

NOTA PALEONTOLOGICA

TRIDIMENSIONAL ANGEL SHARK JAW ELEMENTS (ELASMOBRANCHII, SQUATINIDAE) FROM THE MIOCENE OF SOUTHERN ARGENTINA



DANIEL ALFREDO CABRERA¹, ALBERTO LUIS CIONE¹ AND MARIO ALBERTO COZZUOL²

¹CONICET -División Paleontología de Vertebrados, Museo de La Plata, FCNyM, UNLP, Paseo del Bosque s/nº, B1900FWA, La Plata, Argentina. dcabrera@museo.fcnym.unlp.edu.ar; acione@museo.fcnym.unlp.edu.ar

²UFMG -Universidade Federal de Minas Gerais, Belo Horizonte, Brazil. cozzuol@icb.ufmg.br

Key words. *Squatina*. Neogene. Patagonia. Tessellated cartilage. Taphonomy

Palabras clave. *Squatina*. Neógeno. Patagonia. Cartílago teselado. Tafonomía

SURVEYING the basal beds of the middle–late Miocene Puerto Madryn Formation near the city of Puerto Madryn, north-eastern Chubut Province, Argentina (Fig. 1), one of us (MC) collected the proximal half of a palatoquadrate (upper jaw) and Meckel's cartilage (lower jaw) of an angel shark (*Squatina* Dumeril, 1806).

Fossil chondrichthyans are usually represented by isolated teeth, spines, and scales whereas endoskeletal remains are extremely rare due to their low preservation potential (Capetta, 1987). The most abundant cartilage preserved is the vertebral centrae.

The endoskeleton of elasmobranch fishes (sharks, rays, and relatives) is composed by cartilage instead of bone as in other vertebrates. This cartilage may be mineralized to varying degrees with crystals of hydroxyapatite, providing stiffness to the skeletal system. There are two types of skeletal cartilage in sharks: the vertebral cartilage (present only in vertebrae) and the tessellated cartilage (present in the rest of the skeleton) (Fig. 2.1).

The tessellated cartilage consists of a mosaic of hexagonal tiles called tesserae (Fig. 2.2–5), joined together by inter-tesseral collagen fibers. The tesserae are lying just beneath the fibrous perichondrium and overlaying a core of unmineralized extracellular matrix containing chondrocytes (Kemp and Westrin, 1979; Dean and Summers, 2006). Tridimensionally preserved endoskeletal cartilages are uncommon in the fossil record because tessellated tissues tend to collapse after the decay of the unmineralized inner core and other

soft tissues. Tessellated cartilages are often found as bidimensional elements, patches of tesserae or isolated tesserae. In southern South America, endoskeletal elements other than vertebrae are restricted to the skeleton of a primitive batomorph from the Jurassic of Patagonia (Cione, 1999).

Squatina is a neoselachian genus known since the Cretaceous (Welton and Farish, 1993). In southern South America, teeth of *Squatina* have been reported from the Upper Cretaceous, probably the Paleocene and Miocene of Chile (Gutstein *et al.*, 2008; Muñoz-Ramírez *et al.*, 2008), and the Miocene of Argentina (Ameghino, 1906; Cione, 1988; Cione *et al.*, 2000, 2005). In the Puerto Madryn Formation, teeth of *Squatina* were previously preserved as stomach content of the pinniped *Kawas benegasorum* Cozzuol, 2001. In this note, the jaws of *Squatina* sp. found in the Puerto Madryn Formation are described, and the taphonomic context is discussed.

GEOGRAPHIC AND STRATIGRAPHIC PROVENANCE

The jaws of *Squatina* sp. come from the basal strata of the Puerto Madryn Formation, cropping out at cliffs located to the west of the city of Puerto Madryn (65°06'W; 42°46'S) (Fig. 1.1). The Puerto Madryn Formation ("Entrerriense" plus "Rionegrense marino" of Feruglio, 1949) corresponds to the late part of the extensive marine encroachment that lasted from the late Oligocene until the late Miocene ("Mid Tertiary Transgressive Onlap Sequence" of Williams and

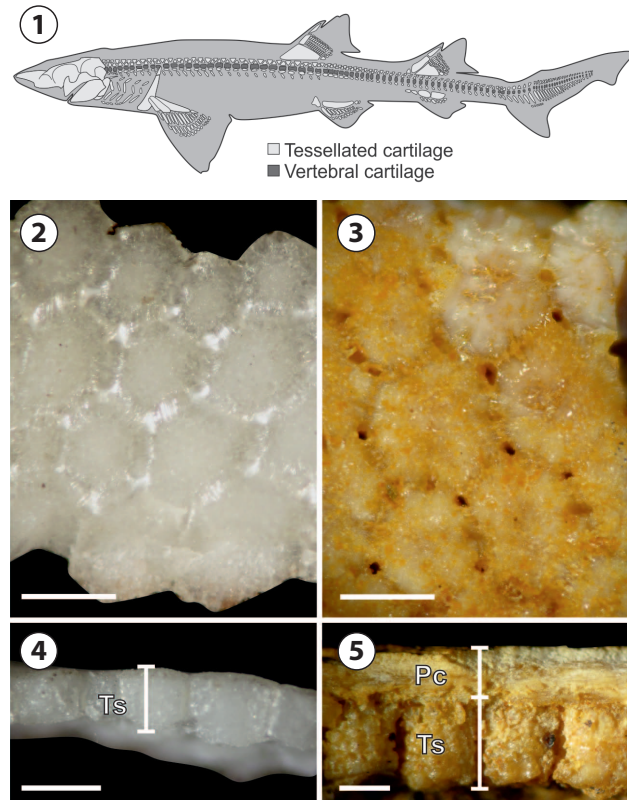
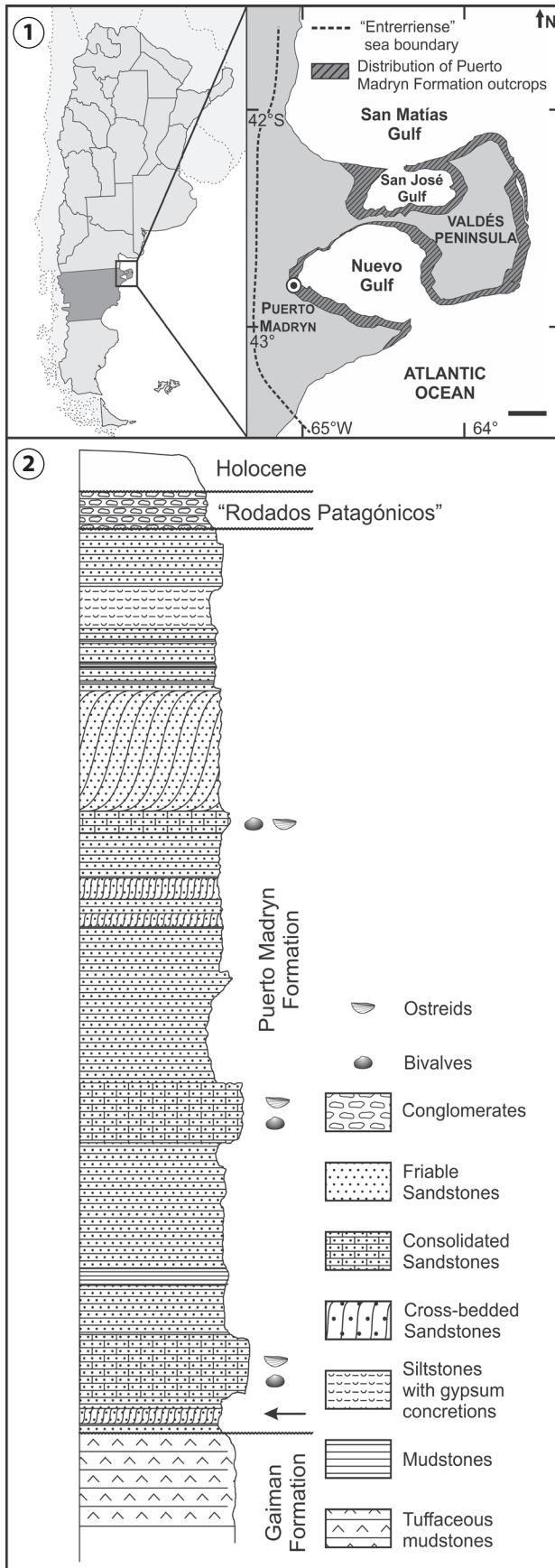


Figure 2. 1, Schematic draw showing the distribution of the tessellated cartilage and the vertebral cartilage in elasmobranchs (modified after Dean and Summers, 2006)/ dibujo esquemático mostrando la distribución del cartilago teselado y cartilago vertebral en elasmobranchios (modificado de Dean and Summers, 2006); 2, 4, tessellated cartilage of a extant specimen of *Squatina*. Internal surface and cross section view respectively. Scale bar= 500 µm/ cartilago teselado de un ejemplar actual de *Squatina*. Superficie interna y vista en sección transversal respectivamente. Escala= 500 µm; 3, 5, tessellated cartilage of the fossil palatoquadrate MPEF-PV 3804. Internal surface and cross section view respectively. Scale bar= 500 µm/ cartilago teselado del palatoquadrate fósil MPEF-PV 3804. Superficie interna y vista en sección transversal respectivamente. Escala= 500 µm; Pc, perichondrium/ pericondrio; Ts, tesserae/ teselas.

Hubbard, 1984) paralleling the early Neogene trend of the global eustatic rise (Uliana and Biddle, 1988; del Río, 1991; del Río *et al.*, 2001). The Puerto Madryn Formation overlies the Gaiman Formation (early Miocene) in the Península Valdés and lower Chubut river area. The large areal extent of Miocene marine deposits reveals that the mean freeboard of the plate interior was low (Uliana and Biddle, 1988).

The Puerto Madryn Formation consists of a sequence of coquinas, cross-bedded sandstones, shales with heterolithic

Figure 1. 1, Locality map of Puerto Madryn (modified after Cozzuol, 2001)/ mapa de la localidad de Puerto Madryn (modificado de Cozzuol, 2001); 2, stratigraphic section exposed at the cliff near the local race-track (modified after Haller, 1981). The arrow points to the fossil bearing level/ perfil expuesto en cercanías del autódromo local (modificado de Haller, 1981). La flecha señala el nivel donde provienen los fósiles.

lamination and massive shales totally bioturbated or laminated (Haller, 1981; del Río, 2000). According to Scasso and del Río (1987), the sequence belongs to a transgressive-regressive cycle within an overall regressive sequence. These sediments were deposited on a shallow shelf with storm influence, evolving upwards into a tide-dominated estuarine environment.

The material described herein was obtained in the middle section of the cliffs located west of Puerto Madryn city, near the local racetrack. The fossil-bearing beds correspond to accumulations of the Transgressive Phase of del Río *et al.* (2001) located at the base of the Puerto Madryn Formation (Fig. 1.2).

The age of the Puerto Madryn Formation has been widely discussed. In recent years, it has been referred to the middle Miocene (biostratigraphic evidence; del Río 1988) and more recently to the early late Miocene (strontium datations; del Río *et al.*, 2001; Scasso *et al.*, 2001). However, according to cetacean evidence, the deposition appears to have started during the middle Miocene up to the Tortonian (Cione *et al.*, 2005). We agree with this later hypothesis.

SYSTEMATIC PALEONTOLOGY

Subclass ELASMOBRANCHII Bonaparte, 1838

Order SQUATINIFORMES Buen, 1926

Family SQUATINIDAE Bonaparte, 1838

Genus *Squatina* Dumeril, 1806

Type species. *Squalus squatina* Linnaeus, 1758.

Squatina sp.

Figures 2–4

Distribution. Recent species lives in temperate European and North African deep waters, to at least 150 m (Compagno, 1984).

Material. MPEF-PV 3804, right palatoquadrate (upper jaw) and MPEF-PV 3805, right Meckel's cartilage (lower jaw), corresponding to a single specimen.

Repository. Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina.

Description. The material consists of a partial right palatoquadrate and Meckel's cartilage, both tridimensionally preserved. The symphyseal area is missing. The palatoquadrate is elongated and has a shallow dental groove on the mesial surface. The most proximal portion is developed into an articular process of the palatoquadrate, which articulates with the concave articular fossa of Meckel's cartilage. Immediately mesial to the articular process, there is the shallow quadrate concavity, which in turn receives the mandibular knob. The quadrate process is a small and dorsally-directed triangular process located in the proximal one-third of the dorsal surface (Carvalho *et al.*, 2008; Fig. 3.1). The Meckel's cartilage has a sharp dental groove on the mesial surface. A well-developed mandibular knob is preserved on the articular area, but the mandibular articular fossa is worn. The palatoquadrate and the Meckel's cartilage have well-preserved tessellated tissue. In cross section, individual tesserae can be clearly observed, and overlaying them, there is a thin layer that ap-

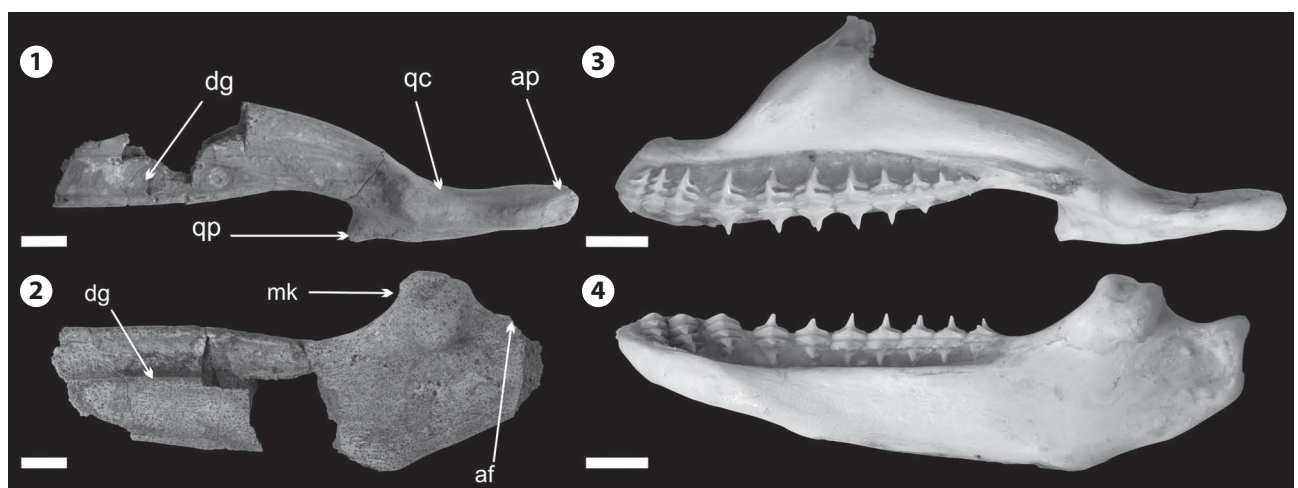


Figure 3. *Squatina* jaws in lingual view/ mandíbulas de *Squatina* en vista lingual. **1**, MPEF-PV 3804 fossil right palatoquadrate (upper jaw)/ MPEF-PV 3804 palatocuartado fósil derecho (mandíbula superior); **2**, MPEF-PV 3805 fossil right Meckel's cartilage (lower jaw)/ MPEF-PV 3805 Cartilago de Meckel fósil derecho (mandibular inferior); **3–4**, extant *Squatina* palatoquadrate and Meckel's cartilage respectively/ palatocuartado y cartilago de Meckel respectivamente de un ejemplar actual de *Squatina*. **af**, articular fossa/ foseta articular; **ap**, articular process/ proceso articular; **dg**, dental groove/ surco dental; **mk**, mandibular knob/ perilla mandibular; **qc**, quadrate concavity/ concavidad cuadrada; **qp**, quadrate process/ proceso cuadrado. Scale bar/ escala= 10mm.

pears to be the calcified perichondrium (Fig. 4). Tesserae are hexagonal in shape and they are higher than wide, ranging from 600–800 μm wide and 800–1000 μm high (Fig. 2.3, 2.5). Both cartilages have an inner cavity completely filled by fine-grained sand. No associated teeth were found.

DISCUSSION

The material agrees with the jaws of species of *Squatina* and differs from other neoselachians in the general shape, the size and proportions of the dental groove, the position and shape of the mandibular knob, the elongate proximal

section of Meckel's cartilage (the articular process and quadrate concavity are widely separated), and the small size and peculiar shape of the quadrate process (which has no direct suspensory function and is a derived feature of angel sharks; see Compagno, 1977; Carvalho *et al.*, 2008) (Fig. 3.3–4).

As tessellated cartilage is very labile, its preservation requires scarce transport, lack of scavengers, and rapid burial (Martin, 1999). Schäfer (1972) studied under experimental conditions the modes of disintegration of fish carcasses and the time it involves. In the case of chondrichthyans, soft tissues were completely disintegrated 20 days after death and only the jaws, teeth, remains of fin rays, and some placoid scales survived. Moreover, this rate of decay increases steeply in well-oxygenated waters. The fossil-bearing stratum corresponds to the transgressive phase and was deposited in an environment above the storm-wave base, swept by strong tidal currents (Scasso and del Río, 1987; del Río *et al.*, 2001). This kind of environment is characterized by a high level of oxygenation and aerobic degradation, which has an important role in soft tissue decay. Aerobic degradation often entails body flotation because of gas developed in the abdominal cavity. As soon as the carcass sinks back to the bottom, it disintegrates rapidly and most skeletal remains are scattered across the sediment and lost due to action of waves or currents (Schäfer, 1972). This might be the reason why no other skeletal remains, even teeth, were found in association with the jaws. The jaws probably had been transported after decay of soft tissues and disarticulation. However, as there is no evidence of abrasion, horizontal transport might have been limited. The palatoquadrate and Meckel's cartilage were found in close association. Therefore, the mandibular articulation should have been intact at the moment of burial, and as the ligamentous connections decay very fast after death (Schäfer, 1972; Holz and Simões, 2002), the residence time on the seafloor should have been short. This rapid burial allowed the isolation of the jaw from destructive biostratigraphic processes such as scavenging, fragmentation due to transport, and bioerosion (Martin, 1999; Schäfer, 1972).

Above the tesserae, there is a layer of well-developed mineralized tissue, which has a linear arrangement and a fibrous appearance as the perichondrium (Fig. 4.2–4). The perichondrium is a connective tissue composed by bundles of collagen fibrils and elastic fibers and is attached to the outer surface of the tesserae (Egerbacher *et al.*, 2006). This tissue has not been shown to calcify (see Kemp and Westrin, 1979; Dean and Summers, 2006) and in the literature there is no reference to perichondrium neither in fossils nor extant

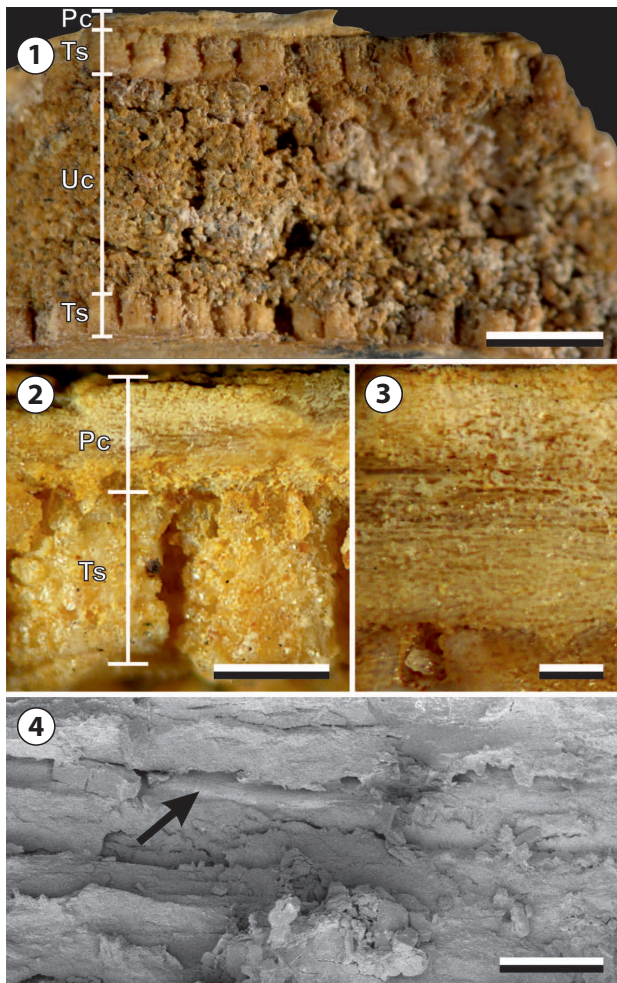


Figure 4. Tesselated cartilage of the palatoquadrate (MPEF-PV 3804)/ cartilago teselado del palatocuatrado (MPEF-PV 3804). **1**, general view in cross section. Scale bar= 2.5 mm/ vista general en sección transversal. Escala= 2.5 mm; **2**, detail of tesserae and perichondrium. Scale bar= 500 μm / detalle de las teselas y el pericondrio. Escala= 500 μm ; **3**, detail of the perichondrium showing the linear arrangement of the perichondral fibers. Scale bar= 200 μm / detalle del pericondrio mostrando la distribución lineal de las fibras pericondriales; **4**, detail of a perichondral fiber (arrow), under SEM. Scale bar= 20 μm / detalle de una fibra pericondral (flecha), bajo MEB. Escala= 20 μm . **Pc**, perichondrium/ pericondrio; **Ts**, tesserae/ teselas; **Uc**, uncalcified cartilage zone/ zona del cartilago no calcificado.

sharks. Because the well oxygenated environment favor the decay of unmineralized tissues by aerobic degradation, we interpret that the perichondral fibers might have been mineralized while the shark from Puerto Madryn was alive and that the mineralized perichondrium avoided the disarticulation of the tessellated tissue during decay.

The jaws are preserved without any indication of flattening. Briggs (1990) mentioned some factors that determine the nature and degree of flattening, including size and composition of sediment (coarser-grained sediments are more resistant to compaction) and the infilling of cavities. In the fossil described here, the inner core is filled with sandy sediments with similar lithological composition as the fossil-bearing level. The filling of the inner core should have been immediately after (or even simultaneous with) the decay of the unmineralized cartilage. Otherwise, a hollow jaw with only the tessellated tissue would have collapsed under the weight of the overlying sediment.

Summarizing, this specimen represents the first tessellated cartilage tridimensionally preserved from Argentina and the first record of mineralized perichondrium. A rapid burial, the rapid filling of the inner core, and the low sediment compaction of sands have allowed the exceptional preservation of the jaws. The presence of mineralized perichondrium represents a previously little appreciated way by which the elasmobranch skeleton might be strengthened and reinforced. The possibility of this being common should be studied in extant species.

ACKNOWLEDGEMENTS

We thank the Agencia Nacional de Promoción Científica y Tecnológica, Consejo Nacional de Investigaciones Científicas y Técnicas, and Universidad Nacional de La Plata for financial support. The Centro Nacional Patagónico (Puerto Madryn) and the Museo Egidio Feruglio (Trelew) are acknowledged for providing the material. We also thank M. Manceñido (Museo de La Plata), the editor A. Forasiepi and the reviewers M. Dean and J. Kriwet for their helpful suggestions that improved the manuscript.

REFERENCES

- Ameghino, F. 1906. Les formations sédimentaires du crétacé supérieur et du tertiaire de Patagonie: avec un parallèle entre leurs faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional de Buenos Aires* 15: 1–568.
- Bonaparte, C.L. 1838. Selachorum tabula analytica. *Nuovi Annali delle Scienze Naturali* 1: 195–214.
- Briggs, D.E.G. 1990. Flattening. In: D.E.G. Briggs and P.R. Crowther (Eds.) *Palaeobiology - a synthesis*. Blackwell Scientific Publications, Oxford, p. 244–247.
- Buen, F. 1926. Catálogo ictológico del Mediterráneo Español y de Maruecos, recopilando lo publicado sobre peces de las costas mediterráneas y próximas del Atlántico (Mar de España). *Resultados de las Campañas Realizadas por Acuerdos Internacionales, Instituto Español de Oceanografía* 2: 1–221.
- Cappetta, H. 1987. Chondrichthyes II: Mesozoic and Cenozoic Elasmobranchii. In: H.-P. Schultze (Ed.), *Handbook of Paleichthyology*, 3B. G. Fischer Verlag, Stuttgart & New York, 193 p.
- Carvalho, M.R.de, Kriwet, J. and Thies, D. 2008. A systematic and anatomical revision of Late Jurassic angelsharks (Chondrichthyes: Squatinidae). In: G. Arratia, H.-P. Schultze and M.V.H. Wilson (Eds.), *Mesozoic Fishes 4: Homology and Phylogeny*. Verlag Dr. Friedrich Pfeil, Munich, p. 469–502.
- Cione, A.L. 1988. [Los peces de las formaciones marinas del Cenozoico de Argentina. Tesis doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 588 p. Inédito].
- Cione, A.L. 1999. First report of a Jurassic ray outside Europe. In: G. Arratia and H.-P. Schultze (Eds.), *Mesozoic Fishes 2: Systematics and Fossil Record*. Verlag Dr. Friedrich Pfeil, Munich, p. 21–28.
- Cione, A.L., Azpelicueta, M.M., Bond, M., Carlini, A.A., Casciotta, J.R., Cozzuol, M.A., de la Fuente, M., Gasparini, Z., Goin, F.J., Noriega, J.I., Scillato-Yané, G.J., Soibelzon, L., Tonni, E.P., Verzi, D. and Vucetich, M.G. 2000. The Miocene vertebrates from Paraná, eastern Argentina. In: F.G. Aceñolaza and R. Herbst (Eds.), *El Neógeno de Argentina. Serie Correlación Geológica (INSUGEO)* 14: 191–237.
- Cione, A.L., Casciotta, J.R., Azpelicueta, M.M., Barla, M. and Cozzuol, M.A. 2005. Peces marinos y continentales del Mioceno del área mesopotámica argentina, procedencia estratigráfica y relaciones biogeográficas. *Miscelánea (INSUGEO)* 12: 49–64.
- Compagno, L.J.V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist* 17: 303–322.
- Compagno, L.J.V. 1984. Sharks of the world. An annotated and illustrated catalogue of sharks species known to date. *FAO Species Catalogue* 4: 1–249.
- Cozzuol, M.A. 2001. A “northern” seal from the Miocene of Argentina: implications for phocid phylogeny and biogeography. *Journal of Vertebrate Paleontology* 21: 415–421.
- Dean, M.N. and Summers, A.P. 2006. Mineralized cartilage in the skeleton of chondrichthyan fishes. *Zoology* 109: 164–168.
- Del Río, C.J. 1988. Bioestratigrafía y cronoestratigrafía de la Formación Puerto Madryn (Mioceno medio). Provincia del Chubut - Argentina. *Academia Nacional de Ciencias Exactas, Físicas y Naturales de Buenos Aires, Anales* 40: 231–254.
- Del Río, C.J. 1991. Revisión sistemática de los bivalvos de la Formación Paraná (Mioceno medio), provincia de Entre Ríos, Argentina. *Monografías de la Academia Nacional de Ciencias Exactas, Físicas y Naturales* 7: 11–90.
- Del Río, C.J. 2000. Malacofauna de las Formaciones Paraná y Puerto Madryn (Mioceno marino, Argentina): su origen, composición y significado bioestratigráfico. In: F.G. Aceñolaza and R. Herbst (Eds.), *El Neógeno de Argentina. Serie Correlación Geológica (INSUGEO)* 14: 77–101.
- Del Río, C.J., Martínez, S.A. and Scasso, R.A. 2001. Nature an origin of spectacular marine Miocene Shell beds of northeastern Patagonia (Argentina): paleoecological and bathymetric significance. *Palaios* 16: 3–25.
- Dumeril, A.M.C. 1806. *Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile à l'aide de tableaux synoptiques*. Allais, Paris, 344 p.
- Egerbacher, M., Helmreich, M., Mayerhofer, E. and Böck, P. 2006. Mineralisation of hyaline cartilage in the small-spotted dogfish *Scyliorhinus canicula* L. *Scripta Medica* 74: 199–212.
- Feruglio, E. 1949. *Descripción geológica de la Patagonia, volumen 2*. Ministerio de Industria y Comercio de la Nación, Dirección General de Yacimientos Petrolíferos Fiscales, Buenos Aires, 333 p.
- Gutstein, C.S., Yury-Yáñez, R.E., Soto-Acuña, S., Suárez, M.E. and Rubilar-Rogers, D. 2008. Fauna de vertebrados y aspectos tafonómicos del

- "bonebed" (Mioceno tardío) de la Formación Bahía Inglesa. *I^{er} Simposio Paleontología en Chile* (Santiago, 2008), *Actas*: 102–108.
- Haller, M. 1981. Descripción geológica de la hoja 43h, Puerto Madryn: provincia del Chubut. *Servicio Geológico Nacional, Boletín* 184: 5–44.
- Holz, M. and Simões, M.G. 2002. *Elementos Fundamentais de Tañonomia*. Editora da Universidade UFRGS, Porto Alegre, 232 p.
- Kemp, N.E. and Westrin, S.K. 1979. Ultrastructure of calcified cartilage in the endoskeletal tesserae of sharks. *Journal of Morphology* 160: 75–101.
- Linnaeus, C. 1758. *Systema naturae...* (Tenth edition). Salvi, Stockholm, 824 p.
- Martin, R.E. 1999. *Taphonomy: A Process Approach*. Cambridge University Press, 508 p.
- Muñoz-Ramirez, C., Moyano, H. and Palma-Heldt, S. 2008. Dientes fósiles de tiburones y rayas presentes en el área de la Bahía de Concepción, VIII Región, Chile Central. *I^{er} Simposio - Paleontología en Chile* (Santiago), *Actas*: 69–73.
- Scasso, R.A. and Del Río, C.J. 1987. Ambientes de sedimentación, estratigrafía y proveniencia de la secuencia marina del Terciario Superior de la región de Península Valdés, Chubut. *Revista de la Asociación Geológica Argentina* 42: 291–321.
- Scasso, R.A., McArthur, J.M., Del Río, C.J., Martínez, S. and Thirlwall, M.F. 2001. $^{87}\text{Sr}/^{86}\text{Sr}$ Late Miocene age of fossil molluscs in the 'En-terriense' of the Valdés Peninsula (Chubut, Argentina). *Journal of South American Earth Sciences* 14: 319–329.
- Schäfer, W. 1972. *Ecology and Palaeoecology of Marine Environments*. University of Chicago Press, Chicago, 568 p.
- Uliana, M.A. and Biddle, K.T. 1988. Mesozoic–Cenozoic paleogeographic and geodynamic evolution of southern South America. *Revista Brasileira de Geociências* 18: 172–190.
- Welton, B.J. and Farish, R.F. 1993. *The Collector's Guide to Fossil Sharks and Rays from the Cretaceous of Texas*. Before Time, Lewisville. 204 p.
- Williams, B.G. and Hubbard, R.J. 1984. Seismic stratigraphic framework and depositional sequences in the Santos Basin, Brazil. *Marine and Petroleum Geology* 1: 90–104.

doi: 10.5710/AMGH.v49i1(469)

Recibido: 1 de febrero de 2011

Aceptado: 30 de diciembre de 2011