

TWO NEW PLEURODIRAN TURTLES FROM THE PORTEZUELO FORMATION (UPPER CRETACEOUS) OF NORTHERN PATAGONIA, ARGENTINA

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ABSTRACT—The chelonian fauna of the Portezuelo Formation (Turonian-Coniacian), outcropping at Sierra del Portezuelo (Neuquén province, Argentina), is reported. Two new taxa of pleurodiran turtles are described. One of them is *Prochelidella portezuelae* new species, a short-necked chelid closely related to extinct species of the Lohan Cura (Albian), Candeleros (Cenomanian), and Bajo Barreal (Turonian) formations from northwestern and central Patagonia, and to the extant species of the genus *Acanthochelys*. The other is *Portezueloemys patagonica* new genus and species, a member of the epifamily Podocnemidoidea, and is considered the sister group of the family Podocnemididae. This discovery confirms the coexistence in northwestern Patagonia of a north gondwanan component (Pelomedusoides) and a south gondwanan element (Chelidae) during the Turonian-Coniacian.

INTRODUCTION

FIELDWORK CONDUCTED by Dr. Fernando Novas from 1990 to 1998 at the outcrops of the Portezuelo Formation (Late Turonian–Early Coniacian, see Hugo and Leanza, 1998; Leanza, 1999) Neuquén Basin, in northwestern Patagonia resulted in the discovery of several fossil reptiles. The crew was from the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires), Museo “Egidio Feruglio” (Trelew, Chubut province), and Museo “Carmen Funes” (Plaza Huincul, Neuquén province). These findings notably increased the known vertebrate fauna of the Portezuelo Formation, yielding theropod maniraptorans (*Patagonykus puertai* Novas, 1997; *Unenlagia comahuensis* Novas and Puerta, 1997; *Megaraptor namunhuaiquii* Novas, 1998), crocodylomorphs, and turtles. The turtles are represented by three side-necked specimens of moderate size. One of them was assigned to the Family Chelidae because of the chelid-like morphology of the shell, and the fifth and eight biconvex cervical vertebrae. The two others have the shell design and cranial morphology of podocnemidoid pelomedusoid turtles.

In this article the chelonian fauna of the Portezuelo Formation is described. Chelonians are represented by two new taxa, one of a short-necked chelid and the other of a podocnemidoid turtle. These species add new information on the paleobiodiversity of the gondwanan side-necked turtles. In addition, this is the first record of an association of taxa belonging to the two main groups of pleurodiran turtles (Chelidae and Pelomedusoides) in an Upper Cretaceous horizon of Patagonia. This discovery confirms the coexistence in northwestern Patagonia of north gondwanan (Pelomedusoides) and south gondwanan (Chelidae) representatives during the Turonian-Coniacian. The paleobiogeographic significance of this discovery is discussed.

MATERIAL AND METHODS

Specimens examined for this study are deposited in the “Museo Carmen Funes de Plaza Huincul” (MCF-PVPH), Neuquén Province, Argentina; Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” de Buenos Aires (MACN); and Museo Provincial “Carlos Ameghino” de Cipolletti, Río Negro Province (MCRN). Because the cladistic analysis on the morphological characters of extant chelid species (Gaffney, 1977) was made using mostly traits of the skull, not preserved in the holotype of *Prochelidella portezuelae*, alpha taxonomy was used for the systematic treatment of *Prochelidella portezuelae* n. gen and sp. and related taxa; however, a cladistic analysis was performed to establish the phylogenetic relationships of *Portezueloemys patagonica*. Characters were analyzed using parsimony to elucidate Hennigian synapomorphies (Hennig, 1968). Morphological data were

examined using Goloboff’s parsimony based on NONA (1993). Terminal taxa included in the analysis are *Notoemys*, Chelidae, *Araripemys*, Pelomedusidae, Bothremyididae, *Brasilemys*, *Hamadachelys*, *Portezueloemys*, Erymnochelyinae, and Podocnemidinae. The taxa of the epifamily Podocnemidoidea (see Lapparent de Broin, 2000) are included in the ingroup, the other taxa are outgroups. The main sources of the fifty morphological characters used in this analysis were the studies of Gaffney and Meylan (1988), Gaffney et al. (1991), Meylan (1996), Lapparent de Broin and Murelaga (1999), and Lapparent de Broin (2000). Multistate characters were treated as non-additive to avoid a priori assumption of polarity. Appendix 1 includes the character description and data matrix analyzed with NONA (Goloboff, 1993). Consistency (Kluge and Farris, 1969) and retention (Farris, 1989) indices were calculated excluding autapomorphies. NONA was run using heuristic searches with random additional sequences. Optimization of characters (slow optimization) was performed using WINCLADA Beta version (Nixon, 1999–2000). This DELTRAN optimization is followed because, as Hirayama (1998) suggested, it is slightly more conservative in terms of assigning synapomorphies to clades in a data matrix with a significant amount of missing data.

SYSTEMATIC PALEONTOLOGY

Order CHELONII Brongniart, 1800

Infraorder PLEURODIRA Cope, 1864

Family CHELIDAE Gray, 1825

Genus PROCHELIDELLA Lapparent de Broin and de la Fuente, 2001

Type species.—*Prochelidella argentinae* Lapparent de Broin and de la Fuente, 2001; figured in Lapparent de Broin and de la Fuente, 2001, figure 3.

Emended diagnosis.—Chelid turtle having a low and wide carapace with slight cervical notch. Carapace length from small (120 mm) to moderate size (270 mm). Shell having a dense microvermiculation with rounded ridges as in the extant species of *Acanthochelys*. Differs from the extant taxa assigned to *Phrynosops* sensu lato in the quadrangular neural 1, and in the narrow anterior plastral lobe. Differs from *Acanthochelys* in the moderate elongation of the anterior border of the carapace, in the nuchal and cervical width, the presence of neurals, and the more anteriorly placed axillary processes.

PROCHELIDELLA PORTEZUELAE new species

Diagnosis.—Short-necked chelid having a carapace with a wide nuchal bone and a wide cervical scale. First neural in a narrow contact with nuchal. Short, wide, laterally placed mesoplastra. Plastral bridge extends from the posterior part of third

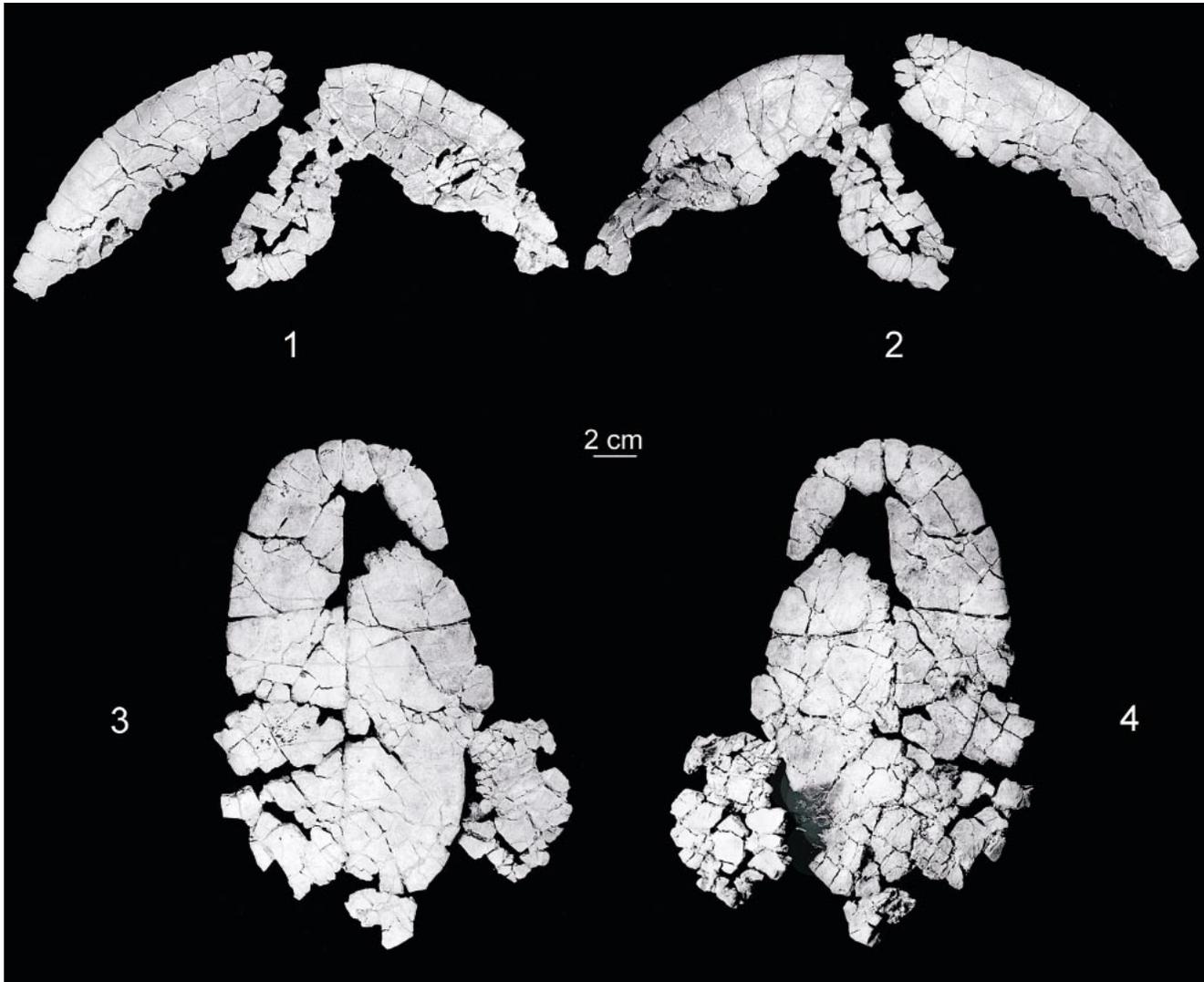


FIGURE 1—*Prochelidella portezuelae* n. sp. MCF-PVPH- 161. Carapace; 1, dorsal view; 2, visceral view. Plastron; 3, ventral view; 4, visceral view.

peripheral bone and first pleural to seventh peripheral. Third to eighth cervical vertebrae all slightly longer than high. Differs from *Prochelidella argentinae* in the moderate shell size, in the more posterior axillary buttress, and in the form and proportion of the first and second marginal scutes. Differs from the other extant species of *Acanthochelys* in the presence of postzygapophyseal articular facets broadly expanded and nearly joined in the fifth cervical vertebra, and in the strong development of the ventral keel of the eighth cervical vertebra.

Etymology.—"Portezuelae," from Sierra del Portezuelo toponymic locality of Neuquén, Argentina.

Type.—Holotype, Museo Municipal "Carmen Funes" of Plaza Huincul MCF-PVPH- 161. Anterior margin of the carapace and nearly complete plastron, left atlantal arch, and other five cervical vertebrae (third or fourth, fifth, sixth, seventh and eighth), both pectoral girdles, left and right humeri and medio-distal extremities of the femora.

Occurrence.—Portezuelo Formation (see Leanza, 1999). Upper Cretaceous (Late Turonian-Early Coniacian); Hugo and Leanza (1998), Leanza (1999). Sierra del Portezuelo, Neuquén Province, Argentina (see locality map Novas, 1997, fig. 1).

Description.—The carapace is low and wide (Figs. 1.1, 1.2, 2.1, 2.2) with a slight nuchal notch, moderate in size (estimated carapace length 270 mm), equivalent in size to large specimens of *Acanthochelys macrocephala*. The carapace ornamentation consists of dense microvermiculation with rounded ridges, and locally fine sulci delimiting irregular polygons around microvermiculations, as observed in extant *Acanthochelys macrocephala*, *A. radiolata*, *A. pallidipectoris*, and *Phrynops gibbus*. *Prochelidella portezuelae* is a primitive relative to *Acanthochelys* based on the moderate elongation of the anterior border of the carapace. The nuchal is anteriorly and posteriorly wide, with a relatively wide cervical scute. The lateral border is upwardly curled and rounded from peripheral 2; slightly medially elongated peripheral 2, and peripheral 1 is as much elongated medially as laterally. Neurals: 1 quadrangular, then hexagonal, short sides in front. Pleural 1 is not elongated. Axillary processes are midway to peripherals 3; costals and vertebral scute 1 overlapping the peripherals (on 1/3) as in *Prochelidella argentinae* Laparent de Broin and de la Fuente, 2001; anteriorly wide vertebral 1 up to the suture between posterior border of peripherals 1–2 and narrowing posteriorly.

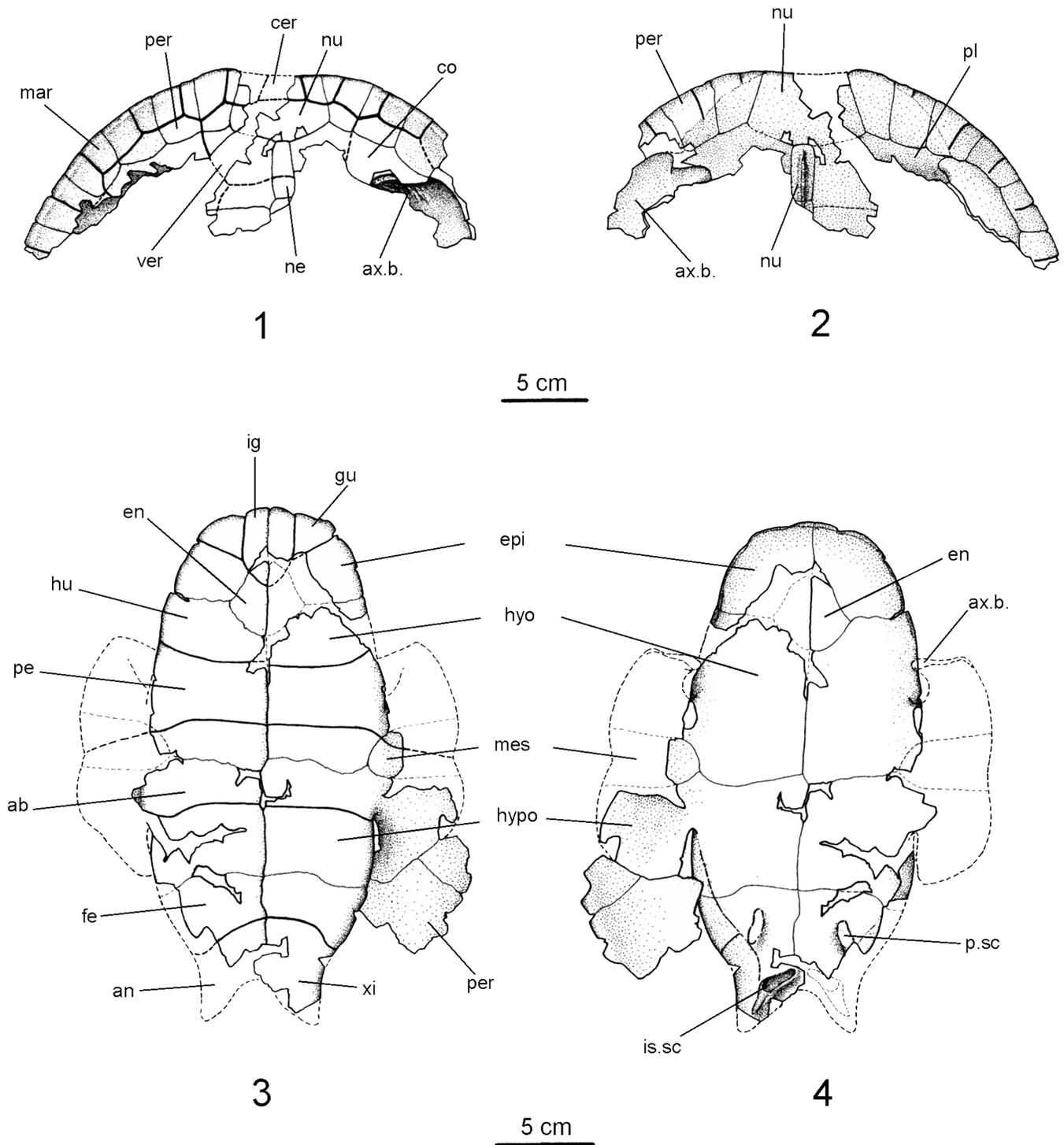


FIGURE 2—*Prochelidella portezuelae* n. sp. MCF-PVPH-161. Carapace; 1, dorsal view, 2, visceral view. Plastron; 3, ventral view; 4, visceral view. Abbreviations: ab = abdominal scale, an = anal scale, ax.b. = axillary buttress, cer = cervical scale, co = costal scale, en = entoplastron, ep = epiplastron, fe = femoral scale, gu = gular scale, ig = intergular scale, gu = gular scale, hyo = hyoplastron, hypo = hypoplastron, hu = humeral scale, is.s. = ischium scar, mar = marginal scale, mes = mesoplastron, ne = neural, nu = nuchal bone, pe = pectoral scale, per = peripheral bone, pl = pleural bone, p. sc. = pubic scar, ver = vertebral scale.

The plastron (Figs. 1.3, 1.4, 2.3, 2.4) is moderate in size (249 mm length on the midline). The narrow anterior plastral lobe is subquadrangular in shape with subparallel lateral margins, in contrast to the enlarged lobe in *Acanthochelys radiolata* or

Phrynops gibbus. The plastron has a primitive scute pattern, including a simple gular-intergular scheme with gular scutes on the epiplastra and a small intergular scute, a humeropectoral sulcus well posterior to a long entoplastron, and relatively short

and wide lateral mesoplastra (compared to *Bonapartemys* Lapparent de Broin and de la Fuente, 2001) crossed by the pectoroabdominal sulcus. Although slightly longer than the anterior lobe, the posterior plastral lobe is the longest plastral element. The posterior lobe is almost twice the axillo-inguinal length of the bridge. The relatively small intergular scute has parallel sides and extends to the anterior third of the entoplastron, in contrast to the large intergular scute of *Palaeophrynops patagonicus* Lapparent de Broin and de la Fuente, 2001. The interfemoral seam is longer than any of the medial seams of the plastron. The interanal and interpectoral seams are the shortest, while the subequal interhumeral and interabdominal seams are of intermediate length. The curved lateral sides of the posterior plastral lobe are slightly constricted at the level of the femoro-abdominal scute sulci and strongly constricted at the femoroanal scute sulci. On the visceral side of the left xiphiplastron the elongated pubis and ischium scars are apparent.

A fragment of the left atlantal neural arch (Fig. 3.1, 3.2) is preserved in *Prochelydella portezuelae* n. sp., one of the four elements of the atlas complex (a pair of neural arches, one intercentrum, and one centrum are usually present). As is typical for turtles, this neural arch is divided into a dorsal portion covering the spinal cord, and a ventral portion bearing an articular facet for the occipital condyle. The posteriorly directed postzygapophysis that normally articulates with the axis is not preserved. The morphology of the atlantal arch is consistent with the generalized chelonian pattern of short-necked chelids. In long-necked chelids such as *Hydromedusa* or *Chelodina* the sutures between the different atlantal elements vanish and this first cervical vertebra reaches a great length.

A possible third or fourth cervical vertebra is partially preserved (Fig. 3.3–3.7). The cotyle is convex and distinctly subpentagonal. The right prezygapophysis is nearly horizontal. The left transverse process is well developed. On the base of the neural arch, a shallow neural crest is more developed than in other cervical vertebrae of the series. The ventral keel is partially broken, but is observed to vanish near the middle of the ventral surface of the vertebra. The posterior articular surface of the centrum and the postzygapophyses are not preserved.

A fifth cervical vertebra is well preserved in *Prochelydella portezuelae* n. sp. (Fig. 4.1–4.6). The prezygapophyses are not preserved and the left transverse process is almost complete. The centrum is narrow with a curved and strong ventral keel that vanishes near the posterior end. The centrum is biconvex. The cotyle is subquadrangular and the condyle is suboval. The fifth cervical is similar to that of *Acanthochelys radiolata*, though larger and with other peculiarities that differentiate it from this and other living species of *Phrynops* s.l. Contrary to the condition present in *Acanthochelys* and other species of *Phrynops* s.l., the postzygapophyseal articular facets of *Prochelydella portezuelae* n. sp. are more developed and though separated, they are very close together. However, the postzygapophyses are not joined to form a discontinuous semicircular articular surface. Joined postzygapophyses are seen in long-necked species of the *Chelodina-Hydromedusa* group among chelids and in *Araripemys* among the pelomedusoids (see Meylan, 1996).

A possible sixth procoelus cervical vertebra is partially preserved (Fig. 5.1–5.5). A strong ventral keel is developed. The transverse processes are well developed. The cotyle is concave and heart-shaped. The prezygapophyses are slightly raised from horizontal. The condyle and the postzygapophyses are not preserved.

The seventh cervical vertebra is biconcave (Fig. 6.1–6.6) and is well preserved. The cotyle is subquadrangular in outline and slightly wider than high, while the condyle is subquadrangular,

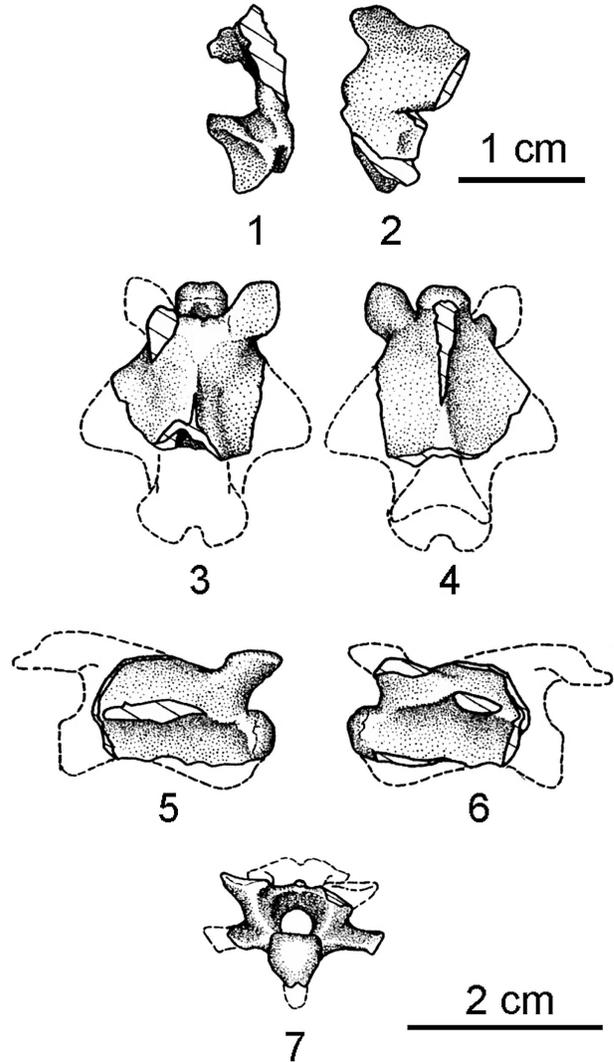


FIGURE 3—*Prochelydella portezuelae* n. sp. MCF-PVPH-161. Atlantal arch; 1, anterior view, 2, lateral view. Third or fourth cervical vertebra; 3, dorsal view; 4, ventral view; 5, right lateral view; 6, left lateral view; 7, anterior view.

but higher than wide. The centrum of the seventh cervical vertebra is narrow with a curved ventral keel as strongly developed as on the fifth vertebra. This keel extends almost to the ventral margin of the condyle. The neural arch contributes to the transverse process, and forms widely spaced prezygapophyses, of which only the right one is complete. The articular facets of the prezygapophyses are slightly inclined from the horizontal, as in those of *Phrynops hilarii*, but not so angled as in *Acanthochelys radiolata* or *A. macrocephala*. The postzygapophyses are completely separated from each other as in other extant species of the *Phrynops* group. The zygapophyseal facets are ventro-laterally oriented.

A nearly complete eighth cervical vertebra (Fig. 7.1–7.6) is also preserved. The centrum is biconvex, with a subquadrangular cotyle and a subcircular condyle. The neural arch contributes to the transverse process. The left transverse process is completely preserved and well developed. The prezygapophyses are not preserved. The neural spine is more strongly developed than the

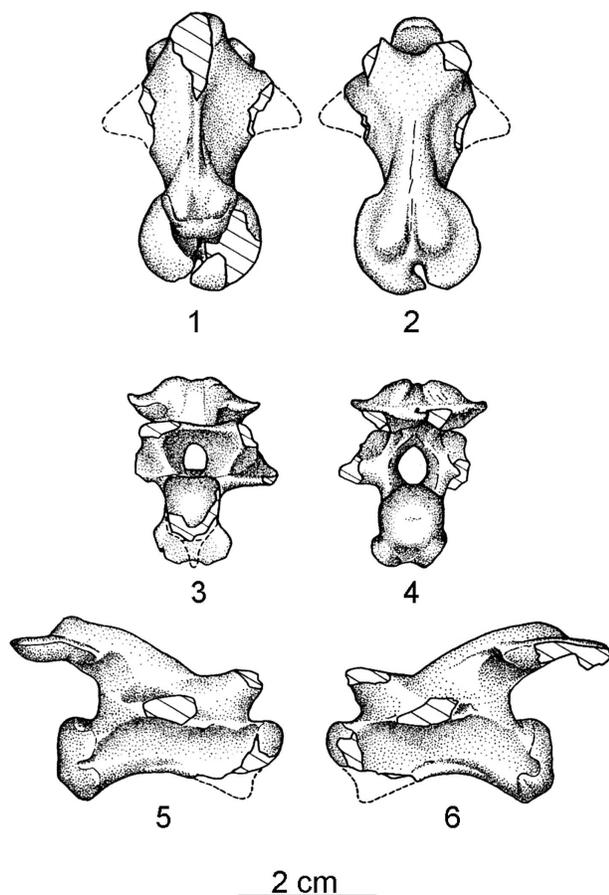


FIGURE 4—*Prochelidella portezuelae* n. sp. MCF-PVPH-161. Fifth cervical vertebra; 1, ventral view; 2, dorsal view; 3, anterior view; 4, posterior view; 5, right lateral view; 6, left lateral view.

neural spines of other cervicals and is relatively low and continuous with the process bearing the postzygapophyses. Although the postzygapophyses are joined, unlike the condition seen in *Acanthochelys* spp., these articular structures are two distinct facets separated by a weak crest and are both oriented ventrolaterally. Contrary to the condition in *Acanthochelys* spp., *Platemys platycephala*, and *Phrynops* spp. a ventral keel is strongly developed on the centrum.

Parts of the right and left scapulae (with a short glenoid neck) and both coracoids are preserved (Fig. 8.1, 8.2). The morphology of the dorsal and acromion processes of the scapula is similar to those of *Acanthochelys radiolata*. The flat proximal acromion process and part of the scapular prong (with more ovoid section) are preserved in both scapulae and join at an angle of 86 degrees. The coracoid is shorter than the scapula. The coracoid is considerably expanded distally, although never as wide as long as in some chelids (e.g., *Chelus* or *Chelodina*).

The left humerus (Fig. 8.3) is almost complete, but only the distal end of the right humerus is preserved. The general morphology is similar to that in other pleurodiran humeri. It has an oval articular head, a wide proximal end with a shallow intertubercular fossa lying between the large medial process (well-preserved) and a small lateral process (not preserved). The humerus narrows to a shaft, subcylindrical in section, that arches dorsally. Distally the shaft flattens dorsoventrally and ends in a broad extremity. The distal articular surface is not preserved.

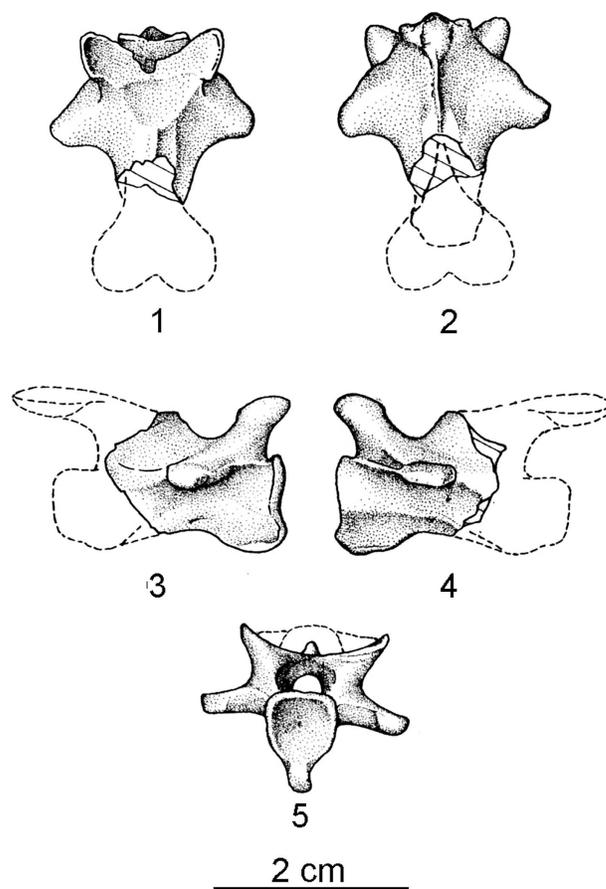


FIGURE 5—*Prochelidella portezuelae* n. sp. MCF-PVPH-161. Sixth cervical vertebra; 1, dorsal view; 2, ventral view; 3, right lateral view; 4, left lateral view; 5, anterior view.

Only the distal part of the right femur (Fig. 8.4) is preserved. The subcylindrical shaft arches dorsally. As is typical, the femur expands distally and forms a large tibial condyle which is poorly preserved.

The right tibia (Fig. 8.5) is well preserved. This bone does not vary greatly among chelonians. It has an expanded head with a broad articular surface which articulates with the tibial condyle of the femur. A cnemial crest extends along the dorsal surface of the proximal end of the tibia. Distally the tibia is slightly expanded.

Discussion.—The shell and vertebral morphology of the holotype of *Prochelidella portezuelae* n. sp. compares well with that of chelid pleurodiran turtles. The pubis and ischium are connected by suture with the xiphiplastra, a recognized synapomorphy of Pleurodira (see Gaffney and Meylan, 1988, and references therein). This condition, associated with the presence of a cervical scute, short and wide mesoplastra crossed by humeropectoral sulci, and the presence of fifth and eighth biconvex cervical vertebrae [also present in Jurassic pleurodirans (see Lapparent de Broin, 2000; de la Fuente and Iturralde Vinent, 2001)] loose carapace-plastron and pleuro-peripheral contacts, and narrow vertebrals 2–4, allows the assignment of *Prochelidella portezuelae* n. sp. to the family Chelidae. This peculiar family of pleurodiran turtles has an extensive record in Patagonia, from the Albian to the Oligocene (see Broin and de la Fuente, 1993a, 1993b; Lapparent de Broin and de la Fuente, 1999) with great diversity. Different morphologies of shell and cervical vertebrae of recently named and

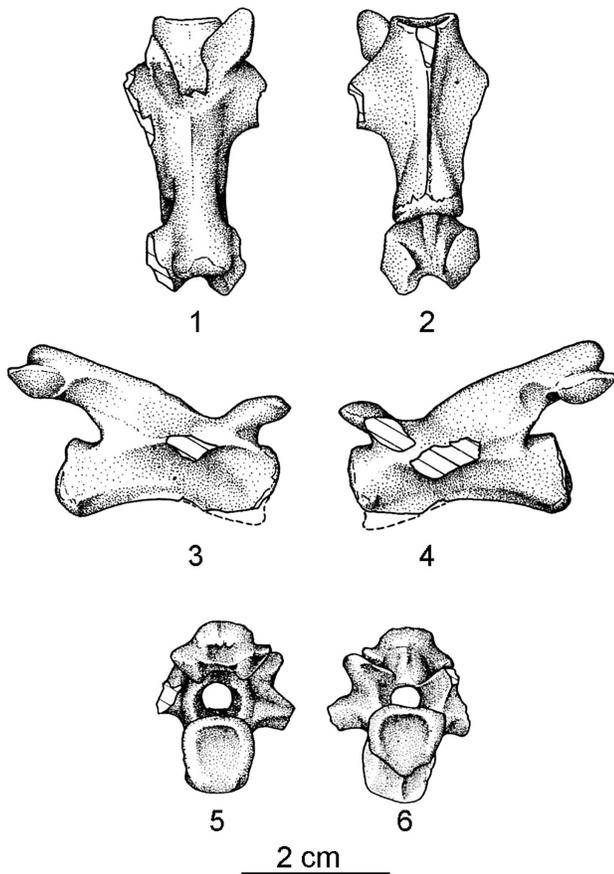


FIGURE 6—*Prochelidella portezuelae* n. sp. MCF-PVPH-161. Seventh cervical vertebra; 1, dorsal view; 2, ventral view; 3, right lateral view; 4, left lateral view; 5, posterior view; 6, anterior view.

unnamed taxa reveal this diversity (Broin and de la Fuente, 1993b, pl. 1, figs. 1–11; Gasparini and de la Fuente, 2000; de la Fuente et al., 2001; Lapparent de Broin and de la Fuente, 2001). In the first study of Upper Cretaceous chelids from the Los Alamos Formation, Broin (1987) already recognized the chelid nature of these chelonians on the basis of shell fragments. More recently, the discovery of isolated cervical vertebrae and more complete shells confirmed this assignment (Broin and de la Fuente, 1993a, 1993b; Gasparini and de la Fuente, 2000). Specimens of *Prochelidella portezuelae* n. sp. with cervical vertebrae articulated to shells provide more corroboration and more information about the chelid groups in the Cretaceous of Argentina.

A basic dichotomy in extant chelid turtles was recognized by Boulenger (1889). Chelids with a neck shorter than the dorsal column (*Pseudemydura*, *Emydura-Elseya* group, and *Phrynops* group) are distinguished from chelids with a neck longer than the dorsal column (*Chelus*, *Chelodina* and *Hydromedusa*). The main difference between these chelid groups is expressed in the length of each cervical vertebra. The comparative study of isolated cervical vertebrae from the Upper Cretaceous of Patagonia and extant chelid species (Broin and de la Fuente, 1993b) confirmed in a general sense the phylogenetic relationships of chelids proposed by Gaffney (1977) on skull characters of extant species. Gaffney's work concluded that the Australian (*Chelodina*) and South American long-necked chelids (*Hydromedusa* and *Chelus*) form a monophyletic group spanning the two continents. In contrast,

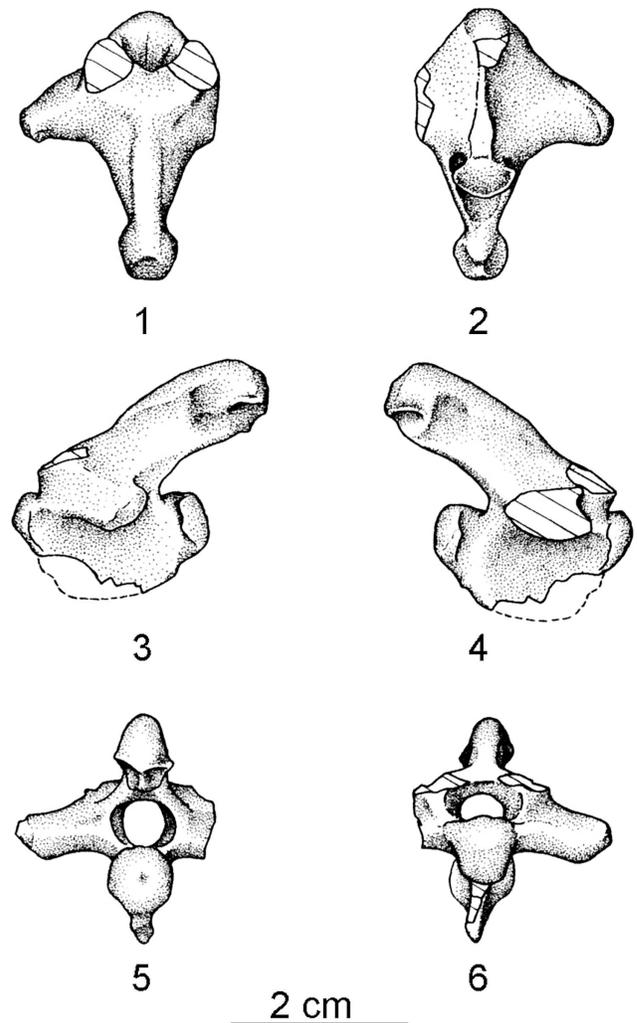


FIGURE 7—*Prochelidella portezuelae* n. sp. MCF-PVPH-161. Eighth cervical vertebra; 1, dorsal view; 2, ventral view; 3, left lateral view; 4, right lateral view; 5, posterior view; 6, anterior view.

based on analyses of morphological and serological data, Burbidge et al. (1974) concluded that all Australian species were more closely related to each other than to any South American species. Coincidentally, recent 12S rRNA and cytochrome b sequencing suggests that the long-necked *Chelodina* are more closely related to the short-necked Australasian genera than to either *Chelus* or *Hydromedusa* (Seddon et al., 1997; Shaffer et al., 1997; Georges et al., 1998). Previously, Pritchard (1984a) proposed that the elongated head and neck structure of *Hydromedusa* and *Chelodina* may have arisen not from a close phylogenetic relationship (as proposed by Gaffney, 1977) but from parallel evolution as they became specialized. However, this scenario is supported neither by phylogenetic analyses nor by recent morphological studies on fossil chelids (de la Fuente et al., 2001; Bona and de la Fuente, 2001) which agree with Gaffney's conclusion. Broin and de la Fuente (1993b) recognized two different morphological conditions in cervical vertebrae among Upper Cretaceous short-necked chelids. A primitive condition with short and high cervical vertebrae, with ventral keels curved or rectilinear, is present in the

extant species of the Australasian *Emydura-Elseya* group [specimens of the extant *Pseumydura urbina*, the basal and more primitive chelid on the basis of cranial morphology (Gaffney, 1977, 1991) was not available for this study]. A second condition is represented by short-necked species referred to *Phrynops* s.l., which have slightly more elongate and lower cervical vertebrae relative to species of the *Emydura-Elseya* group, but with ventral keels curved and reduced posteriorly in relation to central length. This second condition is present in the cervical vertebrae of *Prochelandella portezuelae* n. sp.

Recently, de la Fuente et al. (2001) and Lapparent de Broin and de la Fuente (2001) named five new taxa of chelid turtles. Among them, *Prochelandella argentinae* was based on a partial specimen consisting of the anterior margin of a carapace collected from the Bajo Barreal Formation, Upper Cretaceous (Chubut province, Argentina). Lapparent de Broin and de la Fuente (2001) suggested that this small species might be related to extant species of the genus *Acanthochelys*. This was proposed on the basis of the small size and similar decoration. However, this species retains primitive traits such as a wide and short nuchal bone and cervical scute, the presence of neurals, and the more advanced axillary processes. The anterior carapace of the species described here fits with the diagnostic characters of the genus *Prochelandella* (carapace wide and low with slight nuchal notch, moderate elongation of the anterior border of the carapace, nuchal bone anteriorly and posteriorly wide, neural 1 quadrangular). In contrast to *P. argentinae*, several traits of *P. portezuelae* n. sp. suggest a species-level differentiation between the specimens of the Bajo Barreal and Portezuelo Formations. These include: more posterior axillary processes, form and proportion of the first and second marginal scutes, absence of marked growth annuli and the moderate size.

Lapparent de Broin and de la Fuente (2001) reported additional remains of small forms similar or very close to *Prochelandella* spp. from Lower and Upper Cretaceous sites of Neuquén and Río Negro Provinces (Patagonia). These specimens (most of them isolated shell elements) indicate the presence of several forms of the *Acanthochelys* subgroup. Some characters, such as short pygals (rectangular, or posteriorly widened trapezoid in shape); pygal bone well overlapped by vertebral 5, pygal posterior border transverse (e.g., *A. radiolata*) or slightly notched or rounded border (e.g., *A. spixii* and *A. pallidipectoris*), primitive plastral scute pattern, but with the intergular less dilated (also in *P. portezuelae* n. sp.) support this assignment. Likewise other characters seen in these specimens and in the named species (*P. argentinae* and *P. portezuelae* n. sp.) such as: wide nuchal bone, presence of neural bones, and axillary processes at peripheral 3, differentiate these species from extant species of *Acanthochelys*.

Prochelandella argentinae and *P. portezuelae* appear to be more similar to the older forms from the Lower Albian-Cenomanian (Cerro Leones and El Chocon) than to the more recent forms (El Palomar, El Abra). The latter (Campanian-Maastrichtian) forms have narrowed cervical scales and shortened entoplastra (see Broin and de la Fuente, 1993b; Lapparent de Broin and de la Fuente, 2001). In the specimen from Sierra del Portezuelo assigned to *P. portezuelae*, the series of cervical vertebrae are almost complete, but the *Prochelandella* spp. from other localities (e.g., El Chocón, El Abra) are only known from isolated vertebrae [see Broin and de la Fuente (1993b, pl. 1, fig. 3), Lapparent de Broin and de la Fuente (2001, p. 469)]. In *P. portezuelae* the vertebrae are moderately elongated and lowered, the ventral crest being less notched than in the fourth opisthocelous cervical vertebra of *Palaeophrynops* Lapparent de Broin and de la Fuente, 2001, and overall in the extant species of the paraphyletic *Phrynops* group.

Hyperfamily PELOMEDUSOIDES Cope, 1864
Superfamily PODOCNEMIDOIDEA Cope, 1868
Epifamily PODOCNEMIDOIDAE Cope, 1868
Genus PORTEZUELOEMYS new genus

Type species.—*Portezueloemys patagonica* new species.

Diagnosis.—A podocnemidoid pleurodiran turtle with a podocnemidoid fossa, enlarged carotid canal and lacking prolonged pterygoid wings. Foramen jugulare posterius not separated from fenestra postotica; small epiplastral gular scutes, pectoral scutes contacting entoplastron posteriorly but not extending over the epiplastra and mesoplastra. Differs from *Brasilemys* in the extensive skull roof formed by enlarged areas of the postorbital, jugal, and quadratojugal, and in the narrow interorbital space; differs from *Hamadachelys* in having less extended temporal emargination which does not expose the foramen stapedio temporale, and in a dorsoanterior enlargement of the opening in the podocnemidoid fossa; differs from extant and fossil South American Podocnemidinae in having the pterygoid flange end at the border of the pterygoid on the infratemporal fossa.

Etymology.—“Portezuelo,” from Sierra del Portezuelo; “emys,” from the Greek “aquatic turtle.”

PORTEZUELOEMYS PATAGONICA new species
Figures 9–12

Diagnosis.—As for the genus, by monotypy.

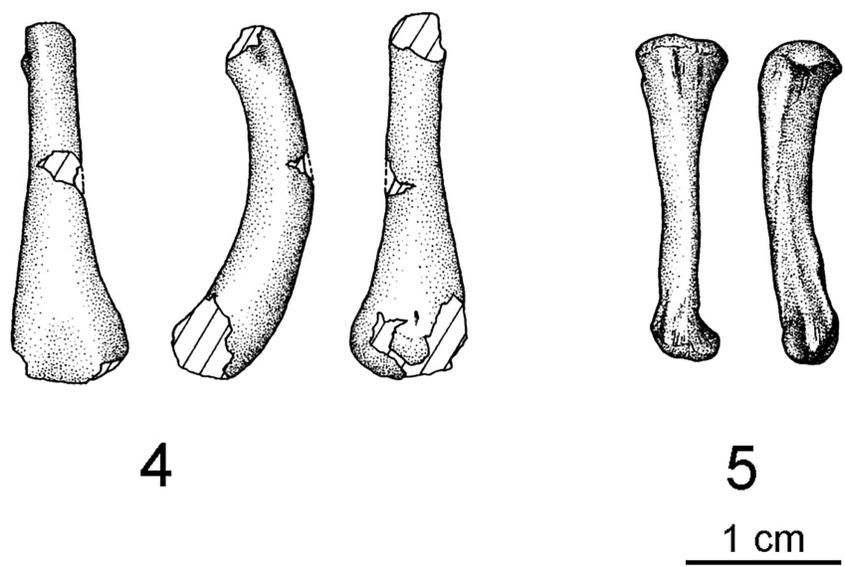
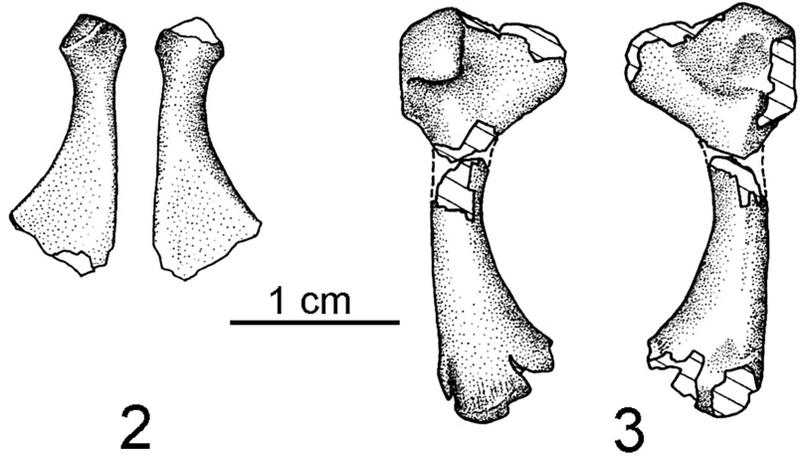
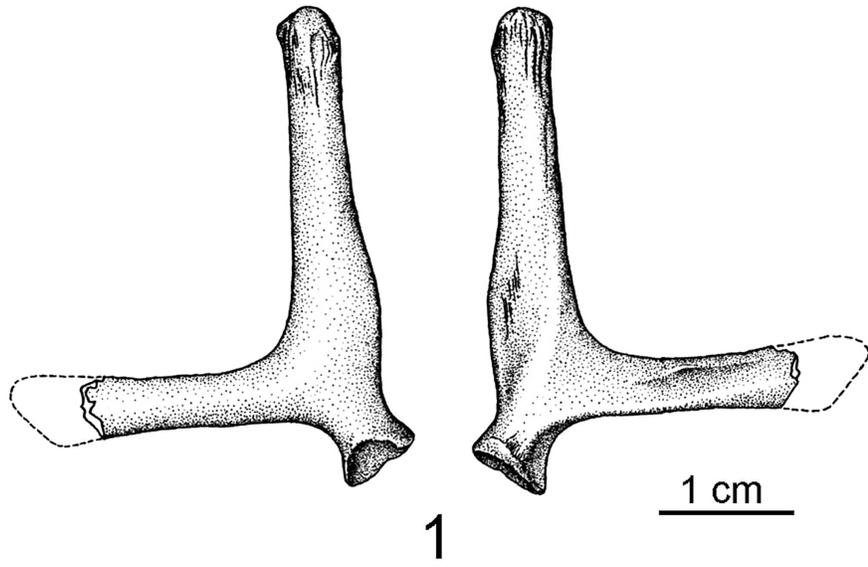
Type.—Holotype, specimen of the “Carmen Funes” Museum of Plaza Huincul, Neuquen province, MCF-PVPH-338: A skull and partial carapace and plastron.

Other material examined.—MCF-PVPH-339: A nearly complete plastron.

Occurrence.—As for *Prochelandella portezuelae* n.sp.

Description.—The skull of *Portezueloemys* (MCF-PVPH-338) is partially filled by fine sandstone in the dorsal and lateral cranial openings with adhering fragments of parietal, frontal, quadrate, and squamosal bones. The palatal and basicranial bones are visible in ventral view (Figs. 9, 10). The sandstone endocast preserves the morphology of the orbital and posterior nasal cavities (prefrontal), as well as infilling of sulcus olfactory (frontal) and adductor chambers (under the quadratojugal and parietal bones), (Figs. 9.1–9.3, 10.1–10.3). The anteriormost part of the snout is not preserved, and it is not possible to determine the width of the external nares. The orbits are relatively small with a narrow interorbital space, unlike the condition in *Brasilemys* (see Lapparent de Broin, 2000, fig. 1).

The prefrontal and anteriormost parts of the frontal are missing. The orbits are relatively small and dorsolaterally directed, contrary to those of *Bauruemys elegans* (Suarez, 1969). Most of the dorsal surface, including the fossa temporalis superior under the parietal and quadratojugal, is filled with fine sandstone. The posterior edges of this sandstone endocast (below the quadratojugal and parietal) forms the border of the posterior emargination (Figs. 9.1, 10.2), which extends slightly beneath the level of the posterior border of tympanic ring of the cavum tympani. This condition suggests the presence of a secondary skull roofing like that of *Hamadachelys* (see Tong and Buffetaut, 1996) and Podocnemididae, and unlike that of in *Brasilemys* (see Lapparent de Broin, 2000, pl. 1, fig. 1). The foramen stapedio-temporale lies on the dorsal surface of the otic chamber and opens dorsally as with chelids and most turtles. As with *Podocnemis*, and contrary to the condition seen in *Hamadachelys*, the foramen stapedio-temporale is not visible in dorsal view. The supraoccipital crest is prolonged slightly beyond the parietals. The opisthotic is characterized by a long paroccipital process that may be prolonged behind the squamosal extremity, as seen in *Hamadachelys* and other pelomedusoids (e.g. *Pelomedusa*).



In transverse section, the skull is not domed as in extant *Podocnemis*. The foramen magnum is roughly oval. The supraoccipital crest slightly exceeds the level of the foramen magnum. The exoccipitals end on the border of this foramen, at three quarters its height. The two exoccipitals meet ventrally with the basioccipital. Laterally, the external border of both exoccipitals in *Portezueloemys* form the medial margins of the foramen jugulare posterius. The lateral border of this foramen is open and confluent with the fenestra postotica (Figs. 9.4, 10.4). A different condition is seen in the extant species of *Podocnemis* and *Peltecephalus dumerilianus*. Contrary to *Portezueloemys patagonica* n.sp., in extant Podocnemidinae the lateral margin of the foramen jugulare posterius is limited by the opisthotic. The descending processus interfenestralis of the opisthotic is seen lateral to the braincase. This process limits the recessus scalae tympani anteriorly (filled by sandstone). Laterally is the cranioquadrate space. The fenestra postotica is roofed by the quadrate and opisthotic, and is crossed posteriorly by the notch of the columella. Only a partial cast of the ventral facet of right articular process of the quadrate is preserved in the holotype of *Portezueloemys patagonica*.

Although the snout is broken, the area of the internal choanae is partially preserved. In ventral view the posterolaterally-curved margins of two large choanae are preserved. The interchoanal bar is formed mostly by the palatines and from a relatively short and narrow vomer that is partially preserved. The foramen palatinum posterior is wide (Figs 9.2, 10.1). The processus trochlearis pterygoidei is well developed laterally. Posterior to the processus trochlearis pterygoidei, the pterygoid flanges are developed ventrally. Although the distal ends of the pterygoid flanges are partially broken in *Portezueloemys patagonica* n. gen n.sp., it may be seen that, as in *Brasilemys* and *Hamadachelys*, the proximal margin of the right pterygoid flange is curved medially. This suggests that the pterygoid wings end at the border of the pterygoid on the infratemporal fossa, and do not extend posteromedially to the suture with the basisphenoid as in podocnemidids. The basisphenoid is roughly subtriangular, although the anterior end is broken. Lateral to the basisphenoid lies the podocnemidoid fossa, forming the pterygoid channel or enlarged carotid canal (see Gaffney, 1979; Lapparent de Broin and Werner, 1998). This fossa is recognized posterior to the base of the pterygoid flange, as a depression on the suture between the pterygoid and the basisphenoid medially. It extends posteriorly to the descending process of quadrate laterally. This condition is present in Podocnemidoidea with the quadrate extended medially to the basisphenoid and the basioccipital covering the processus interfenestralis ventrally. On the left side, the posteriormost end of the pterygoid wing is broken, exposing the foramina area. However, as this area is damaged, only the medial opening for the carotid artery, directed towards the sella turcica can be delimited. The other foramina usually present in the Podocnemidoidea, one anterior leading to the sulcus cavernosus for the palatine branch of the facial nerve, and another lateral one for the facial nerve may be present in a damaged large lateral opening.

Originally the carapace (Figs. 11.1, 12.1) must have measured about 240 mm in length. In transverse section it is low arched. Unfortunately, the anterior margin is broken and most of the nuchal and peripheral bones are fragmented into small pieces overlapping each other. Despite this damage, these bones appear to be relatively short and the anterior margin of the carapace appears to be rounded. The carapace is suboval in shape with rounded

anterolateral and curved lateral margins. A similar condition is present in podocnemidid specimens from the Rio Colorado subgroup at Planicie Banderitas (Neuquén province) and Paleocene specimens of the Maiz Gordo Formation at Casa Grande (Jujuy province, Argentina) (see Broin, 1991; de la Fuente, 1993). Behind the nuchal bone fragments, the neural series continues with six neural bones. The first is subquadrangular, while the remaining four neural bones are roughly hexagonal with short anterolateral margins. The sixth may be heptagonal. The seventh and eighth pairs of pleural bones meet in the midline. Unfortunately, the posterior third of the carapace is not preserved in MCF-PVPH-338, and the suprapygal, pygal and posterior peripheral bones are unknown. Traces of the sulci for the first to fourth vertebral scales are seen over the carapace. The first and the fourth are the smallest and narrowest scales, while the second and third are the largest of the series, with both scales wider than long.

The plastral bridge is considerably longer at its base (=axillo-inguinal distance) than the posterior plastral lobe, but the anterior lobe is the shortest plastral element (Figs. 11.2, 12.2). The anterior plastral lobe is U-shaped, with anterolateral margins diverging to the axillary notches. This condition is typical in extant and fossil podocnemidid species (e.g., *Podocnemis expansa*, *P. vogli*, *P. venezuelensis*). The anterior lobe also does not extend beyond the anterior border of the carapace. The intergular-gular scutes are arranged in a simple scheme: a narrow intergular extends over the first third of the entoplastron and there are small gular scutes on the epiplastra. The entoplastron is diamond shaped and is only crossed posteriorly by the humeropectoral scute sulcus. The interabdominal seam is twice the length of the interpectoral seam. The right mesoplastron is pentagonal and placed laterally at the base of the bridge. The pectoro-abdominal sulcus does not cross the mesoplastron. The interabdominal seam is slightly longer than the interfemoral seam. The lateral margins of the posterior lobe are straight rather than curved, and inclined medially as is usual in some podocnemidid species (i.e., *P. vogli* or *P. venezuelensis*). The posterior ends of the xiphiplastra are not preserved, and preclude the accurate determination of the anal notch shape.

Discussion.—Some of the pleurodire synapomorphies listed by Gaffney and Meylan (1988) are recognized in *Portezueloemys patagonica*: such as the processus trochlearis pterygoidei, the quadrate process below the cranio-quadrate space, foramen palatinum behind the orbit, and pelvis suturally attached to carapace and plastron. Likewise, *Portezueloemys* is a member of the Pelomedusoides (sensu Broin, 1988) based on the vomer reduced to the anterior interchoanal part, and rounded lateral mesoplastra (see character listed in Lapparent de Broin, 2000). Other derived characters of *Portezueloemys* [e.g., the podocnemidoid fossa becoming the true enlarged carotid canal or pterygoideous channel (Gaffney, 1979), forming a deeper fossa inside the skull] allow referral of this new taxon to the epifamily Podocnemidoidea.

Although the skull and shell morphology of *Portezueloemys* is podocnemid-like in the general arrangement of bones and scales and with an enlarged podocnemidoid fossa, the suggests that the pterygoid wings stop at the border of the pterygoid on the infratemporal fossa, and do not extend posteromedially up to the suture of the basisphenoid as in the Podocnemidoidea. The skull, like that of *Podocnemis* is rather flat and oblong, with small orbits directed dorso-laterally and with a narrow interorbital space, but retains some primitive characters (the foramen jugulare posterius confluent with the fenestra postotica and a well developed paraoccipital

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FIGURE 8—*Prochelidella portezuelae* n. sp. MCF-PVPH- 161. 1, dorsal and ventral view of the left scapula; 2, dorsal and ventral view of the left coracoid; 3, dorsal and ventral view of the left humerus; 4, dorsal, lateral and ventral view of the right femur; 5, dorsal and medial view of the right tibia.

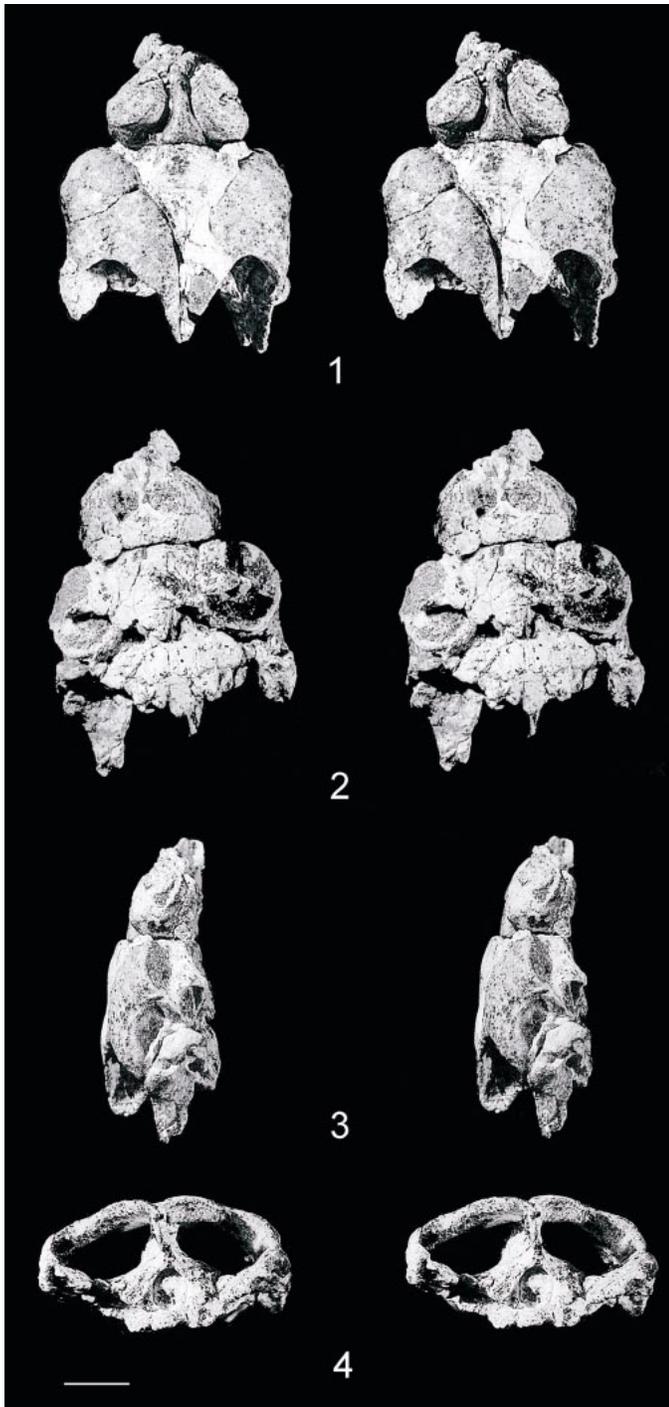


FIGURE 9—*Portezueloemys patagonica* n. gen. n. sp. MCF-PVPH-338. Skull in stereoscopic views; 1, dorsal view; 2, ventral view; 3, lateral view; 4, posterior view. Scale bars = 1 cm.

opisthotic process). The shell is oval in shape rather than quadrangular, and moderately high with a rounded anterior border. The gular scales are small, and the pectoral scales do not contact the mesoplastra, but only the posterior third of the entoplastron and hyoplastra.

The Lower Cretaceous pelomedusoids turtles from South American include several species such as: *Araripemys barretoi*,

the unnamed specimen FR 4922, *Brasilemys josei* and *Cearachelys placidoi* (see Price, 1973; Gaffney and Meylan, 1991; Meylan and Gaffney, 1991; Lapparent de Broin, 2000; Gaffney et al., 2001). All of these taxa were recovered from the Romualdo Member of the Santana Formation (Aptian-Albian), in Chapada do Araripe, Brazil. *Portezueloemys patagonica* n. sp. and *Brasilemys josei* can be differentiated from the other Early Cretaceous taxa because they share the characters present in the epifamily Podocnemidoidea (see Lapparent de Broin, 2000). *Portezueloemys* also differs from *Brasilemys* in the extensive skull roof produced by the enlarged areas of the postorbital, jugal, and quadratojugal, and the narrow interorbital space.

Later South American podocnemidoids are included in the subfamily Podocnemidinae. This subfamily includes species of the genus *Peltocephalus* and *Podocnemis*, the extinct species of the *Roxochelys* group [*R. harrisi* (Pacheco) 1913 = *R. wanderleyi* Price, 1953, *R. vilavilensis* Broin, 1971] (see Broin, 1991); *Bauruemys elegans* (Suarez, 1969) (see Kischlat, 1994); and *Stupendemys geographicus* Wood, 1976. *Portezueloemys* is easily distinguished from the South American podocnemid taxa in the retention of primitive characters such as the pterygoid wing extending only above the anteromedial part of the podocnemidoid fossa and the pterygoid flange not extending behind the quadrate ramus. Likewise, *Portezueloemys*, with a *Podocnemis*-like skull, differs strongly from *Peltocephalus dumerilianus*. Also the skull morphology in *Portezueloemys* is clearly distinguished from *Podocnemis* in the retention of the same primitive cranial characters mentioned above. Among the South American podocnemidids, *Bauruemys elegans* was originally described by Suarez (1969) as *Podocnemis elegans* from the Upper Cretaceous Adamantina Formation, Bauru Group. More recently, Broin (1988, 1991) suggested the exclusion of this species from *Podocnemis* and referred it provisionally to *Roxochelys*. Kischlat (1994) instead referred Suarez's species to the new genus *Bauruemys*. According to Kischlat (1994), *B. elegans* is characterized by a short, wide and relatively low skull, lacking the sulcus interorbitalis, and with a wide, step-like palatal crest. Tong and Buffetaut (1996) recently referred this species to the genus *Hamadachelys*. This genus was described from a single skull as *H. escullei*, from the Albian-Cenomanian horizon of Hamada du Guir, Morocco. However, the derived condition present in the pterygoid wing of *B. elegans*, extending above the anteromedial fossa, precludes the assignment of this species to *Hamadachelys*, a genus considered basal to the family Podocnemididae (see Lapparent de Broin, 2000). The structure of the basicranium in *Bauruemys elegans* was described by Broin (1991), who found a morphology of the rostrum basisphenoidal similar to that of the large *Podocnemis* species [i.e., *P. expansa* and *P. cayenensis* (*unifilis auctoris*)] and *Erymnochelys*.

Other possible podocnemidine species are represented by an assemblage of insufficiently known species indeterminate at the generic level (see Broin, 1991). Among them *Podocnemis argentinensis* Cattoi and Freiberg, 1958, was found in the Late Paleocene of the Aimara Basin, Maiz Gordo Formation (= "Margas verdes o Multicolores"), in Jujuy province, northwestern Argentina. The holotype (MACN 17988), an almost complete plastron, and the specimen referred to it (MACN 16553) figured by Cattoi and Freiberg (1958, figs. 62 and 67) are specimens from different sites ("Quebrada Queñoal," the former and "Quebrada de Ajita," the latter). As was suggested by Broin (1991) this taxon has affinities with *Podocnemis*, although its generic assignment is indeterminate. The plastron of "*Podocnemis*" *argentinensis* does not have the thickening seen in *?Roxochelys vilavilensis* Broin, 1971. Furthermore, the gular scales are short and restricted to the epiplastra, the intergular scale is wide, and the humeropectoral sulcus crosses over the entoplastron as in *Podocnemis*. Additional shells, smaller than the holotype have been found at the Río Casa

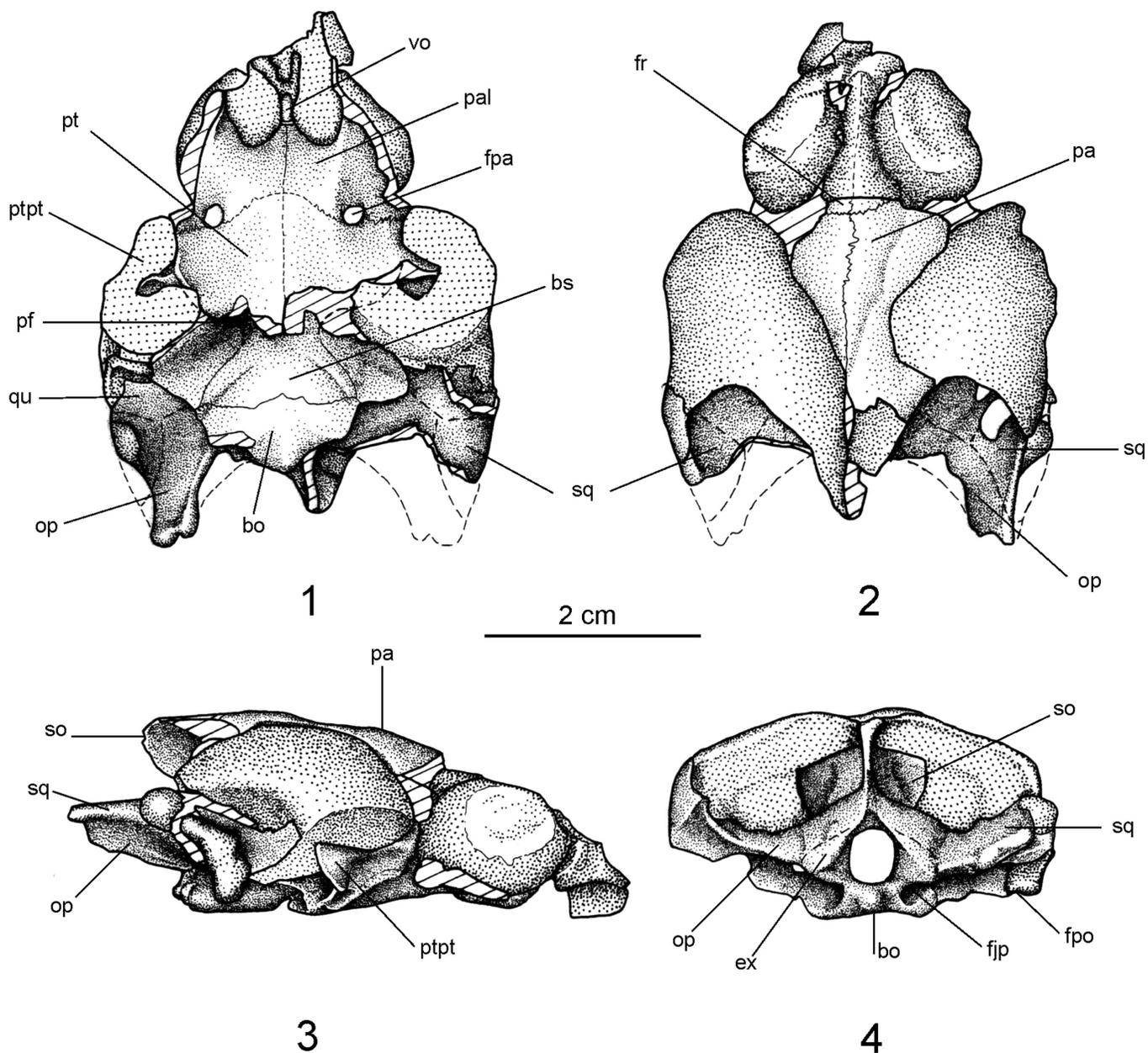


FIGURE 10—*Portezueloemys patagonica* n. gen. and sp. MCF-PVPH-338. Skull; 1, ventral view; 2, dorsal view; 3, lateral view; 4, posterior view. Abbreviations: bo = basioccipital, bs = basisphenoid, ex = exoccipital, fr = frontal, fjp = foramen jugulare posterius, fpa = foramen palatinum posterius, fpo = fenestra postotica, op = opisthotic, pa = parietal, pal = palatine, pf = podocnemidoid fossa, pt = pterygoid, ptpt = processus trochlearis pterygoidei, so = supraoccipital, sq = squamosal; vo = vomer.

Grande locality in the same lithostratigraphic unit (see Gasparini and Báez, 1975; Broin and de la Fuente, 1993b). These specimens have similar plastral morphology to the holotype, and the anterior margin of the carapace is rounded. Likewise, undescribed specimens referable to "*Podocnemis*" *argentinensis* are recognized in the collections of the American Museum of Natural History. However these specimens are considerably smaller than the holotype. A skull is preserved with one of the specimens, and is characterized by its short beak, lateral orbits, high maxilla, and weak posterior elevation as in *Peltocephalus*, but with lateral emargination and a strong vomer. A different *Podocnemis*-like morphology is found in the skull of *Portezueloemys*.

Another Upper Cretaceous podocnemidoid from northern Patagonia was recently described (de la Fuente, 1993). This turtle is represented by a single shell (MCRN 7049) from an unknown horizon of the Río Colorado Subgroup (outcropping at Planicie Banderitas, Neuquén province) and was referred to ?*Podocnemididae* indet. (de la Fuente, 1993). This specimen may be the same species or a close relative of *Portezueloemys patagonica*. Both specimens have a rounded anterior margin of the carapace and a similar pattern of plastral bone and scales. Minor differences are seen in the pectoro-abdominal sulci (that touch the top of mesoplastra) and in the convergence of the lateral margins of the posterior lobe in the specimen from Planicie Banderitas.

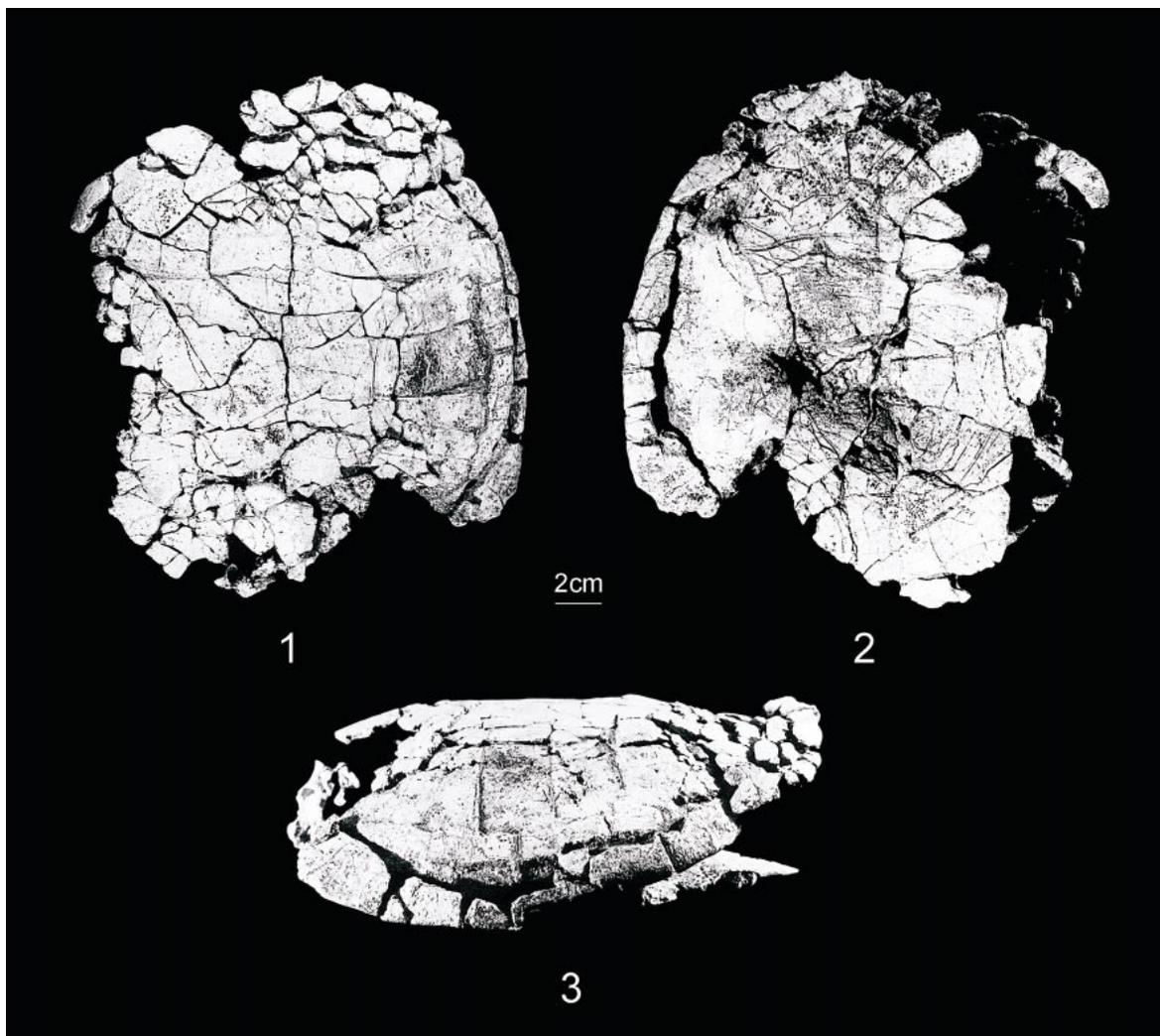


FIGURE 11.—*Portezueloemys patagonica* n. gen. and sp. MCF-PVPH- 338. Shell; 1, dorsal view of the carapace; 2, ventral view of the plastron; 3, lateral view of the shell.

Phylogenetic analysis.—A data matrix of 50 osteological characters for 10 pleurodiran taxa was used to assess the phylogenetic relationships of *Portezueloemys*. This phylogenetic approach was based on previous analyses carried out by other authors (Gaffney and Meylan, 1988; Gaffney et al., 1991; Meylan, 1996; Lapparent de Broin, 2000). The data matrix was analyzed using NONA (Goloboff, 1993). The characters were treated as unordered to preclude any a priori polarity assumptions of character evolution. The analysis of the data matrix yielded one most parsimonious tree (Fig. 13) with a tree length of 61 steps, a consistency index (C.I.) of 0.86 and a retention index (R.I.) of 0.89. Slow optimization was made by using the WINCLADA Program (Nixon, 1999–2000). The analysis suggests that the epifamily Podocnemidoidae (Node 1) is a monophyletic group supported by the presence of an enlarged carotid canal (10 (1)). Node 2 (including *Hamadachelys*, *Portezueloemys*, and Podocnemididae) is supported by the following synapomorphies: 5 (1) parietal-quadratojugal contact, and 7 (2) short postorbital, with parietal-jugal contact. Node 3 (including *Portezueloemys* plus their sister taxa Podocnemididae, Fig. 13) is supported by the following synapomorphies: 15 (1) a dorsoanterior enlargement of the foramen in the podocnemidoid

fossa, 20 (1) processus trochlear pterygoidei at right angle to skull axis, 34 (1) pectoral scale not in contact with the mesoplastron. The family Podocnemididae (Erymnochelyinae plus Podocnemidinae, Node 4) is supported by: 3 (1) parietal-jugal contact, 11 (1) pterygoid covers prootic, 21 (1) pterygoid flange extends posterior to quadrate ramus, 25 (1) development of prolonged pterygoid wing above anteromedial part of the podocnemidoid fossa.

Palaeobiogeography.—Although gondwanan in origin, both groups of the Eupleurodira (Pelomedusoides and Chelidae; see Pritchard, 1984b; Pritchard and Trebbau, 1984) differentiated in opposite areas of Gondwanaland (see Broin, 1987, 1988; Broin and de la Fuente, 1993a, 1993b; de la Fuente, 1992, 1993). While the Pelomedusoides diversified in northern Gondwana (northeastern South America–northwestern Africa block), chelid turtles originated in the southern part of the gondwanan continent (southern South America, Antarctica, and Australasia). The oldest record of pelomedusoids is from the Late Aptian of Gadoufaua, Niger (*Taquetochelys decorata* Broin, 1980; *Teneremys lapparenti* Broin, 1980, aff. *Platycheloides* sp.; see Broin, 1980; Lapparent de Broin, 2000) and the Early Cretaceous, Aptian–Albian boundary, Santana Formation, Ceará, Brasil (*Araripemys barretoii* Price,

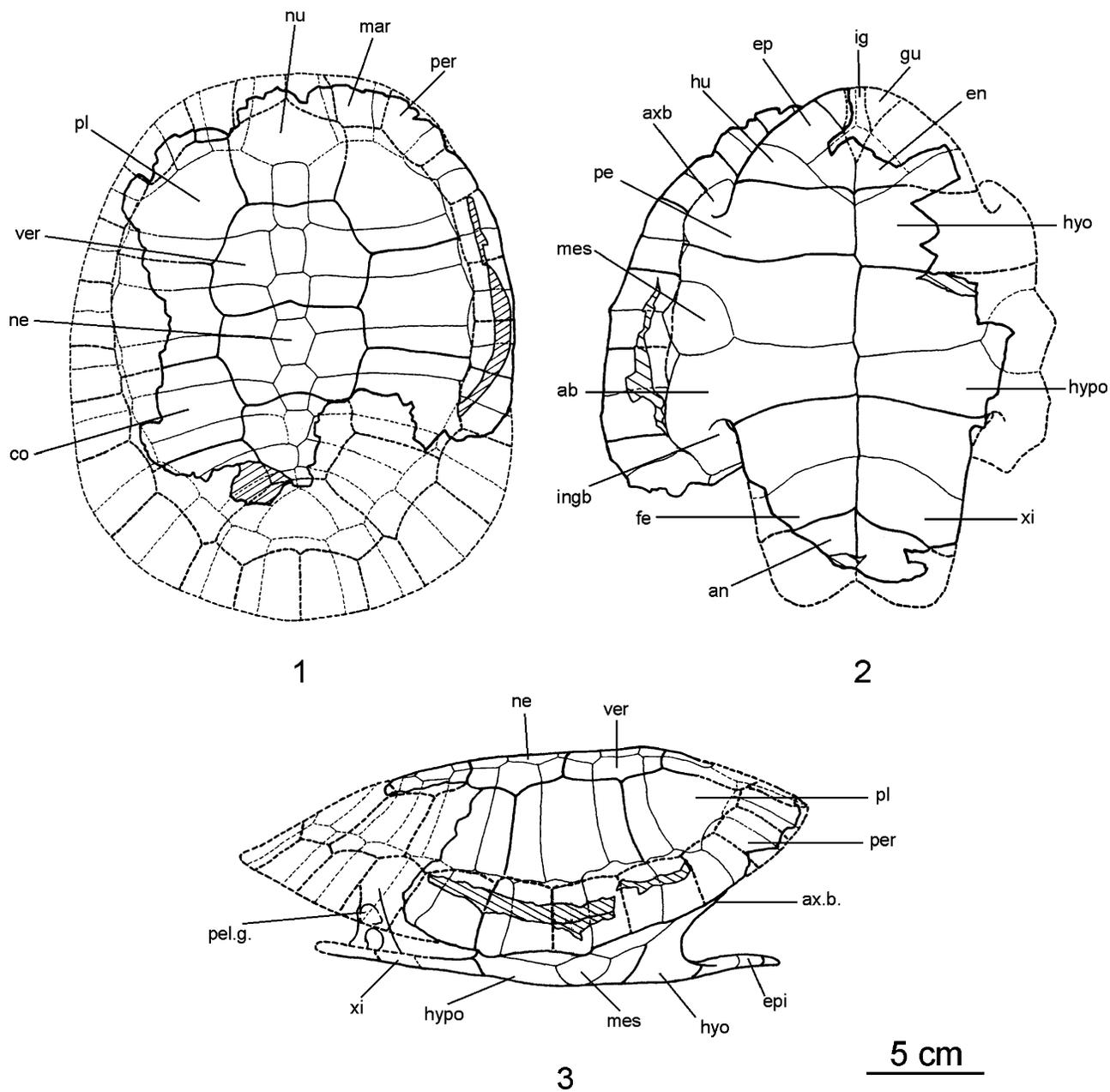


FIGURE 12—*Portezueloemys patagonica* n. gen. and sp. MCF-PVPH-338. Schematic shell reconstruction; 1, dorsal view of the carapace; 2, ventral view of the plastron; 3, lateral view of the shell. Abbreviations: ab = abdominal scale, an = anal scale, ax.b. = axillary buttress, co = costal scale, en = entoplastron, ep = epiplastron, fe = femoral scale, gu = gular scale, hyo = hyoplastron, hypo = hypoplastron, hu = humeral scale, ingb = inguinal buttress, ig = intergular scale, is.s. = ischium scar, mar = marginal scale, mes = mesoplastron, ne = neural, nu = nuchal bone, pe = pectoral scale, pel.g. = pelvic girdle, per = peripheral bone, pl = pleural bone, ver = vertebral scale

1973; *Brasilemys josei* Lapparent de Broin, 2000). The earliest record of chelid tortoises is represented by unnamed species tentatively assigned to *Prochelidella* (see Lapparent de Broin and de la Fuente, 1999, 2001) from the lower Albian of the Lohan Cura Formation outcropping in northern Patagonia (see Leanza, 1999; Leanza and Hugo, 1995). The record given in the present paper of a new podocnemidoid and a new chelid species in the same Turonian-Coniacian horizon documents the coexistence of one lineage from northern Gondwanaland extending to northern Patagonia (*Pelomedusoides* Podocnemidoidae) and another lineage

of chelids that was restricted to central and northern South America in post-Eocene time.

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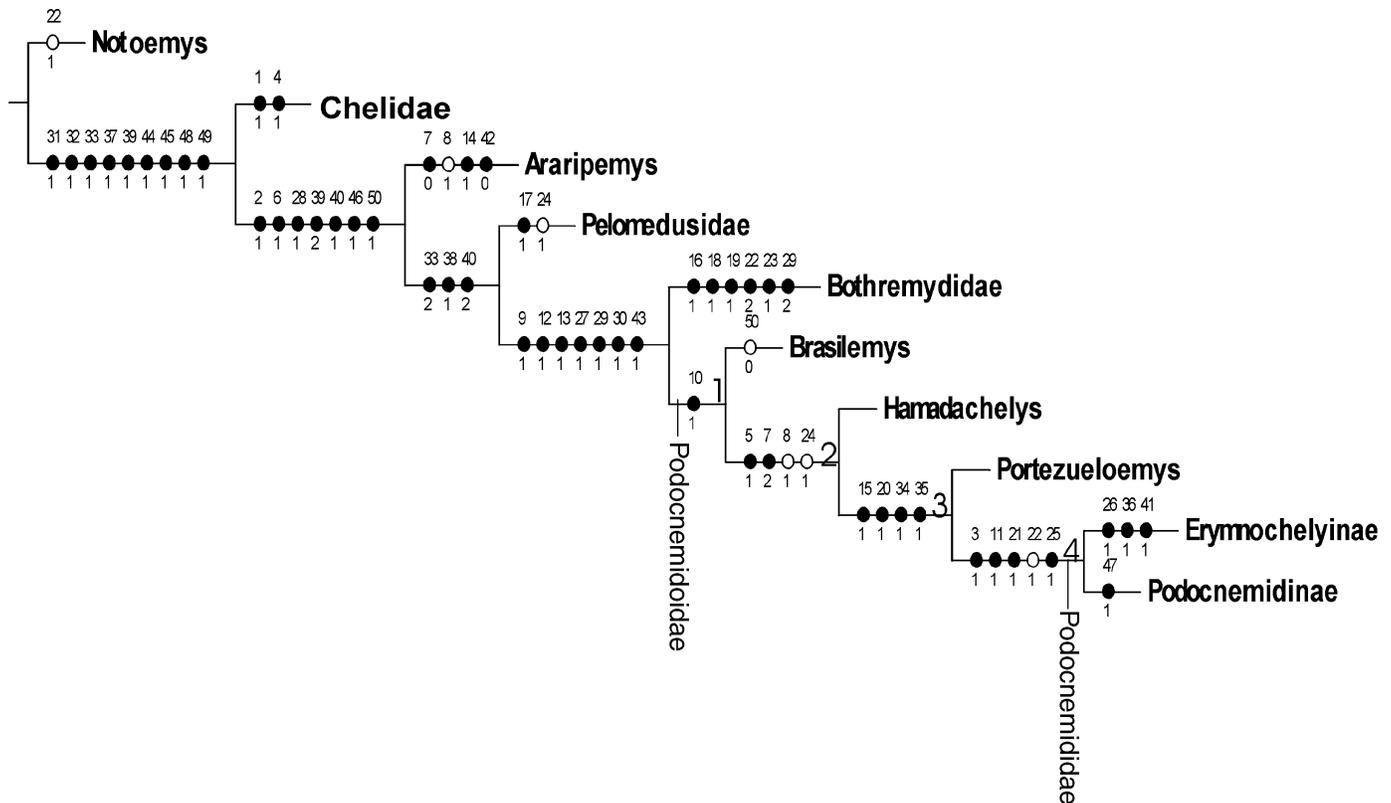


FIGURE 13—Cladogram showing the relationships among selected pleurodiran turtles and character optimization. Solid circles represent non homoplastic characters, open circles represent homoplastic characters. Node 1 (epifamily Podocnemidoidea), Node 2 (unnamed), Node 3 (unnamed), and Node 4 (family Podocnemididae).

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APPENDIX 1

Character, character states, and character matrix used to determine the phylogenetic position of *Portezueloemys*. Explanation of coding for polymorphism: a = (01), b = (12)

Characters gathered from Gaffney (1977), Gaffney and Meylan (1988), Gaffney et al. (1991), Meylan (1996), Lapparent de Broin and Murelaga (1999), Lapparent de Broin (2000), and de la Fuente and IturraldeVincent (2001).

1. Skull emargination.—Posterior skull emargination extended anteroven-trally (0), lateral skull emargination extended dorsoposteriorly (1)
2. Nasal bone.—Present (0), absent (1)

3. Parietal-jugal contact.—No (0), yes (1)
4. Quadratojugal.—Present (0), Absent (1)
5. Parietal-quadratojugal contact.—No (0), yes (1)
6. Jugal quadratojugal contact.—Absent (0), present (1)
7. Postorbital long.—Yes (0); no, short, but lacking parietal-jugal contact (1); no, but with parietal-jugal contact (2)
8. Vomer.—Present and strongly developed (0), reduced or absent (1)
9. Vomer reduced to its anterior interchoanal part.—No (0), yes (1)
10. Enlarged carotid canal.—Absent (0), present (1)
11. Pterygoid covers prootic.—No (0), yes (1)
12. Quadrate-basisphenoid contact behind the prootic.—No (0), yes (1)
13. Quadrate-basioccipital contact.—No (0), yes (1)
14. Basisphenoid.—Long and extending between pterygoid up to palatine (0), only extending between part of pterygoid (1)
15. Dorsoanterior enlargement of the foramen in the podocnemidoid fossa.—Absent (0), present (1)
16. Stapedial canal opens anteriorly.—No (0), yes (1)
17. United foramen posterior carotici interni and foramen facialis in the middle of the ventral face of the prootic.—No (0), yes (1)
18. Salient processus articularis of the quadrate below the level of the lateral border of the skull.—No (0), yes (1)
19. Elongation of the skull between the orbit and the cavum tympani.—No (0), yes (1)
20. Processus trochlearis pterygoidei at right angle to skull axis.—No (0), yes (1)
21. Pterygoid flange extends posterior to quadrate ramus.—No (0), yes (1)
22. Antrum postoticum.—Large (0), moderate (1), very small or absent (2)
23. Eustachian tube.—In incisura columellae auris (0), separated from incisura columellea auris (1)
24. Incisura columellae auris.—Open (0), closed (1)
25. Development of prolonged pterygoid wing above the anteromedial part of the podocnemidoid fossa.—Absent (0), present (1)
26. Highly reduced roof of the enlarged carotid canal.—No (0), yes (1)
27. Podocnemidoid fossa in prootic area.—Absent (0), present (1)
28. Splenial bone.—Present (0), Absent (1)
29. Processus retroarticularis of the articular developed behind the articular facet of the lower jaw.—Not visible dorsally (0), small (1), large (2)
30. Chorda tympani entering the processus retroarticularis.—No (0), yes (1)
31. Carapace short and wide.—Yes (0), no (1)
32. Carapace shape pointed or expanded posteriorly.—Yes (0), no (1)
33. Nuchal bone.—Width \gg length (0), width $>$ or $=$ length (1), length $>$ width (2)
34. Pectoral scales contact mesoplastra.—Yes (0), no (1), hinge intervenes (2)
35. Pectoral scales contact entoplastron.—No (0), yes (1)
36. Pectoral scales contact epiplastra.—No (0), yes (1)
37. Neural bone series.—Irregular (0), regular (1)
38. Neural bone series complete to suprapygal bone.—Yes (0), no (1)
39. Cervical scale.—Present with a width \gg length (0), present with width $>$ or $<$ length (1), absent (2)
40. Mesoplastra.—Lateral cuneiform (0), absent (1), lateral rounded (2), midline contact when hinge intervenes (3)
41. Short humeral scales with an advanced humeropectoral sulcus anterior to mid-length of the entoplastron.—No (0), yes (1)
42. Posterior ischiatic process.—Present (0), absent (1)
43. Elongated plastral bridge.—No (0), yes (1)
44. First thoracic ribs.—Partly reduced in size and laterally linked to rib 2 (0), much reduced in size to a thin and medially linked to rib 2 (1)
45. Costo-vertebral tunnel.—Wide and with slight posterior reduction in width (0), reduced in width all along (1)
46. Procoelous cervical centra from third to eighth vertebrae.—Absent (0), present (1)
47. Cervical centra with posterior condyles saddle shaped.—Absent (0), present (1)
48. Pedicel processes bearing the postzygapophyses.—Absent (0), present (1)
49. Transverse apophyses of cervical vertebral centrum.—At anterior central position (0), at midlength central position (1)
50. Horizontal position of the axis prezygapophyses.—Yes (0), no (1)

