

***Euclastes meridionalis* (DE LA FUENTE & CASADÍO) (Testudines: Pancheloniidae) from Danian levels of the Jagüel Formation at Cerro Azul, Northern Patagonia, Argentina**

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With 9 figures

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Abstract: Complementary cranial and postcranial material of the Pancheloniidae *Euclastes meridionalis* (DE LA FUENTE & CASADÍO, 2000) from Danian levels of the Jagüel Formation (late Maastrichtian-Danian) at Cerro Azul locality (Río Negro province, Argentina) is described. The new finding of *E. meridionalis* represents one of the few instances in which turtles with cranial remains similar to those previously referred to *Osteopygis* have well associated postcrania. This association allows recognition of the stem-Cheloniid condition of crania and postcrania of *E. meridionalis* (e.g. extremely extended secondary palate, shovel-like mandible, lateral process of the humerus close to the caput humeri, coracoid slightly shorter than the humerus, and a dorsal process of scapula forming relatively narrow angle with acromion).

Keywords: Testudines, Pancheloniidae, Danian, Patagonia, Argentina.

1. Introduction

Fieldwork conducted by Dr. ZULMA BRANDONI (and co-workers of the Museo de La Plata, La Pampa, and Comahue Universities) during summer of 2007 at latest Late Cretaceous-Paleogene outcrops of the Neuquén Basin – northwestern Patagonia – resulted in the discovery of a Danian sequence at Cerro Azul. The site is located south-east of Lago Pellegrini (38° 50' 48" S, 67° 52' 20" W), Río Negro province (Fig. 1). This section begins with laminated pelites of the Jagüel Formation, and continues with bioclastic limestones, sandstones and siltstones with heterolithic lamination and evaporitic levels of the Roca Formation. Invertebrates (bivalves, corals, gastropods,

crabs, serpulids, ostracods, benthic and planktic foraminifers, and calcareous nannofossils) are abundant through the whole section. Remains of a lower jaw and postcranial material of the sea turtle *Euclastes meridionalis* (DE LA FUENTE & CASADÍO, 2000) were recovered from the bottom of the section (Fig. 2). As this species was only known through a posterior skull fragment (discovered from outcrops of the Roca Formation, Danian, at Cerros Bayos, La Pampa province, Argentina), the additional elements were essential to complete the knowledge of its anatomy. Likewise, this discovery represents one of the few instances in which turtles with cranial remains similar to those previously referred to *Osteopygis* have well associated postcrania. This association allowed us to

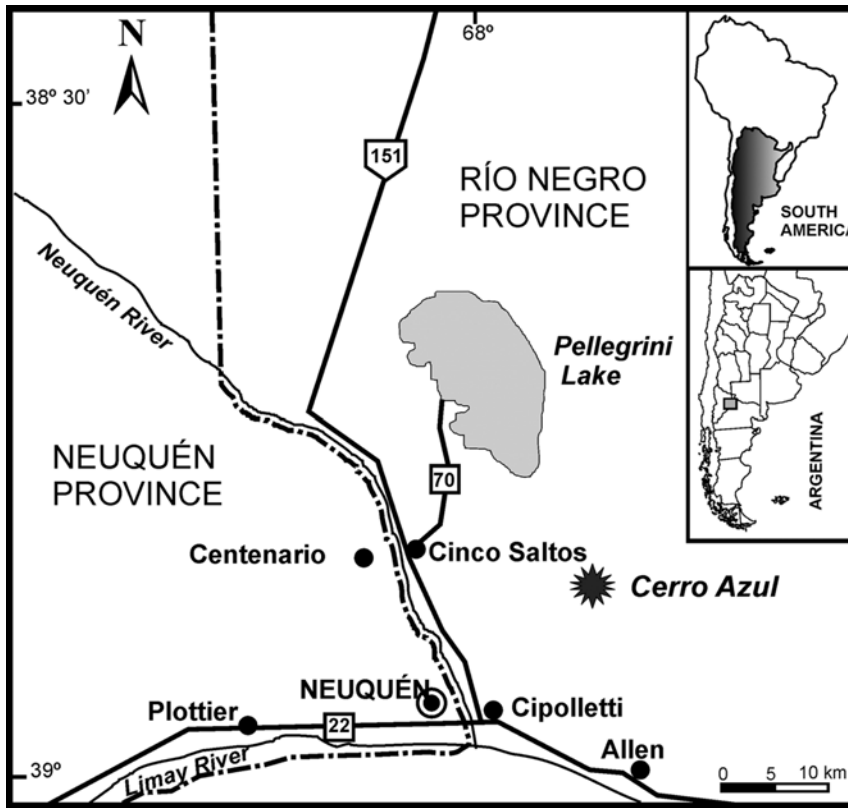


Fig. 1. Location map of the Cerro Azul section, at southeastern Lago Pellegrini, Río Negro province.

recognize the stem-Cheloniid condition of skull and postcrania of *E. meridionalis*.

2. Material and methods

All higher taxon names *sensu* JOYCE et al. (2004). Testudines BATSCH, 1788; Cryptodira COPE, 1868; Pancheloniidae JOYCE et al. (2004). In this contribution we follow the taxonomic decision of MOODY (1980) and consider *Erquelinesia gosseleti* DOLLO, 1886, from the Landenian of Belgium, as a junior synonym of *Erquelinesia planimenta* (OWEN, 1841), from the Lower London Clay of England. To analyze its phylogenetic position, *Euclastes meridionalis* was scored using PARHAM & FASTOVSKY (1997) and LYNCH & PARHAM (2003) data sets with the addition of a new character (Character 6, Appendix 1). The dataset was analyzed in TNT (GOLOBOFF et al. 2003) under equally weighted parsimony.

Stratigraphic section was measured at Cerro Azul locality using a Jacob staff. Geometry of the beds, bounding surfaces, lithology, sedimentary structures and fossil content of the rocks were recorded (Fig. 2).

Abbreviations: GHUNLPam – Cátedra de Geología Histórica of the Universidad Nacional de La Pampa, Argentina. MCSPv – Museo Cinco Saltos, Río Negro, Argentina. SFMF – Museum Senckenberg, Frankfurt am Main, Germany. Q – Museo Paleontológico del Departamento de Geociencias de la Universidad de Concepción, Chile.

3. Geological setting

In the Neuquén Basin, northwestern Patagonia, the Late Cretaceous is characterized by a thick clastic terrestrial succession with dinosaur remains, followed by marginal marine and shallow marine sediments deposited by an Atlantic flooding, produced during the Cretaceous-Paleogene transition, during a period of tectonic quiescence. This shallow sea covered wide areas of northern Patagonia, which was devoid of large topographic barriers (ULIANA & BIDDLE 1988; MALUMIÁN 1999). Those sedimentary rocks are included in the Malargüe Group, which encompass the Cretaceous-Paleogene boundary, and represents the first Atlantic transgression into the Neuquén Basin (WINDHAUSEN 1926; BERTELS 1979; ULIANA & DALLAPÉ 1981). The Malargüe Group, which is well

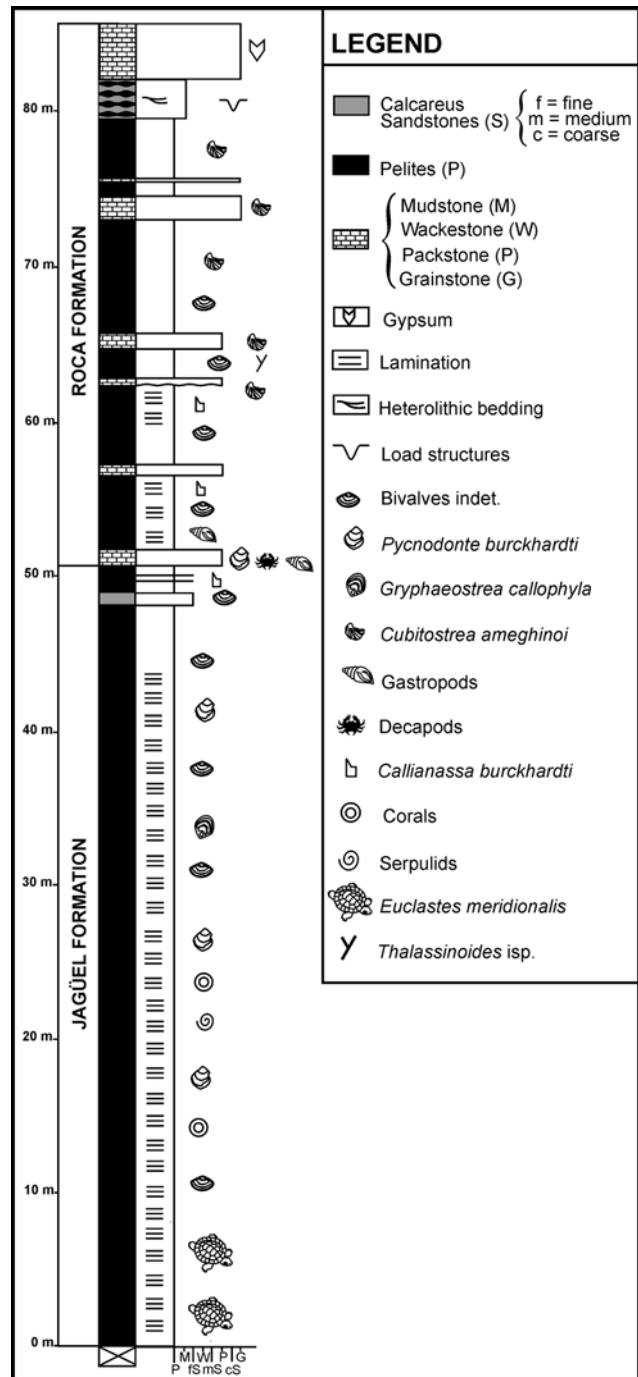


Fig. 2. Stratigraphic section at Cerro Azul, with the localization of the *Euclastes meridionalis* (DE LA FUENTE & CASADÍO) bearing-level.

exposed in southern Mendoza, northeastern Neuquén, western La Pampa and northern Río Negro, had a definite west to east sedimentary supply and active depositional systems ranging from continental to fully marine (LEGARRETA et al. 1989). The onset of marine influx occurred in the late Campanian, the peak of marine flooding during the late Maastrichtian and a

decreasing marine influence within a dominantly continental setting was established during the Paleocene (LEGARRETA et al. 1989; PARRAS & CASADÍO 1999). In the east of the Neuquén Basin, the Malargüe Group includes, from bottom to top, the tide-dominated estuarine and tidal-flat deposits of the Allen Formation, the marine inner to outer shelf

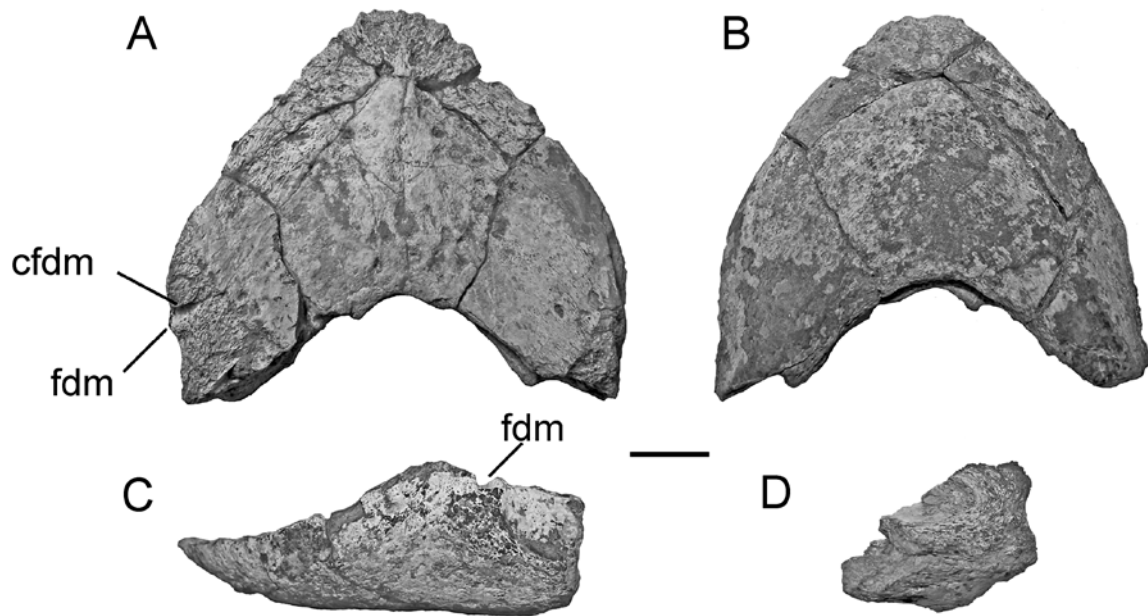


Fig. 3. *Euclastes meridionalis* MCSPv 158. Lower jaw. **A–C** dentary; **A** – dorsal view; **B** – ventral view; **C** – left lateral view; **D** – left surangular in lateral view. Abbreviations: cfdm, canalis foramen *dentofaciale majus*; fdm, foramen *dentofaciale majus*. Scale 2 cm.

pelites of the Jagüel Formation, the shallow marine, intertidal to subtidal calcareous facies of the Roca Formation, and is topped by sandstones, tuffs and evaporites of the El Carrizo Formation, deposited under lacustrine to fluvial environments (ULIANA & DELLAPÉ 1981; LEGARRETA et al. 1989; PARRAS et al. 1998).

Because these rocks provide an excellent opportunity to study the changes operated in mid-latitude continental and marine ecosystems of the southern hemisphere at the end of the Cretaceous and beginning of the Paleogene, they have been lately subject to renewed interest (CASADÍO et al. 2005).

The studied fossils come from the bottom of a shallowing up section of the Malargüe Group cropping out at Cerro Azul locality, southeast of Lago Pellegrini, northwestern Patagonia (Figs. 1–2). These beds are referred to the Jagüel Formation, which comprises 50 m of laminated mudstones and siltstones, and have been deposited in an inner shelf to subtidal environment. This formation transitionally grades into 35 m of the shallow marine, subtidal to supratidal calcareous facies (bioclastic packstones to rudstones, mudstones and sandstones with heterolithic lamination, and evaporites) of the Roca Formation. Bivalves (mostly oysters), gastropods, decapods, corals,

and serpulids are very abundant in all the section. The micropaleontological analysis has revealed the presence of ostracods, benthic and planktic foraminifers, and calcareous nannofossils.

The calcareous nannofossils (nannozones NP2 and NP3), the planktic forams and the oysters *Pycnodonte* (*Phygraea*) *burckhardti* (BÖHM), *Gryphaeostrea callophyla* (IHERING) and *Cubitostrea ameghinoi* (IHERING), indicate a Danian age for the entire section (PARRAS et al. 2007).

4. Systematic paleontology

Testudines BATSCH, 1788

Cryptodira COPE, 1868

Pancheloniidae JOYCE, PARHAM & GAUTHIER, 2004

Euclastes COPE, 1867

Euclastes meridionalis (DE LA FUENTE & CASADÍO, 2000)

Figs. 3, 5–7

2000 *Pampaemys meridionalis* DE LA FUENTE & CASADÍO, p. 238, figs. 3–4.

Holotype: GHUNLPam 19137, posteromedial skull fragment.

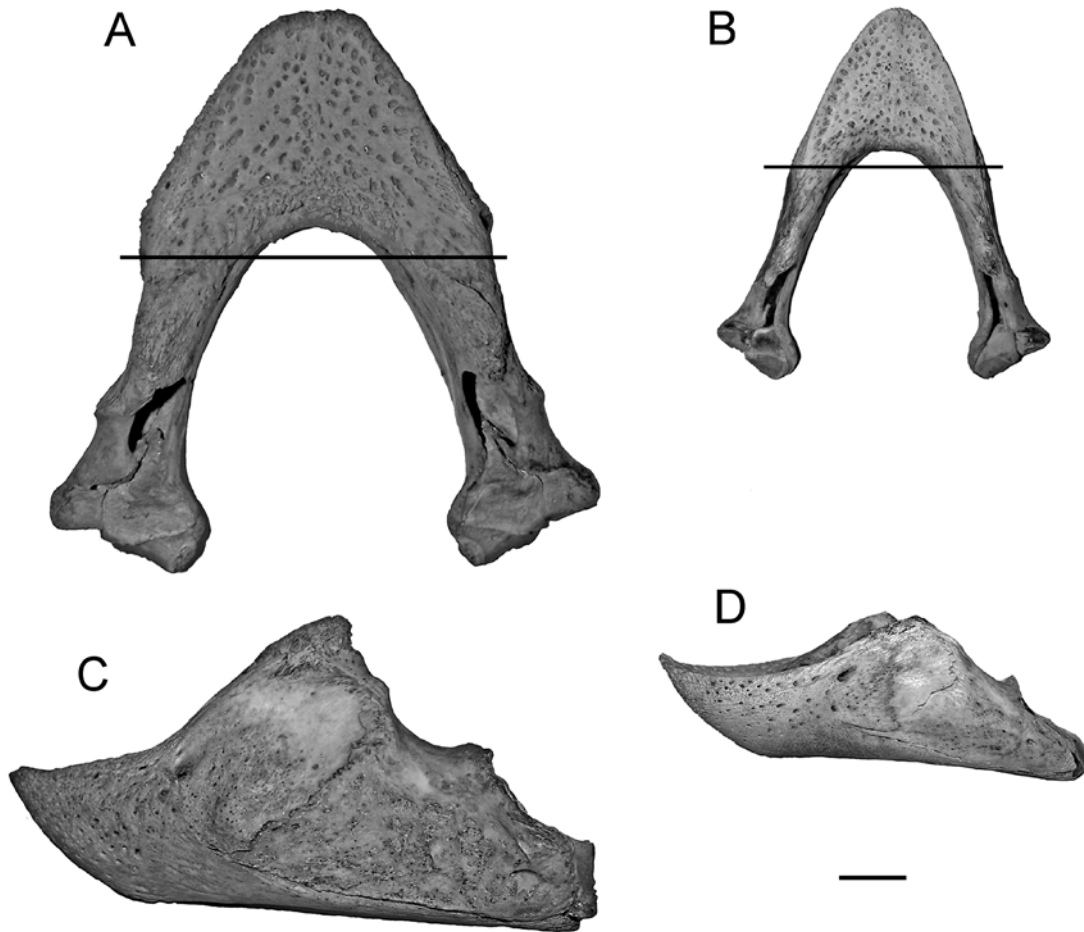


Fig. 4. *Caretta caretta* lower jaws showing the relative position of foramen *dentofaciale majus*. **A** and **C** (MLP uncataloged); **B** and **D** (MLP R.5340). **A-B** – dorsal view; **C-D** – lateral view. Scale 2 cm.

Referred material: MCSPv 158, lower jaw, right scapular girdle, right humerus, caudal vertebrae and carapace fragments of one adult specimen.

Occurrence: Cerros Bayos (37° 35' 50" S, 67° 39' 34" W), Roca Formation (Danian) and Cerro Azul (38° 50' 48" S, 67° 52' 20" W), Jagüel Formation (Danian).

Emended diagnosis: Eucryptodiran marine turtle that can be referred to *Euclastes* on the basis of an extensive secondary palate with elongated maxillae, vomer and palatines, a V-shaped basisphenoid, palatines overshelve pterygoids. Distinguished from other *Euclastes* based on the following set of characters: palatines not fused in midline behind the vomer in ventral view, narrow palate at the level of the pterygoid process, and development of an acute crest posterior to the choana, *fossa masseterica* of the mandible is extended and deepened on the surangular. *E. meridionalis* shares with *E. planimenta* a secondary palate more extensive than the other species of *Euclastes* [*E. platyops*

(COPE, 1867), *E. roundsi* (WEEMS, 1988), *E. wielandi* (HAY, 1908), *E. hutchisoni* LYNCH & PARHAM, 2003].

Description: Mandible: The referred specimen of *E. meridionalis* preserves the dentary and the left surangular (Fig. 3). As typical in *Euclastes* species, in *E. meridionalis* the mandible is broad and flat. The masticatory surface of dentaries shows a medial convexity that divides the triturating surface into concave halves as in the holotype of *E. hutchinsoni* LYNCH & PARHAM, 2003. In *E. meridionalis* the symphyseal length is 71 mm. In another mandible referred to *Euclastes* sp. from the Quiriquina Formation this length is estimated in 97 mm (GASPARINI & BIRO-BAGOCZKY 1986). As the only postdentary preserved element is the surangular, the total length of the mandible in *E. meridionalis* is not available. Nevertheless, based on the preserved elements, the symphyseal length can be estimated as approximately 55 per cent of this lower jaw length (Fig. 3).

A similar relation is calculated in *E. planimenta* (= *E. gosseleti*). These extensive triturating surfaces are related to

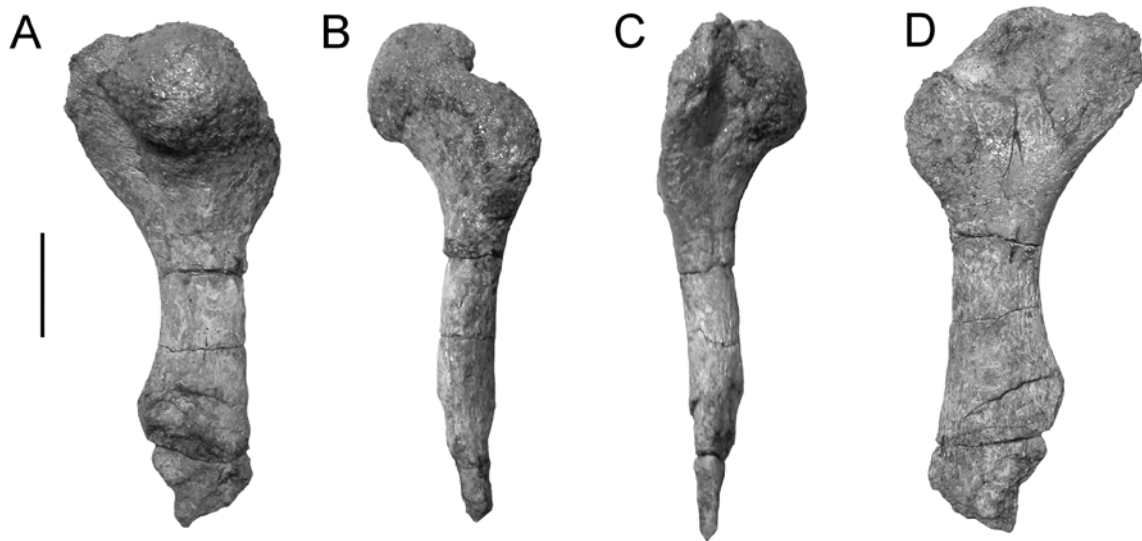


Fig. 5. *Euclastes meridionalis* MCS Pv 158. Right humerus. **A** – dorsal view; **B-C** – lateral views; **D** – ventral view. Scale 2 cm.

the development of a large secondary palate. The triturating surface in *E. meridionalis* is as extensive as in *E. planimenta* and more extensive than *E. hutchinsoni* ZANGERL (1971) proposed as a parameter to estimate the relative size of the triturating surface in cheloniids, the location of a transverse line connecting the *foramina dentofaciale majus* (= *foramina mentalia* in his paper). According to this author, in forms with a relatively less extensive triturating surface (e.g. *Caretta*) this line runs behind the posterior edge of the triturating shelf, while in forms with a more extensive triturating surface this line traverses it near its posterior margin (e.g. *Osteopygis* in his paper) or intersects the symphysis at about the mid-length (e.g. *Erquelinnesia* in his paper). Nevertheless, the location of this line could be variable at intraspecific level, as shown on Fig. 4, and therefore its use as a marker to set up the relative size of the triturating surface is a weak point.

The lower jaw width at the level of the dentofacial foramen is 118 mm, and the angle between cutting edges is close to 84 degrees. As in the other *Euclastes*, there is a strong fossa masseterica on the lateral wall of the dentary. In *E. hutchinsoni* and *E. planimenta* this fossa is deep anteriorly and vanishes posteriorly, while in *E. meridionalis* both the anterior and posterior edges of the fossa deeply excavate the lateral mandible wall.

In lateral view the symphysis of *E. meridionalis*, and of *Euclastes* sp. from Quiriquina, is remarkably low (“shovel like”) in comparison with other cheloniids and also other species of the genus (e.g. height /length of the symphysis = 4). In *E. meridionalis* the foramen *dentofaciale majus* opens at the same level of the labial edge of the triturating surface of the dentary (Fig. 3C).

Humerus: The right humerus of *E. meridionalis* (Fig. 5) is relatively straight as an artefact of deformation. Probably

its shaft was slightly S-shaped in life, but it is slightly compressed dorso-ventrally, and ovoid in cross section. This bone does not differ in morphology from *E. hutchinsoni* humerus (LYNCH & PARHAM 2003: fig. 7B). The proximal end of the MCS Pv 158 is better preserved than the distal end. The general morphology of the humerus is similar to that of basal chelonioids. Although the medial process of the humerus is elongated proximally (as in extant cheloniids) its proximal extent is subequal to the head in ventral view. This condition, as well as the proximal position of the lateral process, differs from those of living cheloniids. The caput humeri sets off from the humerus shaft at an angle of 134 degrees (α angle of ZANGERL 1953), and the head of the humerus is anteroposteriorly compressed. Its convex ventral margin distinctly overhangs the intertubercular fossa. The angle between the main plane of movement and the axis of the shaft is 30 degrees (β angle of ZANGERL 1953).

Scapula: The MCS 158 preserves the complete scapular blade (dorsal process) and the base of the acromion (ventral process) (Fig. 6A-C). The scapular blade and the acromion diverge at an angle of 85 degrees. There is an extended neck separating the glenoid from the diverging scapular processes. The retention of an elongated scapular neck has been considered as a plesiomorphic feature characteristic of many early Cretaceous sea turtles (*Santanachelys*, *Toxochelys*) and modern cheloniids (KEAR 2006). The scapular neck of *E. meridionalis* is more feeble and long than *Toxochelys*. The glenoid articular surface of the scapula is relatively narrow.

Coracoid: The coracoid is relatively short and its length approximately equals that of the scapular blade (Fig. 6D-E). Distally it is expanded forming a plate with a blunt ridge on its ventral face, as is described by ZANGERL (1971) in *E. planimenta*. The coracoid is shorter than the humerus,

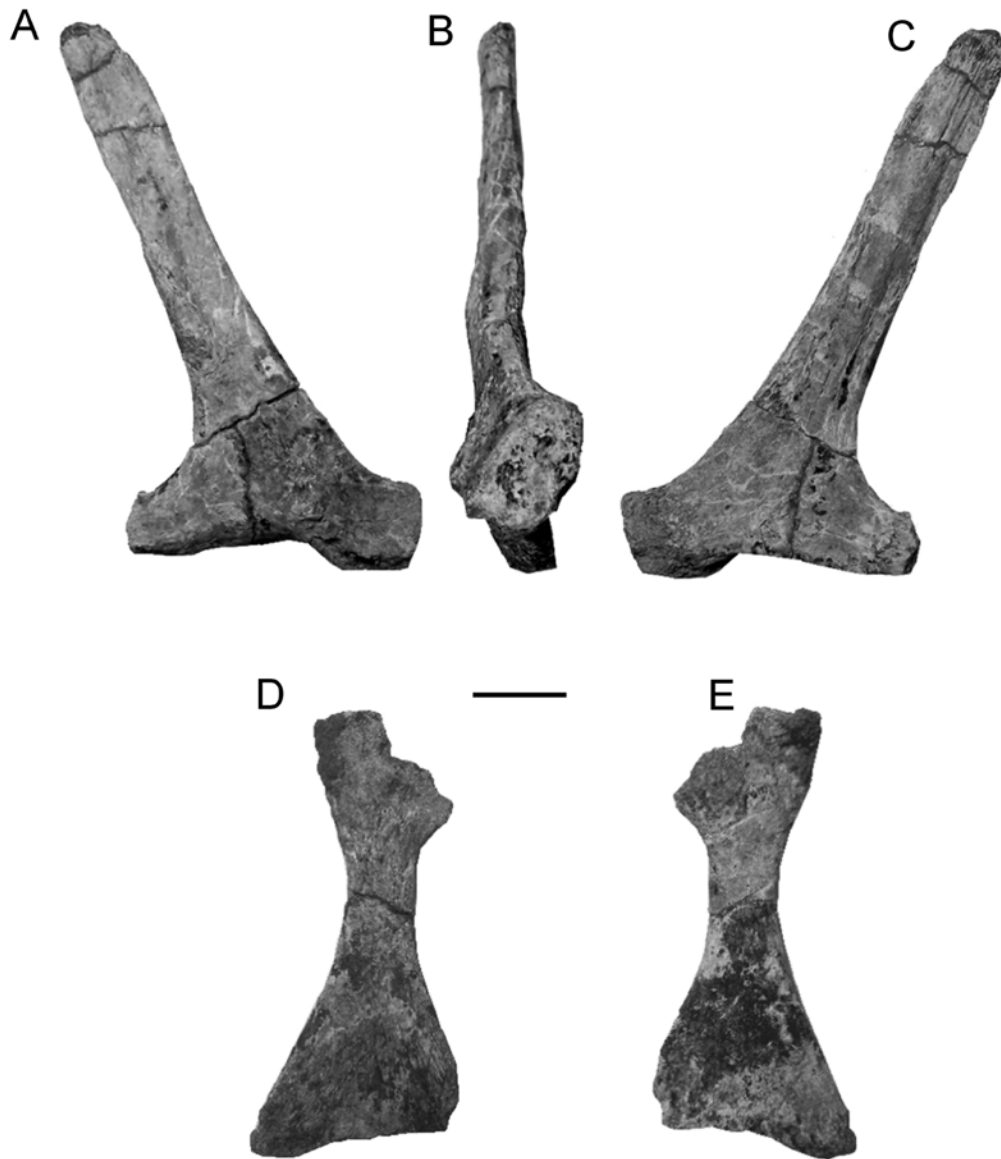


Fig. 6. *Euclastes meridionalis* MCSPv 158. **A-C** – scapula; **D-E** – coracoid. Scale 2 cm.

a primitive condition present in other stem-Cheloniidae such as *Toxochelys* and *Ctenochelys* (see LYNCH & PARHAM 2003).

Caudal Vertebrae: Two anterior isolated centra of caudal vertebrae are preserved (Fig. 7). The procoelus condition of one of them is represented by a wide and depressed cotyle and a prominent convex condyle. In this caudal vertebra the left transverse process is quite prominent, and a strong ventral crest is recognized anteriorly, but vanishes posteriorly. The other centrum is badly preserved, so the presence of a ventral crest cannot be confirmed.

Carapace: The carapace is represented by an isolated peripheral bone of the bridge and a posterior peripheral bone. Unfortunately, the poor preservation of these bones

precludes a detailed description and their location in the carapace is uncertain.

5. Discussion

The holotype of the species *E. meridionalis* (DE LA FUENTE & CASADÍO, 2000) was originally described as *Pampaemys meridionalis* on the basis of a fragmentary skull (GHUNLPam 19137) from the Early Paleogene (Danian) of La Pampa province (Argentina). This species is characterized by an extremely extensive secondary palate. As a consequence of this

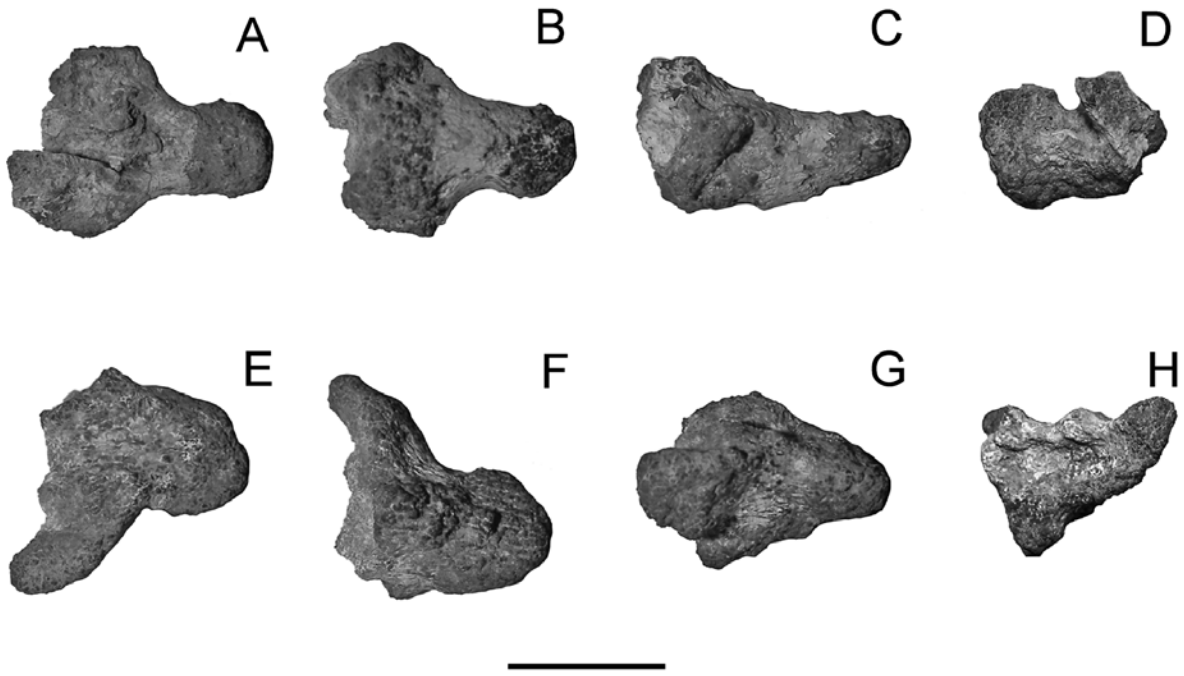


Fig. 7. *Euclastes meridionalis* MCSPv 158. Two caudal vertebrae. **A-E** – dorsal view; **B-F** – ventral view; **C-G** – lateral view; **D-H** – anterior view. Scale 2 cm.

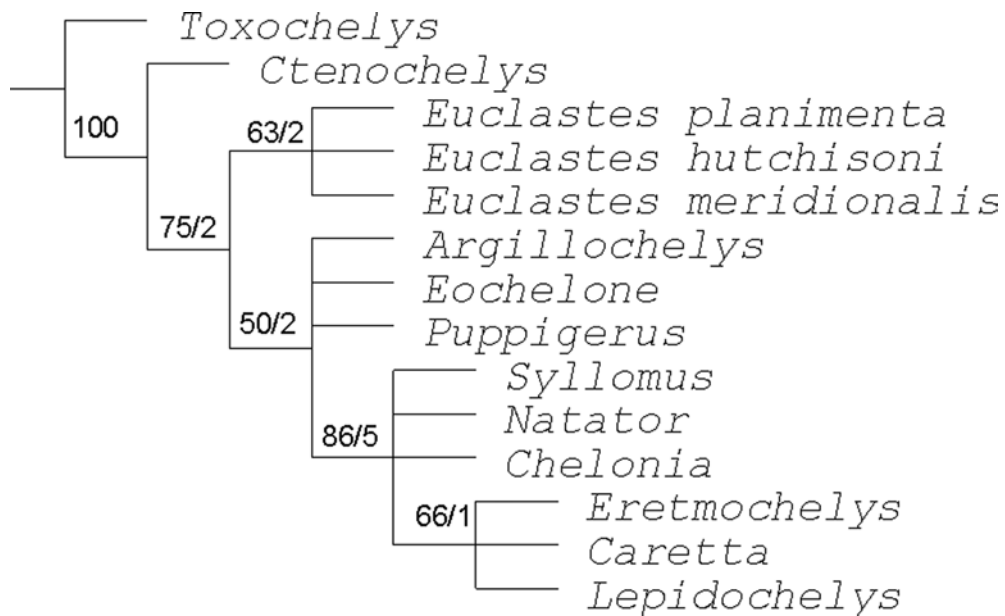


Fig. 8. Cladogram showing *Euclastes meridionalis* relationships among selected chelonoids. The numbers above branches correspond to bootstrap values (1000 replicates) decay indices respectively.

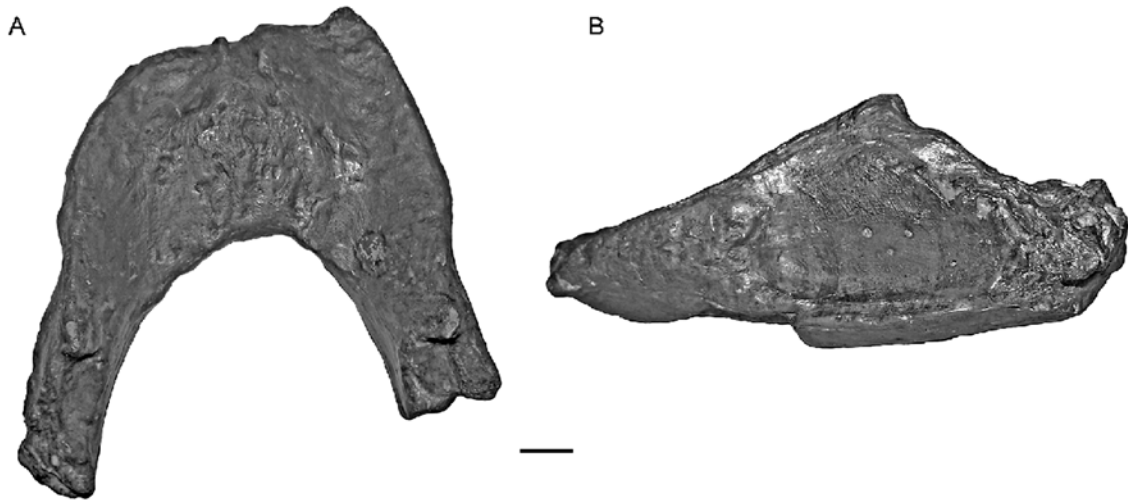


Fig. 9. *Euclastes* sp. from Quiriquina Formation (Q 377). **A** – dorsal view; **B** – left lateral view. Scale 2 cm.

elongation the internal narial opening is located posterior to three quarters of the skull length. The extreme elongation of the secondary palate of GHUNLPam 19137 might be correlated with a long mandibular symphysis as the one observed on the other specimen (MCSPv 158) recovered from the Danian of northern Patagonia, supporting the assignments of the latter to the species described by DE LA FUENTE & CASADÍO (2000). These authors assigned this species to the subfamily Osteopyginae. After the “decapitation” of *Osteopygis* and the assignment of the referral skull to stem-Cheloniidae and the post-crania to stem-Cryptodira proposed by PARHAM (2005), this author recommended that the name Osteopyginae must be discarded.

As non-*Osteopygis* Osteopyginae are represented by monotypic genera, and in order to avoid the proliferation of generic names, LYNCH & PARHAM (2003) and PARHAM (2005) proposed the assignment of all durophagous species, previously referred to Osteopyginae, to a single genus, *Euclastes* COPE, 1867. Because of the nature of the available material from Argentina and until new material is found, LYNCH & PARHAM’S taxonomic decision is followed in this paper.

The species currently assigned to *Euclastes* and the other stem-Cheloniidae taxa (i.e. *Toxochelys* and *Ctenochelys*) were considered members of Toxochelyidae (ZANGERL 1953, 1971), until FASTOVSKY (1985) demonstrated the paraphyletic condition of this family. Three hypotheses on the phylogenetic

relationships of these marine turtles have been proposed. GAFFNEY & MEYLAN (1988) argued that *Ctenochelys* should be considered a sister taxon of all chelonioids except *Toxochelys*. HIRAYMA (1994) and PARHAM & FASTOVSKY (1997) proposed that *Toxochelys*, *Ctenochelys* and *Euclastes* taxa should be considered as Cheloniidae *sensu lato*. More recently, KEAR & LEE (2006) in their phylogenetic analysis of the major sea turtle lineages found *Toxochelys* and *Ctenochelys* as stem sea turtles outside the crown Cheloniodea, rather than allied with derived Cheloniidae.

By the implicit enumeration of all possible trees, eight most parsimonious trees of 60 steps ($ci = 0.61$; $ri = 0.76$) were obtained. The strict consensus tree is shown in Figure 8. *E. meridionalis* forms a clade with the other two species of the genus *E. hutchinsoni* and *E. planimenta* supported by an extensive secondary palate (character 1); shovel-like mandible (character 6); a low tomial ridge (character 7, missing in *E. meridionalis*); broad skull (character 13); and fused premaxilla (character 14, missing in *E. meridionalis*). In most of the topologies found *E. hutchinsoni* basal to the clade formed by *E. meridionalis* and *E. planimenta*.

Two other pancheloniids referable to *Euclastes* sp. have been recovered from the Campanian-Maastrichtian of the Quiriquina Formation, north of the Chilean Patagonia. In 1986, GASPARINI & BIRO-BAGOCZKY described a mandible (Q 377) and referred it to *Osteopygis* sp. Later this material was

referred to *Euclastes* sp. (LYNCH & PARHAM 2003; DE LA FUENTE 2007). However, this mandible could be referred to *E. meridionalis* by the long and extremely low symphysis. Although a shovel-like mandible characterizes *Euclastes* species, in MCSPv 158 and Q 377 this condition is extreme. Thus, the length is more than three times the height of the symphysis (Fig. 9).

The other specimen referable to *Euclastes* sp. is a well preserved skull (SFMF R 4151), also from the Campanian-Maastrichtian of the Quiriquina Formation, originally described as *Osteopygis* aff. *sculptus* by KARL et al. (1998). As noted by BONA & DE LA FUENTE (2005) the name *Osteopygis sculptus* is a junior synonym of the chelid *Yaminuechelys maior* (STAESCHE, 1929). Although SFMF R 4151 is referable to the genus *Euclastes* sensu LYNCH & PARHAM (2003) based on the extensive secondary palate, the extension in this specimen is not as extreme as in *E. meridionalis*, suggesting that it probably corresponds either to a new species of *Euclastes* or to one of the known species of the genus other than *E. meridionalis*. Unfortunately, this topic cannot be resolved until a complete revision of the material housed at the Senckenberg Museum is accomplished.

The finding of *E. meridionalis* in Danian sedimentary rocks of the Jagüel Formation at Cerro Azul, is one of the few instances in which turtles with cranial remains similar to the those previously referred to *Osteopygis* have well associated postcrania. This association allowed recognition of the stem-Cheloniid condition of skull and postcrania of *E. meridionalis*.

The association of cranial and postcranial elements in *Euclastes meridionalis* reveals that, within the Pancheloniids, this species exhibits some derived traits in its cranial morphology (i.e. extremely extended secondary palate, shovel-like mandible) while it retains primitive postcranial features lost in the crown cheloniids: the lateral process of the humerus close to the caput humeri, coracoid slightly shorter than the humerus, and a dorsal process of scapula forming relatively narrow angle with acromion.

Two topics are worth to be remarked. One is referred to the temporal distribution of *Euclastes*. Although both main lineages of marine turtles (i.e. pancheloniids and pandermochelys) are inferred to have survived the Cretaceous/Paleogene extinction (e.g. KEAR & LEE 2006), only *Euclastes* documents this transition. Thus, in northern Patagonia *Euclastes* material has been recovered in Campanian-Maas-

trichtian levels of the Quiriquina Formation, and Danian levels of the Roca and Jagüel formations.

The other topic is referred to the living habits of *Euclastes* based on the known record. Postcranial characters of *E. meridionalis* suggest that this species, as well as the other *Euclastes*, were poor swimmers compared to crown cheloniids, as HIRAYAMA (1992, 1994, 1997) proposed for other stem-Cheloniids (i.e. *Toxochelys* and *Ctenochelys*). The extensive secondary palate and triturant surface of the lower jaw of *Euclastes*, as well as a broad skull, have been associated with a durophagous diet (LYNCH & PARHAM 2003). Although durophagy evolved more than once in the panchelonioida, the striking feature only present in *Euclastes* is the shovel-like mandible. This peculiar mandible might be associated with the adaptation not only for durophagy but also the specialization to feed on benthic semi-infaunal and/or shallow burrower invertebrates; however, this proposal opens further studies.

Acknowledgements

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Appendix 1 – Description of characters used in phylogenetic analyses

1. Secondary palate: (0) absent; (1) present; (2) extensive (PARHAM & FASTOVSKY 1997, character 1).
2. Foramen palatinum posterius: (0) wide; (1) lost (PARHAM & FASTOVSKY 1997, character 2).
3. Contact of vomer with premaxillae: (0) broad; (1) reduced (PARHAM & FASTOVSKY 1997, character 3).
4. Foramen caroticum laterale much larger than foramen arterius canalis caroticus interni: (0) absent; (1) present (PARHAM & FASTOVSKY 1997, character 4).
5. Dentary: (0) flat triturating surface; (1) lingual ridges present; (2) ridge along entire length of symphysis (PARHAM & FASTOVSKY 1997, character 6).
6. Shovel-like mandible: absent (0); present (1).
7. Tomial ridge: (0) pronounced; (1) low (PARHAM & FASTOVSKY 1997, character 7).
8. Surangular extending anteriorly into dentary: (0) absent; (1) present. (PARHAM & FASTOVSKY 1997, character 8).
9. Shape of the anterior portion of the vomer: (0) constant width; (1) variable width (PARHAM & FASTOVSKY 1997, character 9).
10. Prefrontal scutes: (0) one pair; (1) two pair (PARHAM & FASTOVSKY 1997, character 10).
11. Process pterygoideus externus: (0) large; (1) reduced (LYNCH & PARHAM 2003, character 10).
12. Direction of the orbits: (0) dorsolaterally facing; (1) laterally facing (LYNCH & PARHAM 2003, character 11).
13. Skull shape: (0) moderate width; (1) broad; (2) narrow and elongate (LYNCH & PARHAM 2003, character 12).
14. Fused premaxillae: (0) absent; (1) present. (LYNCH & PARHAM 2003, character 13).
15. Dorsal process of scapula forming relatively wide angle with acromion: (0) absent; (1) present (PARHAM & FASTOVSKY 1997, character 11).
16. Metischial processes: (0) pronounced; (1) reduced. (PARHAM & FASTOVSKY 1997, character 12).
17. Femoral trochanters: (0) separated by a fossa; (1) fossa obliterated (LYNCH & PARHAM 2003, character 16).
18. Femoral trochanter ridge: (0) not complete; (1) complete, without a notch (LYNCH & PARHAM 2003, character 17).
19. Tibial pit for pubotibialis and flexor tibialis internus muscles: (0) absent; (1) present (PARHAM & FASTOVSKY 1997, character 15).
20. Centra of the seventh cervical vertebra: (0) procoelous; (1) platycoelous (PARHAM & FASTOVSKY 1997, character 16).
21. Articulations of first and second digits: (0) movable; (1) immovable (PARHAM & FASTOVSKY 1997, character 17).
22. Humerus with V-shaped or triangular lateral process: (0) absent; (1) present (LYNCH & PARHAM 2003, character 21).
23. Coracoid length in relation to humerus: (0) shorter; (1) longer (PARHAM & FASTOVSKY, character 19).
24. Seventh to eighth centrum articulation of the cervical vertebra: (0) single; (1) doubled (LYNCH & PARHAM 2003, character 23)
25. Elongated plastron with a broad bridge: (0) absent; (1) present (PARHAM & FASTOVSKY 1997, character 20).
26. Rib-free peripherals: (0) only anterior and posterior to ribs; (1) between seventh and eighth ribs; (2) between sixth and seventh ribs (unordered) (PARHAM & FASTOVSKY 1997, character 21).
27. Post nuchal fontanelles: (0) present; (1) absent (PARHAM & FASTOVSKY 1997, character 22).
28. Additional peripherals (0) absent; (1) present (PARHAM & FASTOVSKY 1997, character 23).
29. Additional pleural scales: (0) absent; (1) present (LYNCH & PARHAM 2003, character 28).
30. Neurals (0) between eight and nine; (1) usually ten; (2) variable between extensive neural fragmentation and neural reduction (LYNCH & PARHAM 2003, character 29).
31. Textured carapace elements: (0) absent; (1) present (LYNCH & PARHAM 2003, character 30).
32. Shape of pygal: (0) notched posteriorly; (1) not notched (PARHAM & FASTOVSKY 1997, character 24).

Appendix 2 – Character-taxon matrix used for phylogenetic analysis:

	5	10	15	20	25	30
<i>Toxochelys</i>	0	0	0	0	0	0
<i>Ctenochelys</i>	1	0	0	0	0	0
<i>Euclastes planimenta</i>	2	1	1	1	0	0
<i>Euclastes hutchisoni</i>	2	1	1	1	0	0
<i>Euclastes meridionalis</i>	2	1	1	1	0	0
<i>Argillochelys</i>	1	1	0	0	1	0
<i>Eochelone</i>	0	1	0	0	1	0
<i>Puppigerus</i>	2	1	1	1	1	1
<i>Syllomus</i>	1	1	1	1	1	1
<i>Natator</i>	1	1	1	1	1	1
<i>Chelonia</i>	1	1	1	1	1	1
<i>Eretmochelys</i>	1	1	1	1	1	1
<i>Caretta</i>	1	1	1	1	1	1
<i>Lepidochelys</i>	1	1	1	1	1	1