calvo J., Presencia de los mas antiguos quelidos (tortugas pleurodiras) en el Cretácico inferior de ‘El Chocón’, provincia del Neuquén, Argentina, in: XIII Jornadas Argentinas de Paleontología de Vertebrados, La Rioja, 11–15 Mayo 1997, Ameghiniana, 34, 4, 1997, 538 p.
- [16] Lapparent de Broin F. de, Molnar R., Eocene chelid turtles from Redbank Plains, southeastern Queensland, Australia, *Geodiversitas* 23 (1) (2001) 41–79.
- [17] Leanza H.A., The Jurassic and Cretaceous Terrestrial beds from Southern Neuquén Basin Field Guide, Instituto Superior de Correlación Geologica (INSUGEO), Miscelanea 4 (1999) 3–30.
- [18] Leanza H.A., Hugo C.A., Revisión estratigrafica del Cretácico Inferior continental en el ambito sudoriental de la Cuenca Neuquina, *Rev. Asoc. Geol. Argent.* 50 (1–4) (1995) 30–33.
- [19] Leanza H.A., Hugo C.A., Geología y Recursos Minerales de la Hoja Geológica 3966–III, Villa Regina, Servicio Geológico Minero Argentino, Viedma, 1999, pp. 1–91.
- [20] Martinez R., Giménez O., Rodríguez J., Bochaty G., *Xenotarsosaurus bonapartei* nov. gen. et sp. (Carnosauria, Abelisauridae). Un nuevo Theropoda de la Formación Bajo Barreal, Chubut, Argentina, in: IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza, 2, 1986, pp. 23–31.
- [21] Wermuth H., Mertens R., Schildkröten–Krokodile–Brückenechsen, Gustav Fischer Verlag, Jena, 1961, pp. 1–422.