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Trace fossils on penguin bones from the Miocene of Chubut, southern Argentina

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Several traces of biological interaction were found on penguin bones from the basal levels (Aquitanian) of the Miocene Gaiman Formation in the lower Chubut valley of the Provincia del Chubut, Argentina. The fossil-bearing beds were deposited in littoral to sublittoral environments within sediments of mostly pyroclastic origin. We interpret many traces to have been produced by predators and/or scavengers while the penguins were still in a breeding area. Many bones show cracking marks due to aerial exposure. The material is disarticulated as is usual in recent breeding areas. Potential predators were coeval terrestrial mammals, most probably marsupial carnivores. After a marine transgression, these bones were buried or exposed on the sea bottom where they could be colonized by algae, sponges, cnidarians, and other benthic organisms. We identified sponge borings in several bones. Other traces are interpreted to have been produced by echinoderms feeding on sponges or algae. No evidence of other invertebrate predators such as muricid or naticid gastropods, or decapods was found. Finally, other traces appear to have been generated by shark and possibly teleostean vertebrates feeding on epibionts. One coracoid is interpreted to have been marked by a shark that is common in the Gaiman Formation, the carcharhiniform *Galeocerdo aduncus*. From an ethological (Seilacherian) classification, traces on bones from the Gaiman Formation include Domichnia (sponge perforations), Praedichnia (terrestrial marsupials, sharks, teleosteans) and Pasichnia (echinoderms). Remarkably, remains of marine organisms with skeletons made of calcium carbonate are very poorly preserved in the Gaiman Formation. Only large oysters, sparse shell fragments, skeletal moulds, and bioturbation is evident. The fossil assemblage is mainly composed of phosphatic (e.g. teeth, bones, crustacean parts) and siliceous (sponge spicules, diatoms) remains.

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ALTHOUGH marks left by feeding activities of invertebrates, especially molluscs, have been reported frequently from Cenozoic marine sediments (e.g. Buatois *et al*. 2003, Carmona *et al*. 2008), there have been relatively few studies of traces on vertebrate bones (e.g. Frenguelli 1928, Deméré & Cerutti 1982, Cigala Fulgosi 1990, Noriega *et al*. 2007).

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The Leonian beds of the lower Miocene Gaiman Formation, (northeastern Chubut Province; Fig. 1) have yielded numerous penguin bones (Simpson 1972, Acosta Hospitaleche 2004). Notwithstanding that most bones are isolated and fragmentary, several species were identified in the samples (Acosta Hospitaleche 2004): *Eretiscus tonni* (Simpson, 1981), *Palaeospheniscus bergi* Moreno & Mercerat, 1891, *P. patagonicus* Moreno & Mercerat, 1891, and *P. biloculata* (Simpson, 1970). Many of these penguin

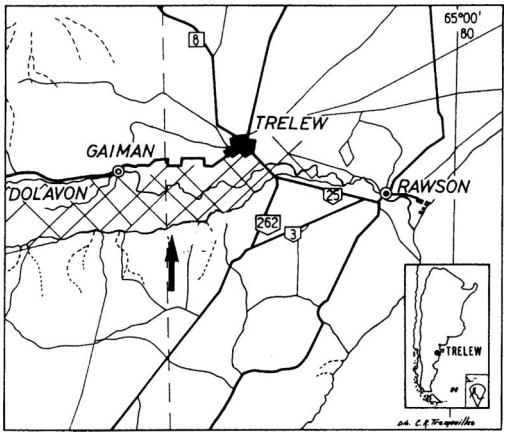

Fig. 1. Map of the Trelew-Gaiman area showing the Bryn Gwyn fossil locality (arrowed).

bones show polygenic traces. We describe these traces here and propose hypotheses about their genesis. A main goal was to establish if traces were antemortem, perimortem or postmortem (Turner & Turner 1999).

Stratigraphic setting

The Gaiman Formation crops out in northeastern Provincia del Chubut, Argentina. It was named by Mendía & Bayarsky (1981) but it has been recognized as a discrete interval since the 19th century. The unit is flat-lying and about 50 m thick at Bryn Gwyn (Simpson 1935, Mendía & Bayarsky 1981; Fig. 1). It is composed of a coarsening-upward succession of mudstones, fine tuffs, tuffs, tuffaceous sandstones, and coquinas (Scasso & Castro 1999). Scasso & Castro (1999) divided the formation into two parts. The lower part is 20 m thick and composed of fine, white, tuffaceous, bioturbated mudstones with sparse thin levels of oysters. The unit begins with a transgressive conglomerate or phosphatic coquina 20 to 80 cm thick with shell hash and swaley or hummocky stratification that grades into a tuff with selachian teeth and vertebrae, and osteichthyan, bird, and mammal bones (T2, see below; Cione 1978, 1986, 1988, Cione & Pandolfi 1984, Cione & Cozzuol 1990, Arratia & Cione 1996, Scasso & Castro 1999). The upper part of the Gaiman Formation is 30 m thick, whitish to light grey and slightly darker than the lower part. Thick beds of tuffaceous sandstones with ripples, and hummocky or parallel stratification are interbedded with the mudstones. Large *Ophiomorpha* Lundgreen, 1891 burrows are present. Some thin coquinas and a 20–40 cm thick phosphatic conglomerate are intercalated; the latter includes bones and teeth (T2; see below; Scasso & Castro 1999).

Scasso & Castro (1999) recognized two types of phosphatic levels: "Type 1" and "Type 2." The second variety is related to reworking, winnowing and mechanical concentration of resistant particles (T2; Fig. 2). It represents reworked beds associated with transgressive surfaces; vertebrate teeth and bones are preserved in these layers.

The Gaiman Formation overlies the continental Trelew Member of the Sarmiento Formation (which includes a terrestrial Colhuehuapian fauna, late Oligocene–early Miocene; Simpson 1935, Cione 1988) and underlies the marine Puerto Madryn Formation (middle–late Miocene; Mendía & Bayarsky 1981, Cione 1986; Fig. 3).

Ameghino (1900–1903, 1906) developed the basic stratigraphic scheme for both marine and continental sequences of the Cenozoic of southern South America with the intent to correlate both sequences. Other authors refined both the terrestrial and marine chronostratigraphic standards (see Pascual *et al.* 1965, Bertels 1975, 1980, Marshall *et al.* 1983, Malumián 1999). The upper Eocene to lower Miocene marine rocks of eastern Patagonia were referred to the Julian and Leonian stages (see Ameghino 1906, Bertels 1970). The Gaiman Formation is correlated with the upper Leonian Stage (Ameghino 1900–1903, Bertels 1970,

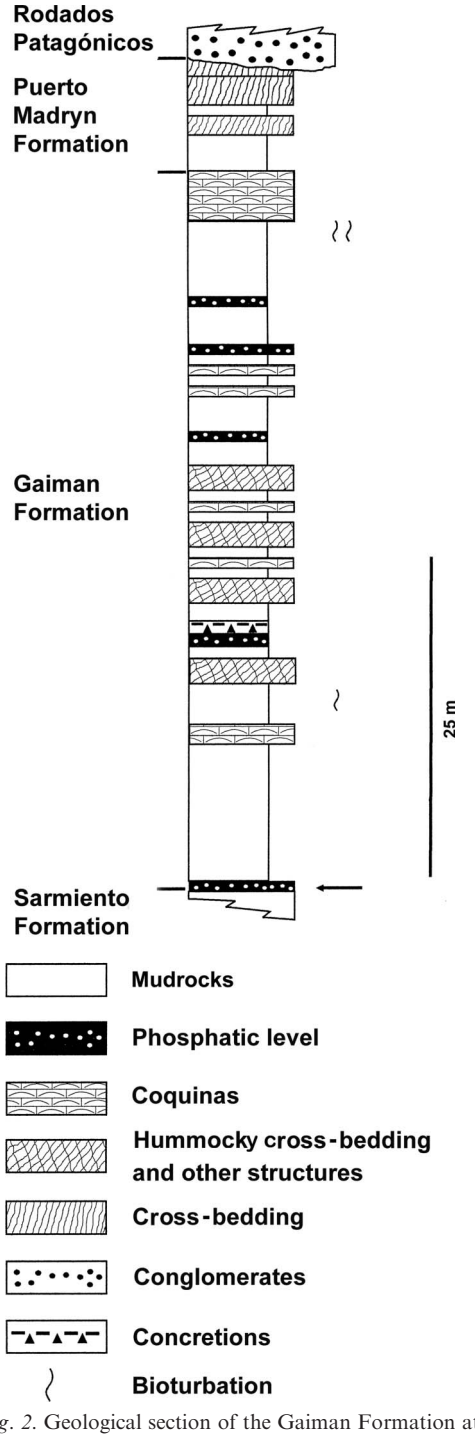

Fig. 2. Geological section of the Gaiman Formation at Bryn Gwyn (modified from Scasso & Castro 1999). Fossil layer arrowed.

Cione 1988). Camacho (1974) introduced a partially different stratigraphic scheme for the marine Cenozoic of Patagonia, based on selected index fossils and lithology. Camacho removed from the Julian and Leonian stages rocks he named "Estratos con *Neoinoceramus*" and "Estratos con *Monophoraster* y *Venericor*" and stated they are of Eocene age (Camacho 1974; see also Legarreta *et al.* 1990). He referred the base of the Gaiman Formation to the "Estratos con *Monophoraster* y *Venericor*". However, the "Estratos con *Neoinoceramus*" and "Estratos con *Monophoraster* y *Venericor*" are correlated with the Leonian Stage (Cione & Expósito 1980, Cione 1986 1988, Cione & Cozzuol 1990).

Correlation of the type Monte León Formation and Gaiman Formation is based on stratigraphic relationships, ash and biogenetic silica content, and fossil evidence (Cione 1978, 1986, 1988, Cione & Expósito 1980). The Gaiman Formation unconformably overlies the continental Trelew Member of the Sarmiento Formation, which includes a Colhuehuapian fauna (Cione 1988) and underlies the marine middle–upper Miocene Puerto Madryn Formation (Simpson 1935, Mendía & Bayarsky 1981, Cione 1986). No radioisotopic dates from rocks with Colhuehuapian fauna are available (Flynn & Swisher 1995). The Deseadan Stage precedes the Colhuehuapian Stage. The Deseadan is currently known to span the interval 24.5–29 Ma (late Oligocene; Flynn & Swisher 1995). ^{40}K-^{40}Ar dates of 15.8 ± 2.5 Ma and 16.6 ± 0.8 Ma have been reported from beds at the base of the Gaiman Formation at Bryn Gwyn (Bown & Larriestra 1990). These dates are close to the Burdigalian and Langhian boundary). However, vertebrate evidence suggests that at least the base of the unit is Aquitanian.

During late Paleogene and early Neogene times, southern South America east of the Andes had relatively stable tectonic conditions and the dominant accumulations

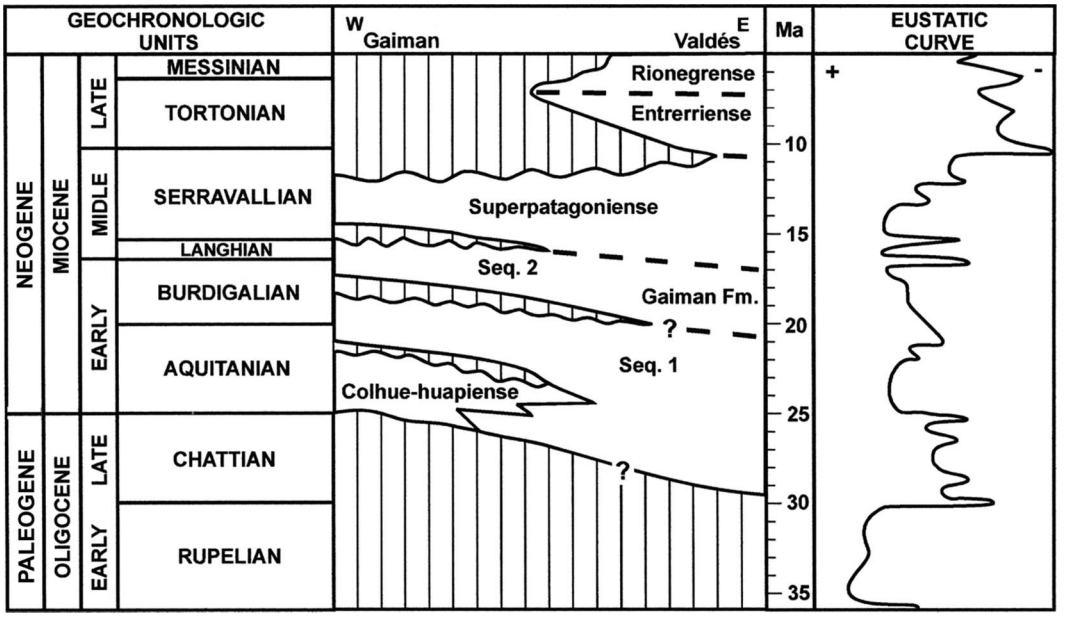

Fig. 3. Main stratigraphic units, age and stratigraphic relationships in the lower río Chubut valley and Valdés Peninsula (Chubut). Correlation with sea level variation taken from Haq *et al.* (1987). Modified from Scasso & Castro (1999). Names in the stratigraphic sequence correspond to informal and formal units in use in the area.

are fine grained (Uliana & Biddle 1988). Marine flooding appears to have peaked when the Gaiman, Pinturas, and part of Monte León, Chenque and Centinela formations were deposited. These formations could correlate with the sequence set of early Aquitanian age (TB1-1.4) or with the sequence of the late Aquitanian and Burdigalian (TB2-2.1) of Haq *et al.* (1987). According to Ogg *et al.* (2008) the Aquitanian begins at 23.03 Ma.

Material

The material (578 bones including: humeri (156), coracoids (78), ulnae (30), tibiotarsi (59), femori (40), carpometacarpi (23), vertebrae (55), tarsometatarsi (33), radii (48), sternae (7), sinsacri (14), scapulae (3), phalangi (26), rostrae (5), skull (1) comes from the marine Gaiman Formation (Mendía & Bayarsky 1981), which is exposed in the southern cliffs of the lower Río Chubut valley, eastern Provincia del Chubut, Argentina. Most were found at the locality Bryn Gwyn (Loma Blanca in the maps). Bryn Gwyn is located 4 km south of the city of Gaiman (43°15′S, 65°30′W; Figs 1, 2; Cione 1986, 1988). Some other material comes from the nearby locality of informal name "Campo de *Pristiophorus*" (43°19′S, 65°17′W; see Cione 1988). Most of the bones derive from the conglomerate located at the base of the Gaiman Formation (lower "Type 2" phosphatic level T2 of Scasso & Castro 1999; Fig. 2). A few bones come from the upper "Type 2" phosphatic level T2 of Scasso & Castro (1999; Fig. 2), located in the middle of the upper section of the Gaiman Formation in this area.

The material was collected during several field campaigns, two of which were led by ALC at Bryn Gwyn during 1977 and 1983. The material is curated in the División Paleontología de Vertebrados, Museo de La Plata, La Plata, Argentina; 128 bones show

predation and/or scavenging marks. Penguin bones were found disarticulated but relatively well preserved, as were most of the other vertebrate fossils (the rare cetacean and teleostean bones and the abundant neoselachian teeth and vertebrae).

Methods

We recognized a range of subaerial taphonomic proceses following Mikuláš (2001) and Behrensmeyer (1978). We use the terminology of Binford (1981; see also Lyman 1994) for categorization of predation traces on our material. In some cases we propose a species or group as the agent that produced the trace. In others, when we lack this precision, we use ichnological nomenclature.

Terrestrial traces

Metatheria (Fig. 4)

Several traces are presumed to represent bite marks of terrestrial mammals such as didelphid or hathliacyniid sparassodont marsupials, common in Patagonia during the Miocene (Colhuehuapian, Pinturan, Santacrucian South American continental ages; Paula Couto 1979, Goin *et al.* 2007). All appear to have been formed before subaerial desiccation cracks developed. Most traces are relatively feeble, differing from others such as those described by Kear & Godthelp (2008). We did not find generalized scooping or scoring (see Binford 1981, Lyman 1994, Martin 2006).

Isolated pits (Fig. 4D)

Material. MLP 20-391 (coracoid), MLP 20-253 (radius, Fig. 4D), MLP 20-428 (complete femur), MLP 20-394 (carpometacarpus), MLP 71-VII-14-2 (coracoid distal end), MLP 20-390 (coracoid distal end), MLP 20-358 (coracoid distal end), MLP 20-486 (humerus), MLP 20-333 (proximal tibiotarsus).

Description. Isolated rounded holes with a rounded or pointed bottom. The compact bone collapsed without fracturing (e.g. MLP 20-394).

Interpretation. These marks are similar to those produced by pointed teeth (canines) or cusps (of molariforms) of mammals.

Aligned pits (Fig. 4B)

Material. MLP 20-477 (humerus).

Description. Three series of aligned and clearly defined pits about 8 mm long. The pits are rounded and about 0.3 mm in diameter. Two series occur on the middle part of the anterior side of the diaphysis and one on the posterior side.

Interpretation. Early Miocene hathliacynid (Sparassodonta) marsupials agree in size and tooth morphology and arrangement with these marks. Moreover, disposition of the three series suggest that they could correspond to a single bite. If we consider that it is the length of the dental series, the marsupial was medium-sized. A less likely hypothesis is that these marks were made by moderate- to large-sized didelphid didelphimorphians. However, by early Miocene times known didelphids were very small, as suggested by a recent review (Goin *et al.* 2007). In contrast, hathliacyniid and borhyaenid sparassodonts were extremely abundant.

Shallow wide furrows (Fig. 4C)

Material. MLP 20-390 (distal end of left coracoid), MLP 20-433 (proximal part of femur), MLP 20-391 (complete right coracoid, Fig. 4C), 77-VII-14-13 (proximal half of humerus).

Description. Shallow wide and narrow transverse marks and a few pits on the anterior and posterior faces. In MLP 20-390, they are fewer and wider. In MLP

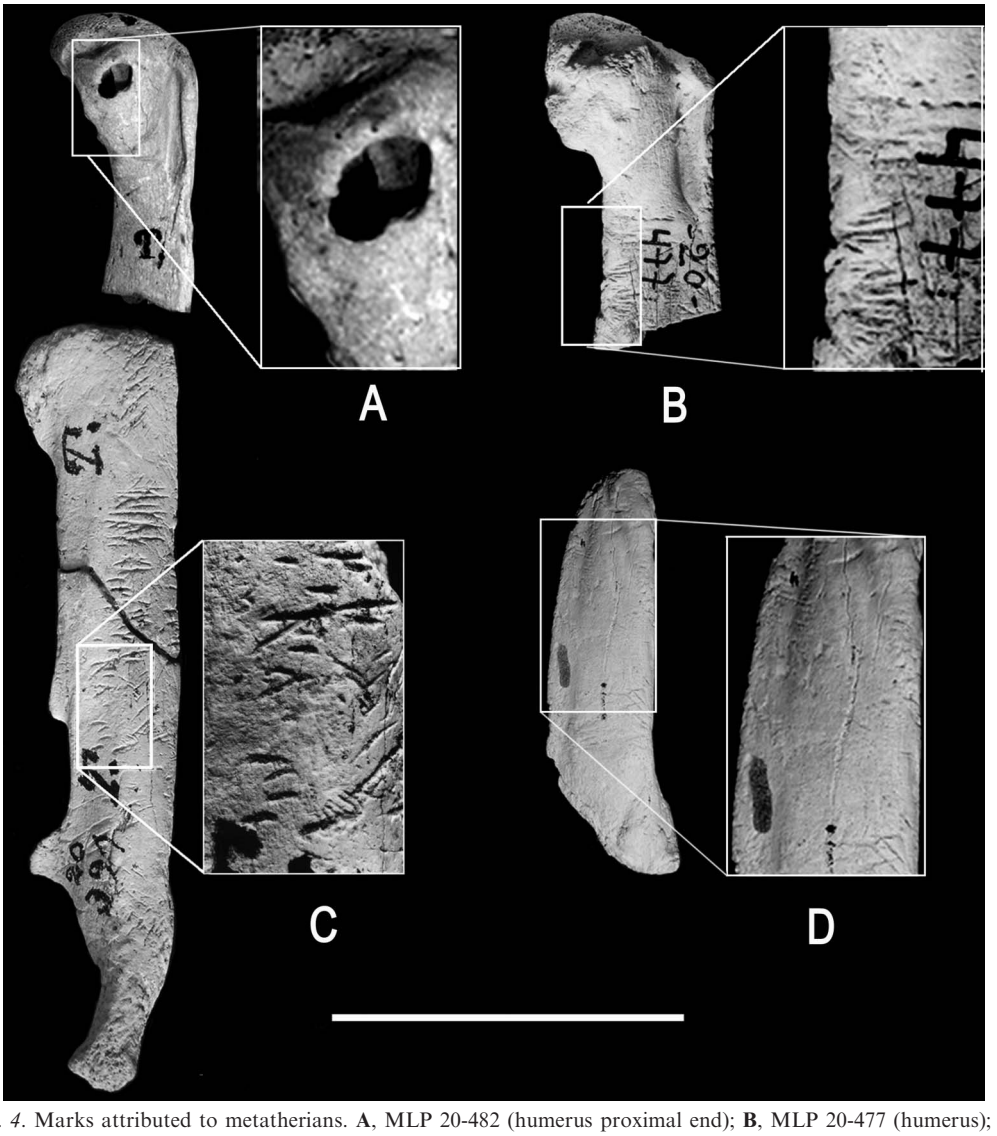

Fig. 4. Marks attributed to metatherians. **A**, MLP 20-482 (humerus proximal end); **B**, MLP 20-477 (humerus); **C**, MLP 20-391 (complete right coracoid); **D**, MLP 20-253 (radius). Scale bar = 50 mm.

20-391 there are many marks, some parallel. Furrows occur in three main directions, all transverse: 90°, 45° proximally, and 45° distally. The second of these are few and short. There are some pits on the anterior face in both bones.

Interpretation. We interpret that a mammal bit the bone with its incisors and scratched it to the right side to generate the four furrows. The other damage appears to correspond to diverse biting and gnawing actions by the same predator.

Deep furrows (Fig. 4A, B)

Material. MLP 20-477 (humerus, Fig. 4B). MLP 20-482 (humerus proximal end, Fig. 4A).

Description. Many short and relatively deep furrows occur across the diaphysis. Most are less than 5–8 mm long.

Interpretation. We interpret these trace fossils to have been generated by the same mammal that made the pits and gnawed the humerus head.

Scoring (Fig. 4B, C)

Material. MLP 20-477 (humerus, Fig. 4B). MLP 20-391 (coracoid, Fig. 4C).

Description. The head of a humerus has been gnawed inwards as to eliminate the periosteal bone.

Interpretation. Recent placental carnivores generate this kind of damage in bone termini.

Marine traces

Ichnogenus **Entobia** Bronn, 1837 (Fig. 5A)

Material. MLP 20-372 (fragmentary coracoid), MLP 71-VII-14-1 (tibiotarsus), MLP 20-486 (humerus), MLP 20-491 (humerus), MLP 20-50 (complete humerus), MLP 20-510 (distal end of humerus), MLP 20-394, MLP 20-486 (humerus).

Description. Subcircular isolated holes on the bone surface with a diameter of about 0.5 mm and without any kind of ornamentation. Holes continue as canals inside the bone. These traces were found alone or combined with *Gnatichnus pentax* (e.g. MLP 20-486, Fig. 5A).

Interpretation. Drillholes assigned to *Entobia* are putatively excavated by clionid sponges (see Bromley & Tendal 1973, Taylor & Wilson 2003). Sponges excavate galleries for habitation. The feeding activities of echinoderms may widen the original borings leaving abundant marginal scratches (see Bromley 1975).

Ichnogenus **Gnathichnus** Bromley, 1975 (Fig. 5B)

Type ichnospecies. *Gnathichnus pentax* Bromley, 1975

Gnathichnus pentax Bromley, 1975 (Fig. 5B)

Material. MLP 71-VII-14-1 (tibiotarsus), MLP 77-XII-22-8 (humerus broken into two pieces), MLP 20-295 (cubit), MLP 20-391 (coracoid), MLP 20-433 (femur), MLP 20-486 (humerus), MLP 20-325 (fragmentary tibiotarsus), MLP 20-510 (humerus distal end), 77-XII-22-11 (humerus distal end), 71-VII-14-2 (coracoid distal end), MLP 20-538 (humerus proximal end), MLP 20-382 (coracoid distal end), MLP 20-491 (humerus).

Description. Traces of this species are very abundant on some bones (e.g. MLP 20-295, MLP 20-486). We distinguish four kinds of *Gnatichnus* marks on our material (*fide* Bromley 1975, Breton *et al*. 1992) varying in morphology on the basis of position.

Type 1. On flat surfaces, a complex arrangement of grooves (MLP 20-486, Fig. 5B).

Type 2. In abrupt convex surfaces, such as bone edges (MLP 20-486, Fig. 5B), grooves densely packed and more or less parallel.

Type 3. Severe erosion around sponge borings consisting of deep radiating grooves that greatly enlarge the original hole (MLP 20-486, Fig. 5B).

Type 4. On a flat surface, a rounded depression of about 5 mm surrounded by marginal grooves. Some of the marks cross the depression.

Interpretation. This species is attributed to dental erosion by regular echinoids (Taylor & Wilson 2003). Echinoids severely erode hard substrates (e.g. mollusc valves, consolidated sediment or bones; e.g. Buitrón-Sánchez & Pantoja-Alor 1994) in order to expose and eat enclosed annelids and

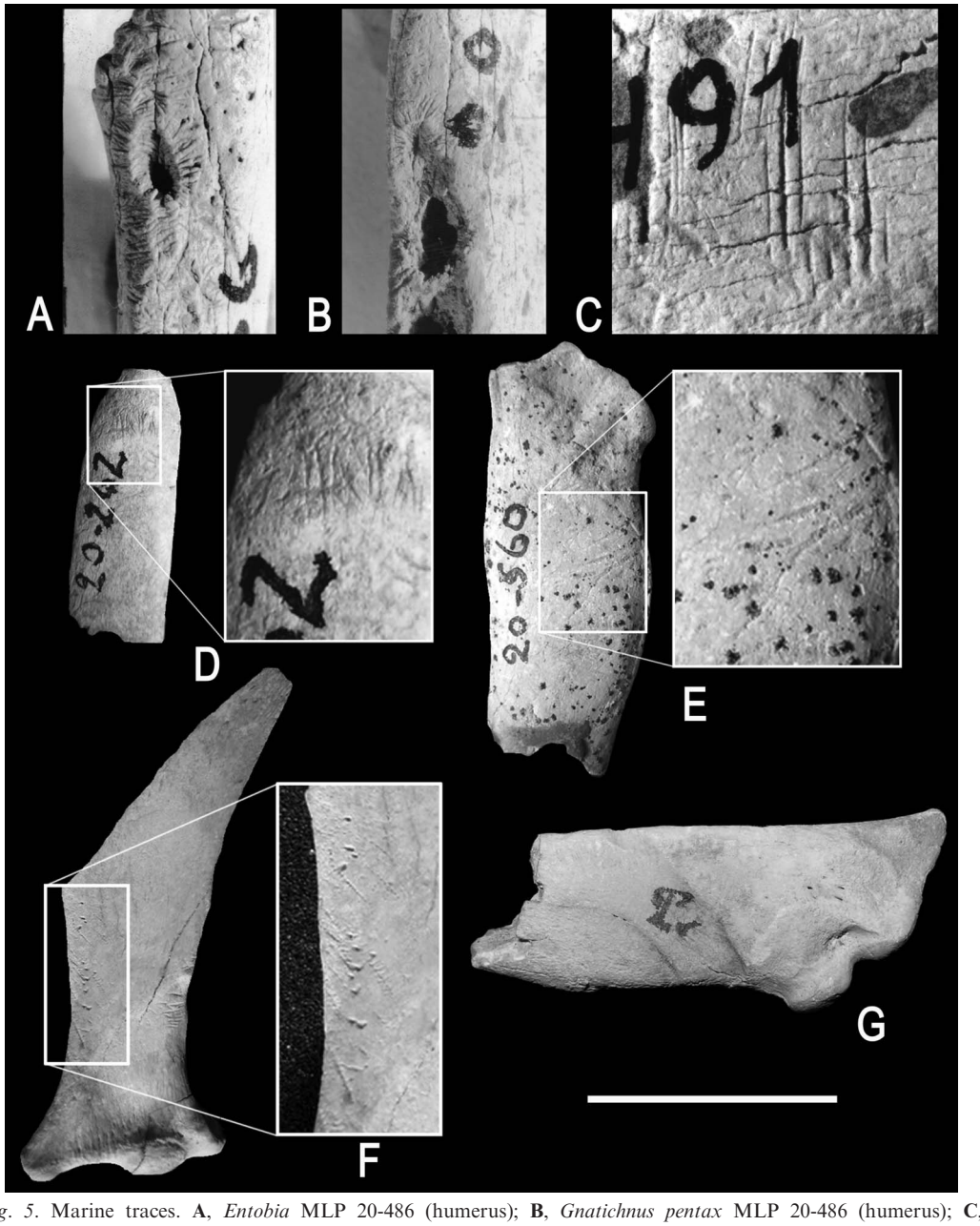

Fig. 5. Marine traces. **A**, *Entobia* MLP 20-486 (humerus); **B**, *Gnatichnus pentax* MLP 20-486 (humerus); **C**, indeterminate, parallel shallow traces MLP 20-491 (humerus); **D**, cf. ichnogenus *Radulichnus* MLP 20-262 (radius); **E**, indeterminate, short curved traces MLP 20-560 (humerus); **F**, *Galeocerdo aduncus* MLP 20-293 (scapula); **G**, indeterminate (wide and short furrows) MLP 20-490 (humerus distal end). Scale bar for A–C = 10 mm; for D–F, and G = 30 mm.

sponges (Bromley 1975) or surficial algae (e.g. Schultz & Verdinelli 1975). We found many sponge drillings of about 0.1 mm that we assigned to ichnogenus *Entobia* (see above). Some of these were greatly enlarged by putative echinoid action that resulted in

very wide holes of about 3–4 mm with numerous marginal and closely packed grooves (MLP 20-486, Fig. 5B). Different markings appear to have been generated by the same agent acting on different surfaces under varying circumstances. The complex Type 1 is interpreted as the recurrent action of echinoids. The simplest form of a regular stellate arrangement of five radiating grooves at angles of *ca* 72° is rarely seen in isolation (see Bromley 1975). In Type 2, teeth employment accommodated to the bone shape. Type 3 is interpreted as the action of echinoids to expose and eat the sponge material. Type 4 may be a variation of type 1, with concentrated browsing in a small area. Although some traces around *Entobia* holes could be produced by small fishes or decapods (Bishop 1975), marks on Gaiman bones appear to have been generated by echinoids.

cf. ichnogenus **Radulichnus** Voigt, 1977 (Fig. 5D)

Material. MLP 20-428 (complete femur), MLP 20-369 (coracoid), MLP 20-433 (femur), MLP 20-522 (proximal end of humerus), MLP 20-262 (radius), MLP 20-266 (radius), MLP 20-326 (tibiotarsus diaphysis), MLP 20-250 (radius), MLP 20-370 (fragmentary coracoid), MLP 20-538 (proximal end of humerus), MLP 20-560 (humerus), MLP 20-429 (femur), MLP 20-253 (radius), MLP 71-VII-14-1 (tibiotarsus), MLP 20-375 (incomplete coracoid).

Description. These traces constitute three linear parallel cuts 0.2–1.1 mm long, separated by spaces of about 0.6 mm. Their orientation is generally transverse or oblique to the main axis of the bone.

Interpretation. Grazing gastropods and chitons are well known to contribute to the erosion of reef surfaces when foraging on algae growing on hard substrates; they damage the surface with their radulae (Taylor & Wilson 2003, Gibert *et al*. 2007, Peyrot-Clausade 2008, Wilson 2008). In Argentina, Farinati *et al*. (2006, 2007) have described marks on molluscs and hard fine-grained substrates in Holocene beds. The material from Gaiman has less-dense traces than other examples (e.g. Gibert *et al*. 2007).

Galeocerdo aduncus Agassiz, 1843 (Fig. 5F)

Material. MLP 71-VII-14-1 (tibiotarsus), MLP 20-372 (coracoid), MLP 20-292 (scapula), MLP 20-293 (scapula).

Description. A scapula (MLP 20-293) bears very small aligned pits (seven pits per 2 mm) on both sides near the edges of the bone and oblique to its longest axis. Several series are laterally displaced. Among the aligned pits, are larger isolated pits. One coracoid (MLP 20-372) bears a parallel set of short and small scratches.

Interpretation. The series of pits and the parallel scratches appear to correspond to the bite of a medium-sized carcharhiniform shark with serrated teeth. Such teeth are abundant in the Gaiman Formation (*Galeocerdo aduncus*; Ameghino 1906, Cione 1988). Large, parallel, numerous, and closely spaced marks are usually attributed to large lamniform sharks such as *Carcharodon carcharias* Linnaeus, 1758 or *Carcharocles megalodon* Agassiz, 1843 (cf. Deméré & Cerutti 1982, Cigala Fulgosi 1990; see comments in Noriega *et al*. 2007). In this case, the marks are similar but much smaller. They resemble marks produced by Cretaceous anacoracid neoselachians (Schwimmer *et al*. 1997). These sharks had dentitions similar to *G. aduncus*. In the Gaiman Formation, another medium-sized shark with serrated cutting edges occurs in abundance (the lamniform *Carcharoides totuserratus* Ameghino, 1901; Ameghino 1906, Cione 1988). However, when we marked plasticine and parafin with teeth of both species, the marks from *Galeocerdo aduncus* most resembled the fossil traces.

Traces of unknown origin

Parallel shallow traces (Fig. 5C)

Material. MLP 77-XII-22-2 (tibiotarsus diaphysis), MLP 71-VII-14-2 (coracoids distal end), MLP 71-VII-14-12 (fragmentary coracoids), MLP 77-XII-22-8 (humerus broken into two pieces), MLP 71-VII-14-1 (tibiotarsus), MLP 77-XII-22-1 (complete humerus), MLP 20-491 (humerus), MLP 20-383 (coracoids distal end), MLP 20-372 (fragmentary coracoids), MLP 20-347 (tibiotarsus proximal end), MLP 20-538 (humerus proximal end), MLP 20-522 (humerus proximal end), MLP 20-250 (fragmentary radius), MLP 20-273 (radius), MLP 20-363 (fragment of coracoids), MLP 20-428 (femur), MLP 20-369 (coracoid), MLP 20-490 (humerus distal end), MLP 20-337 (tibiotarsus distal end), MLP 20-258 (radius), MLP 20-429 (femur), MLP 20-256 (radius), MLP 20-262 (fragmentary cubit), MLP 20-260 (radius), MLP 20-560 (humerus), MLP 20-253 (radius), MLP 20-295 (cubit), MLP 20-370 (fragment of coracoid), MLP 20-423 (bill fragment), MLP 20-418 (bill fragment), MLP 20-325 (fragmentary tibiotarsus), MLP 20-326 (fragmentary tibiotarsus diaphysis), MLP 20-333 (tibiotarsus distal end), MLP 20-331 (fragmentary tibiotarsus diaphysis), MLP 20-334 (tibiotarsus distal fragment), MLP 20-328 (tibiotarsus proximal end), MLP 20-329 (fragmentary tibiotarsus without both ends), MLP 20-257 (radius), MLP 20-251 (radius), MLP 20-438 (femur), MLP 20-510 (humerus distal end), MLP 20-266 (cubit), MLP 20-535 (humerus proximal end), MLP 20-529 (humerus distal end), MLP 20-530 (fragment of humerus), MLP 20-375 (incomplete coracoid), MLP 77-XII-22-45 (humerus proximal end), MLP 20-343 (tibiotarsus distal end), MLP 20-292 (scapula), MLP 20-344 (tibiotarsus distal end), MLP 20-335 (tibiotarsus distal end), MLP 20-350 (tibiotarsus distal end), MLP 20-384 (coracoid distal end), MLP 20-389 (coracoid), MLP 20-367 (incomplete coracoid), MLP 20-371 (incomplete coracoid), MLP 20-379 (incomplete coracoid), MLP 20-381 (coracoid distal end), MLP 77-XII-22-11 (humerus distal end), MLP 20-293 (scapula), MLP 20-559 (incomplete synsacrum), MLP 79-XII-22-2 (incomplete tibiotarsus), MLP 71-VII-14-1 (tibiotarsus), MLP 20-352 (coracoid distal end), MLP 20-349 (coracoid proximal end), MLP 20-56 (tibiotarsus distal end), MLP 77-XII-22-49 (radius), MLP 77-XII-22-52 (humerus proximal end), MLP 77-XII-22-50 (incomplete coracoid), MLP 77-XII-22-51 (femur distal end).

Description. Marks are shallow and narrow only affecting the periosteal bone. They are arranged in series 0.2–25 mm long. Although the main part is oblique or perpendicular to the main axis of the bone, some are parallel to it. They do not cross each other except where abundant. A humerus (MLP 20-491) has thin and parallel cuts about 9–10 mm long perpendicular to the diaphysis. This bone bears slightly curved traces, grouped in series of up to 12 cuts, collectively 12 mm wide. Each trace is initially deep, becoming shallower at the end. A tibiotarsus diaphysis (MLP 20-331) has sets of two traces located on one face with a counterpart of another two on the other face.

Short curved traces (Fig. 5E)

Material. MLP 20-538 (humerus proximal end), MLP 20-560 (humerus), MLP 20-423 (bill fragment).

Description. Subparallel deep and short traces. Most traces are perpendicular to the diaphysis but do not occur in series.

Wide and short furrows (Fig. 5G)

Material. MLP 20-266 (radius), MLP 20-510 (humerus distal end), MLP 20-375 (incomplete coracoid), MLP 20-250 (radius), MLP 20-369 (coracoid), 77-XII-22-2 (humerus distal end), MLP 20-370 (fragment of coracoid), MLP 20-490 (humerus distal end).

Description. Shallow furrows of consistent depth, about 1 mm wide. MLP 20-490 has two parallel traces, slowly curved and oblique to the humerus axis. The longer is 22 mm, corresponding to the total width of the diaphysis, whereas the shorter is 12 mm long. Both are located only on one side of the bone. They are oblique to the diaphysis and are disordered and intercrossed.

Interpretation. It is difficult to identify the agent that made these marks. They may have been generated by various organisms scavenging meat or foraging for algae on bones (e.g. teleosteans, elasmobranchs, molluscs, echinoderms, amongst others).

Discussion

Environment and biota

Marine. Lower Miocene sediments were deposited in a littoral to sublittoral environment supplied with pyroclastic material from volcanic eruptions in the Macizo Norpatagónico areas (central Provincia de Río Negro, northern Patagonia; Ardolino 1981). Well-preserved *Ophiomorpha*, *Skolithos* Haldemann, 1840, *Chondrites* Von Sternberg, 1833 and *Planolites* Nicholson, 1873 burrows are preserved in the Gaiman Formation, and the occurrence of bioturbation belonging to the *Cruziana* ichnofacies indicates that the environment was not deeper than shallow neritic (Scasso *et al*. 1996; see also Ardolino 1981).

Penguin bones were found in two reworked and winnowed lags associated with transgressive surfaces, which display a concentration of phosphatic concretions, ooids, vertebrate bones and teeth, decapod remains and some large shells, collectively constituting condensed deposits (lower and upper T2 levels of Scasso & Castro 1999; Fig. 2). The basal conglomerate is poorly exposed and no sedimentary structures were recorded, but it probably represents a condensed shoreface deposit associated with landward migration of the shoreline during the transgression (Scasso & Castro 1999). The sea transgressed towards the west and reached the longitude of Dolavon (Cortés 1982, Cione 1988, Scasso & Castro 1999; Fig. 2).

Most of the Gaiman Formation fossils come from the base of the unit (Cione 1986, 1988, Scasso *et al*. 1996). Remarkably, most are vertebrate remains. Most of the invertebrates are represented by moulds. However, there are ostreid shells showing evidence of chemical alteration. Crab skeletons and vertebrate bones and teeth are composed of calcium phosphate, which is much more resistant to acid alteration.

Close association of callianasid bioturbation (*Ophiomorpha*) and phosphatic levels suggests a genetic link, via enhanced early-diagenetic water circulation between the ocean bottom and the sediments, coupled with the redox pumping of iron, that allowed phosphate concentration and development of concretions close to the sea bottom (Scasso & Castro 1999). Consequently, the disappearance of most invertebrates with calcium carbonate skeletons is suggested to have occurred during early diagenesis.

Ameghino (1900–1903, 1906), Leriche (1907) and Frenguelli (1928) described the first fossil fishes from the Gaiman Formation. More recently, ALC described elasmobranchs and teleosts (Cione 1978, 1986, 1988, Cione & Pandolfi 1984, Arratia & Cione 1996, Cione & Azpelicueta 2002; see also Cione & Expósito 1980). Fish recorded are hexanchiform hexanchids, lamniform isurids, odontaspidids, cetorhinids, carcharhiniform carcharhinids, heterodontiform heterodontids, squatiniform squatinids myliobatiform myliobatids, perciform oplegnathids and labrids, and tetraodontiform molids. Fish remains are strongly biased to elasmobranches owing to the type of deposit. A high-energy environment easily degrades bones, leaving only the more resistant material (teeth) preserved. Also, teeth are shed through the life of rays and sharks, generating a large quantity of potential fossils. The fish association suggests warm temperate waters. However, the occurrence of a diverse community of penguins suggests that the hydrology could have been complex (Cione 1978, Malumián & Náñez 1991, Scasso & Castro 1999, Malumián 2002, Acosta Hospitaleche 2004).

The most recent study of the penguin fauna revealed the following taxa: *Eretiscus tonni, Palaeospheniscus bergi, Palaeospheniscus patagonicus* and *Palaeospheniscus biloculata* (Acosta Hospitaleche 2004). Cozzuol (1996) revised the cetaceans and recognized Balaenidae, ''Cetotheriidae,''

Physeteridae, Squalodelphidae, Squalodontidae? and Kentriodontidae (see also Cione & Cozzuol 1990).

Continental. The early Miocene (Colhuehuapian, Pinturan and Santacrucian) continental faunas include many metatherians, xenarthrans and rodents. Several traces presumably correspond to didelphid or borhyaenid marsupials, common in Patagonia during the Miocene (Paula Couto 1979, Goin *et al*. 2007). Procyonids, the first mammals of Order Carnivora, entered South America during the Huayquerian (early late Miocene). Canids occur for the first time in the Marplatan (early Pliocene) and felids during the Ensenadan (early Pleistocene; Cione & Tonni 1995, 2005, Woodburne *et al*. 2006). We did not find rodent traces (e.g. as shown by Lyman 1994, Reitz & Wing 1999, Martin 2006). Rodents have been known in South America since the Tinguiririan (earliest Oligocene; Flynn *et al*. 2003).

Taphonomy

Penguin disarticulation sequence in breeding areas. The disarticulation process is relatively fast in birds (Cruz 2007). One of us (CAH) made observations on the sequence of skeletonization and disarticulation of recent Patagonian penguins in breeding areas. The bird dies at the coast, where the body remains for a few weeks; its spine begins to bend backward; then, soft tissues separate from the bones (Fig. 6). Data from modern penguin colonies published by Cruz (2006) largely agree with our own observations in the study area. Disarticulation begins with the skull and then limbs. The rostrum detaches at this time from the rest of the skull. Hindlimbs are more rapidly dismembered than forelimbs, which remain attached as a unit with the coracoid, furculum, scapula, and in some cases the sternum. Moreover, the proximal portions of every limb separate before the distal ones (Cruz 2007). In hindlimbs, the humerus, ulna and radius are exposed, whereas in forelimbs only the tibiotarsus loses its covering. Subsequently, the keel becomes exposed, although the thoracic cage remains most frequently articulated. Dismembering of limb bones begins while the spine, the thoracic cage and pelvis are held together. After burial, disarticulation and dispersal of bones continue in most cases via bioturbation (Cruz 2007).

Weathering. Fresh or slightly weathered bones predominate in colonies (Cruz 2007). This is probably related to the intrinsic features of bird bones. While mammals display the whole range of weathering stages of Behrensmeyer (1978), avian bones rarely exceed stage 2. Cruz (2007), suggested that this is due to rapid burial before advanced weathering (Cruz 2007) whereas Behrensmeyer *et al*. (2003) suggested that they disintegrate rapidly. Certainly, rapid skeletal disarticulation is typical of all birds and increases the vulnerability of bones to destruction. Furthermore, bird bones are small compared to many mammals. When avian bones exceed a certain stage, they are so badly damaged that they essentially disappear (Cruz 2005). That is particularly the case for the thoracic cage and skull, which rarely fossilize.

Based on archaelogical studies, four stages have been proposed for the decomposition of Patagonian marine birds: (1) bones with shallow longitudinal cracks, (2) bones with deep longitudinal cracks, fractures, and porous surface, (3) bones with pronounced cracks, externally flaked, and rounded epiphyses, (4) splintered surface and badly damaged bones (Muñoz & Savanti 1998).

Many fossil penguin bones of the Gaiman Formation bear longitudinal or oblique cracks: MLP 20-337, MLP 20-391, MLP 20-486, MLP 20-50 (Fig. 7B: MLP

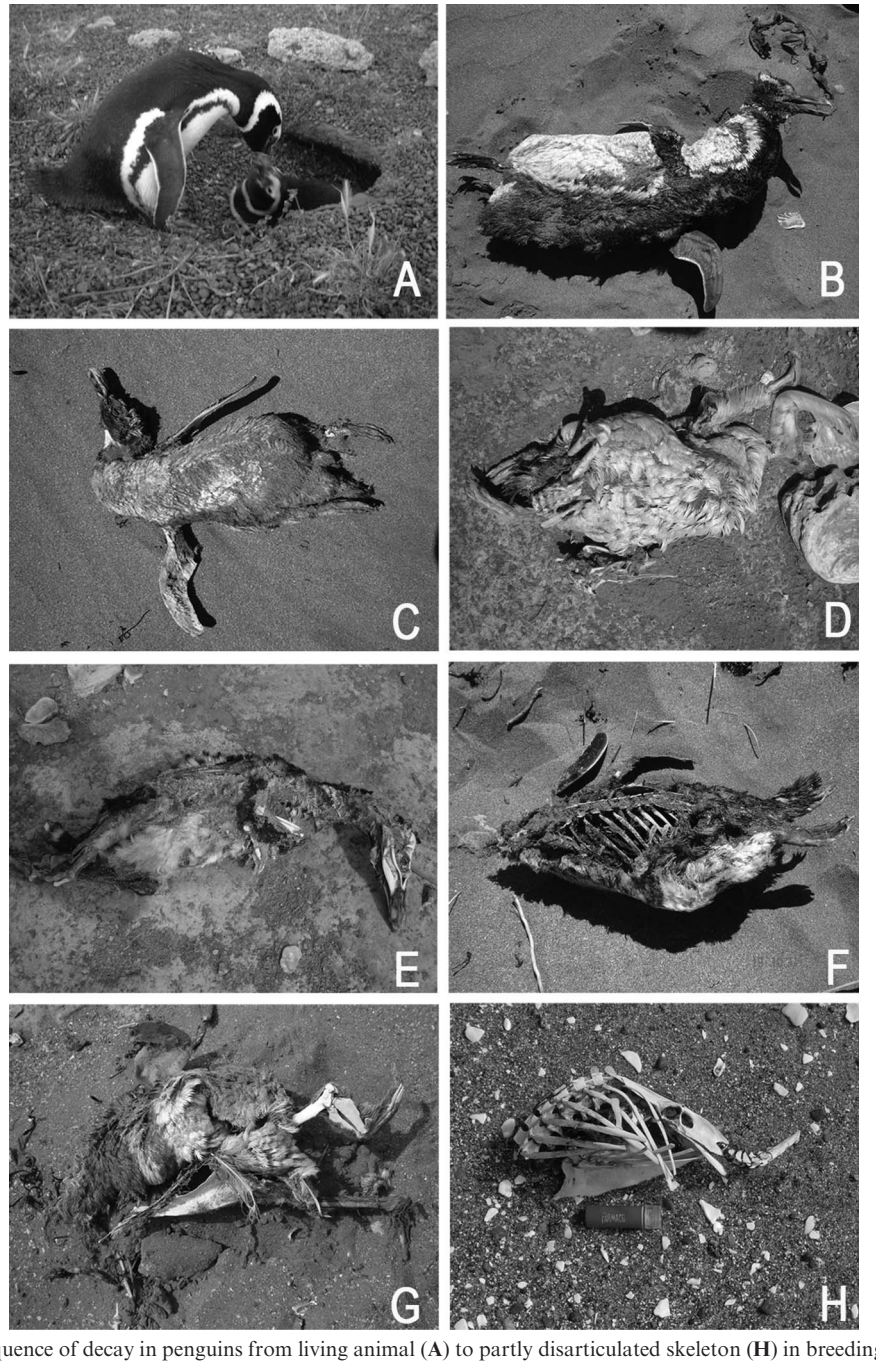

Fig. 6. Sequence of decay in penguins from living animal (**A**) to partly disarticulated skeleton (**H**) in breeding areas of Patagonia (photos of CAH).

20-50), MLP 20-491, MLP 20-535, MLP 20-365, MLP 20-50. Comparing homologous elements, cracks develop in a similar pattern in recent and fossil bones (Fig. 7A, B). Of the penguin bones with predation marks (128 pieces), 70.3% bear weathering cracks

(Appendix 1). We observed flaking in the outer layers of some bones (stage 2 of Behrensmeyer 1978 and 3 of Muñoz & Savanti 1998; MLP 20-365) and deep cracking and a coarse layered fiber structure in others (stage 4 of Behrensmeyer 1978 and Muñoz & Savanti 1998; MLP 20-368, MLP 20-246; Fig. 7C, D).

Weathering indicates that the material was exposed to subaerial conditions for relatively long periods before being drowned by the sea. Large numbers of isolated bones occur in modern penguin breeding colonies. A similar pattern can be assumed for the Gaiman area during the early Miocene. The cracks clearly differ from those generated by burial pressure. The high rate of weathered bones suggests that most animals died in the breeding colony.

Fractures. Flattening, fracturing, disarticulation and burial of carcasses can be attributed to trampling by other members of the penguin colony (Cruz 1999, 2007), especially around nests (Malacalza & Navas 1996). Fractures in appendicular bones are commonly observed in fossil and archaeological penguin material, but not in modern colonies. They can not be attributed to carnivore or root action (Cruz 2007) but probably represent diagenetic processes. Exposed fossil bones from the Gaiman Formation could be more vulnerable to fracturing by the modern harsh weather conditions.

Predation and scavenging. Remarkably, the incidence of land carnivores is extremely low in modern marine bird bone assemblages, being $<1\%$ of samples (Cruz 1999, 2004). When land-bound, marine birds are mainly preyed upon by other birds (Williams 1995). The incidence of predation on adult Magellanic penguins is not high, as predators concentrate on eggs and chicks, and the scavenging of carcasses. The main predators and/or scavengers at colonies are the South American Grey Fox, the little

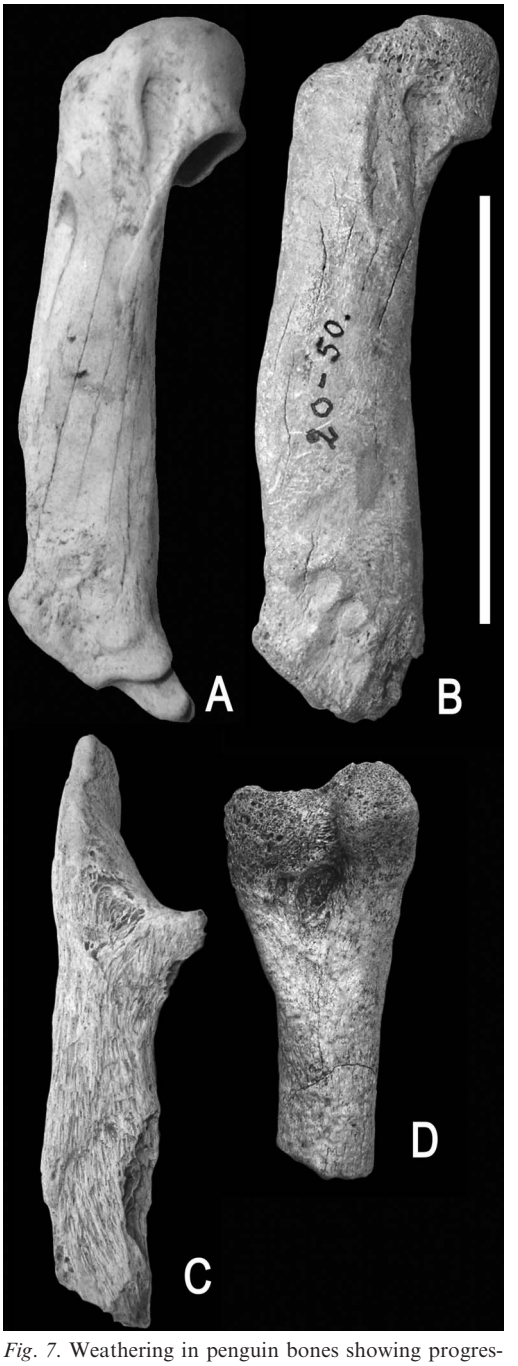

Fig. 7. Weathering in penguin bones showing progressive degradation from **A** to **D** (recent bird bones held in the División Paleontología de Vertebrados, Museo de La Plata). **A**, recent humerus; **B**, MLP 20-50 (humerus); **C**, MLP 20-246 (coracoid); **D**, MLP 20-298 (femur). Scale bar = 50 mm.

Hairy Armadillo, skuas and especially the Kelp Gull (Frere *et al*. 1996, Gandini *et al*. 1996).

The main action of bird predators is puncturing of the thorax, abdomen and cervical and ocular regions, with subsequent skin tearing, muscle damage and gut destruction. Bone modifications are scarce, and those recorded were concentrated especially on the sternum, keel and ribs. The most distinct markings are punctures on the sternum. Another distinct feature of bird predation and scavenging is that it takes place *in situ*, not involving carcass or bone transport.

Element representation. Damuth (1992) studied element representation of recent marine bird bones comparing flying birds, running birds and exclusively diving birds in a taxon free analysis. Each of these bird types displays a particular pattern of element representation due to the influences imposed by locomotion such as bone density (Cruz 2005). According to Livingston (1989), bone structure and functional anatomy are determinant in the constitution of bone accumulations.

In marine birds, hind- and forelimbs are the most commonly preserved elements. The pelvic girdle is less represented (Cruz 2007). There is a tendency towards predominance of humeri, tibiotarsi and femora for limbs, and coracoids for the scapular girdle.

The Gaiman Formation at Gaiman includes the largest and most diverse fossil representation of Spheniscidae in southern South America. Acosta Hospitaleche (2007) identified 578 penguin bones in an assemblage from this unit, of which 73% represent appendicular bones and 14% scapular girdle bones. Humeri are most abundant (27%).

Why is the Gaiman assemblage interpreted as a breeding colony?

The high density of bones in modern breeding areas of Patagonian marine birds is remarkable. Spheniscid remains predominate over those of other vertebrates; bones are mostly disarticulated, limb bones are abundant, carnivore marks on bones are rare, and fractured elements are common. Many of the features evident in modern assemblages are also apparent in fossil avian deposits (Cruz 2007).

Penguin remains have a limited distribution in space and their importance decreases towards the boundaries of the colony (Cruz 1999, 2003, 2004). Another remarkable factor related to bone accumulations is the activity of predators and scavengers (Cruz 1999, 2003, 2004). They usually transport carcasses beyond the limits of the colony and leave recognizable marks on external bone surfaces (Cruz 2007). However, modern studies along the coast of Patagonia (Cruz 2007) and Antarctica (Emslie 1995) indicate that the most important causes of bone accumulations are not carnivory or scavenging but weathering and erosion processes. The differential representation of skeletal parts constitutes an important tool for gauging the degree of bone transportation and their proximity to the colony. Fossil colonies are represented mostly by limbs bones, then scapular girdles, whereas axial skeletons and pelvic girdles are scarce (Emslie 1995; Cruz 1999, 2004, 2005).

The basal sediments of the Gaiman Formation were deposited in a transgressive marine environment that advanced westward. The great abundance of penguin bones, many with cracks, indicates that they were exposed subaerially in a breeding area.

Comparison with other fossil penguin localities

The remarkable penguin record from the Eocene La Meseta Formation at Seymour Island (Antarctic Peninsula) reveals an assemblage in which almost all bones are disarticulated (personal observation; see also Jadwiszczak 2009). No predation marks have

been found although there are weathering cracks (CAH, personal observation).

Few but, in many cases, completely articulated penguin skeletons occur in the middle–late Miocene Puerto Madryn Formation on the Valdés Peninsula (Acosta Hospitaleche 2004). No predation marks were found and burial was interpreted to be even more rapid and certainly subaqueous.

Absence of teleostean marks

We found it very difficult to identify marks left by teleostean fishes on Gaiman Formation penguin bones. Some teleosteans (e.g. Labridae, Sciaenidae; Braga 1984) crush invertebrates or other animals. Others, such as scarid and acanthurid fishes, are typical bioeroders of corals in tropical environments (see Backus 1966, Peyrot-Clausade *et al*. 2000, Brown-Sarracino *et al*. 2007, Peyrot-Clausade 2008) or forage on algae (Backus 1964). Little is known about fish traces in temperate waters although there are good descriptions of bioerosion (e.g. Stearley & Ekkdale 1989). Studies in Denmark, Japan and California have shown that some teleosteans forage on benthic algae, sponges and molluscs, amongst other organisms (Backus 1964). However, the intensity of fish-rasping appears to be considerably less than in the tropics (Backus 1966). The nature of the traces produced by these fishes on bones has not been studied. However, some remains of parrotfish were described from the Gaiman Formation (Cione & Azpelicueta 2002). Although we have no direct linkage, oplegnathids could have left traces on bones when foraging for epibionts. For example, *Oplegnathus insignis* (Kner, 1867) and other species presently feed on benthic algae and fauna (Fishbase 2008).

Conclusions

The abundant penguin remains from the base of Gaiman Formation at Bryn Gwyn are represented by disarticulated bones, of which many show predation marks. They certainly represent a thanatocenosis (*sensu* Fürsich 1990). We found pits, furrows, a few scores but no punctures. This could be due to the small size of predators/scavengers and the penguin bone robustness. Sedimentary and palaeontological features indicate that deposition occurred in an intertidal to subtidal setting.

Marks from desiccation, terrestrial carrion feeders and disarticulation suggest that penguin corpses were exposed in a breeding area (Fig. 8A). We found no healed marks. Carnivores are important in the removal and disarticulation of modern Patagonian penguin corpses. At Bryn Gwyn, terrestrial predators would have been represented by mammals, most probably medium-sized marsupial carnivores (Fig. 8). There are no previous reports of fossil marsupial traces in South America. Birds also probably predated or scavenged penguins, but have not left marks on the bones.

When the sea transgressed onto the continent, the penguin bones were buried in the marine sediments or remained exposed on the sea floor (Fig. 8B). As the sea advanced, the breeding areas likely migrated westward. Those bones exposed on the sea floor were colonized by algae, sponges and other benthic animals. They acted as hard benthic substrates for encrustation and bioerosion (Oschmann 1990). We identified clionid sponge borings in several bones (Domichnia: *Entobia*). Other organisms such as echinoderms foraged for sponges or algae and left traces (Pasichnia: *Gnatichnus pentax*). The *Entobia* holes were enlarged and heavily marked, probably by echinoderms. Other traces may have been generated by sharks feeding on epibionts or on penguin carcasses. One scapula bears traces possibly produced by a shark common in the Gaiman Formation, the carcharhiniform *Galeocerdo aduncus*.

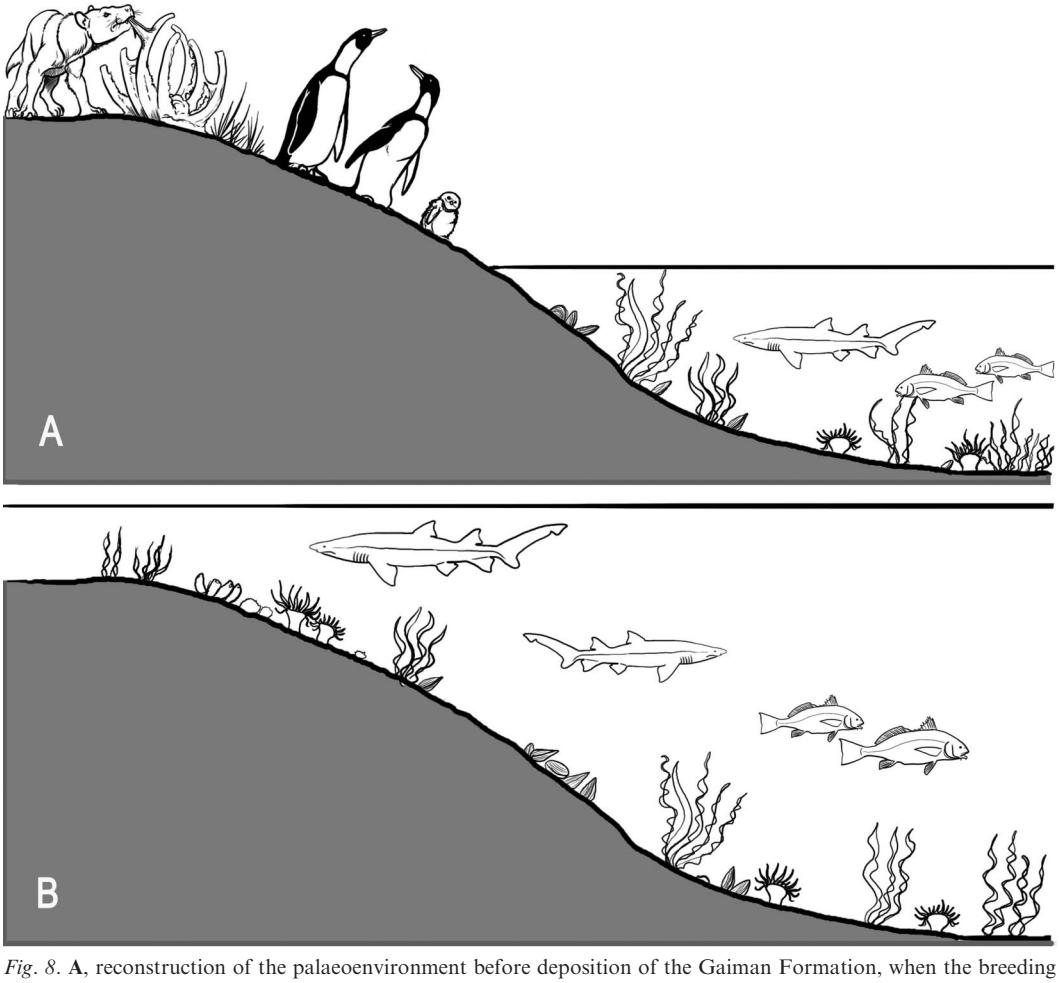

Fig. 8. **A**, reconstruction of the palaeoenvironment before deposition of the Gaiman Formation, when the breeding area was located at Bryn Gwyn; **B**, Reconstruction of the environment during deposition of the Gaiman Formation.

We recognized several ecological guilds in the Gaiman Formation identified by traces: strict predators (*sensu* Bambach 2002) of different levels, scavengers (mammals, sharks, teleostean fishes), grazers (echinoderms and possible molluscs) and suspension feeders (sponges). Other organisms are represented by bodies but not by traces: strict predators (penguins), suspension feeders (oysters, other pelecypods, silicious sponges) and autotrophs (diatoms). The corrosive environment removed most of the calcium carbonate and left almost exclusively calcium phosphate or silica. Consequently, the unit lacks somatic remains of most molluscs, bryozoans, polychaetes and cirripeds.

Traces on the penguin bones can be assigned to the *Trypanites* Ichnofacies (*sensu* Bromley & Asgaard 1991), which is characterized by domichnial borings and grooves made by foragers (see Taylor & Wilson 2003, Farinati *et al*. 2006, 2007). Usually, these are formed in shoreline rocks or in lithified limestone hardgrounds on the seabed.

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References

Acosta Hospitaleche, C., 2004. *Los pingüinos (Aves, Sphenisciformes) fósiles de Patagonia. Sistemática, filogenia, biogeografía y evolución*. PhD Thesis, Universidad Nacional de La Plata, 321 pp. (unpublished).

Acosta Hospitaleche, C., 2007. Revisión sistemática de *Palaeospheniscus biloculata* (Simpson) nov. comb. (Aves, Spheniscidae) de la Formación Gaiman (Mioceno Temprano), Chubut, Argentina. *Ameghiniana 44*, 417–426.

Agassiz, L., 1833–43. *Recherches sur les poissons fossiles*, Vol. 5. Neuchatel, Switzerland, 1420 pp.

Ameghino, F., 1900–1903. L'age des Formations sédimentaires de Patagonie. *Anales de la Sociedad Científica Argentina, 50*, 109–130, 145–165, 209–229; *51*, 20–39, 65–91; *52*, 189–197, 244–250; *54*, 161–180, 220–249, 283–342.

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 Historia Natural de Buenos Aires 15*, 1–568.

Ardolino, A., 1981. El volcanismo cenozoico del borde suroriental de la Meseta de Somuncurá, Provincia del Chubut. *Actas del VIII Congreso Geológico Argentino 3*, 7–23.

Arratia, G. & Cione, A.L., 1996. The fish fossil record of southern South America. *Münchener Geowissenschaft Abhanlungen 30A*, 9–72.

Backus, G.J., 1964. The effects of fish-grazing on invertebrate evolution in shallow tropical waters. *Occasional Papers of the Allan Hancock Foundation 27*, 1–34.

Backus, G.J., 1966. Some relationships of fishes to benthic organisms on coral reefs. *Nature 210*, 280–284.

Bambach, R.K., 2002. Supporting predators: changes in the global ecosystem inferred from changes in predator diversity. In *The Fossil Record of Predation*, M. Kowalewki & P.H. Kelley, eds, Paleontological Society Special Papers 8. Paleontological Society, New Haven, 319–352.

Behrensmeyer, A., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology 4*, 150–162.

Behrensmeyer, A.K., Stayton, C.T. & Chapman, R.E., 2003. Taphonomy and ecology of modern avifaunal remains from Amboseli Park, Kenya, *Paleobiology 29*, 52–70.

Bertels, A., 1970. Sobre el "Piso Patagoniano" y la representación de la época del Oligoceno en Patagonia Austral (República Argentina). *Revista de la Asociación Geológica Argentina 25*, 495–501.

Bertels, A., 1975. Bioestratigrafía del Paleógeno en la República Argentina. *Revista Española de Micropaleontología 7*, 429–450.

Bertels, A., 1980. Estratigrafía y foraminíferos (Protozoa) bentónicos de la Formación Monte León (Oligoceno) en su área tipo, provincia de Santa Cruz, Argentina. In *Actas del II Congreso Argentino de Paleontología y Bioestratigrafía y I Congreso Latinoamericano de Paleontología 2*, 213–273.

Binford, L.R., 1981. *Bones. Ancient Men and Modern Myths*, Academic Press, Orlando, 320 pp.

Bishop, G., 1975. Traces of predation. In *The Study of Trace Fossils*, R. Frey, ed., Springer-Verlag, Berlin, 261–281.

Bown, P. & Larriestra, C.N., 1990. Sedimentary palaeoenvironments of fossil platyrrhine localities, Miocene Pinturas Formation, Santa Cruz Province, Argentina. *Journal of Human Evolution 19*, 87–119.

Braga, L., 1984. *Contribución al conocimiento de la alimentación de los Sciaenidae y las adaptaciones del aparato digestivo a sus respectivos regímenes*. PhD Thesis, Universidad Nacional de La Plata, 210 pp. (unpublished).

Breton, G., Neraudeau, D. & Cuenca-Boulat, C., 1992. *Gnathichnus stellarum* ichnosp. nov., trace de broutage d'un Echnide du Campanien des Charentes (France). *Revue de Paléobiologie 11*, 219–229.

Bromley, R.G., 1975. Comparative analysis of fossil and recent echinoid bioerosion. *Palaeontology 18*, 725–739.

Bromley, R.G. & Asgaard, U., 1991. Ichnofacies: a mixture of taphofacies and biofacies. *Lethaia 24*, 153–164.

Bromley, R.G. & Tendal, O.S., 1973. Example of substrate competition and phobotropism between two clionid sponges. *Journal of Zoology 169*, 151–155.

Bronn, H.G. 1837–1838. *Lethaea geognostica. 2: Das Kreide und Molasse-Gebirge*, Schweizerbart, Stuttgart, 545–1350.

Brown-Sarracino, J., Peckol, P., Curran, A. & Robbart, M., 2007. Spatial variation in sea urchins, fish predators, and bioerosion rates on coral reefs of Belize. *Coral Reefs 26*, 71–78.

Buatois, L., Bromley, R.G., Mángano, M., Bellosi, E. & Carmona, N., 2003. Ichnology of shallow marine deposits in the Miocene Chenque Formation of Patagonia: complex ecologic structure and niche partitioning in Neogene ecosystems. *Publicación Especial de la Asociación Paleontológica Argentina 9*, 85–95.

Buitrón-Sánchez, B.E. & Pantoja-Alor, J., 1994. Esponjas perforantes de moluscos del Cretácico temprano en al región centrooccidental de México. *Revista Mexicana de Ciencias Geológicas 11*, 222–231.

Camacho, H.H., 1974. Bioestratigrafía de las formaciones marinas del Eoceno y Oligoceno de la Patagonia. *Anales de la Academia Ciencias Exactas, Físicas y Naturales 26*, 39–57.

Carmona, N., Butois, L.A., Mangano, M.G. & Bromley, R.G., 2008. Ichnology of the Lower Miocene Chenque Formation, Patagonia, Argentina: animal-substrate interactions and the modern evolutionary fauna. *Ameghiniana 45*, 93–122.

Cigala Fulgosi, F., 1990. Predation (or possible scavenging) by a great white shark on an extinct species of bottlenosed dolphin in the Italian Pliocene. *Tertiary Research 12*, 17–36.

Cione, A.L., 1978. Aportes paleoictiológicos al conocimiento de la evolución de las paleotemperaturas en el área austral de América del Sur durante el Cenozoico. Aspectos zoogeográficos y ecológicos conexos. *Ameghiniana 15*, 183–208.

Cione, A.L., 1986. A new *Megascyliorhinus* (Chondrichthyes, Galeomorphii) from the middle Tertiary of Patagonia. *Journal of Vertebrate Paleontology 6*, 105–112.

Cione, A.L., 1988. *Los peces de las formaciones marinas del Cenozoico de Argentina*. PhD thesis. Facultad de Ciencias Naturales, Universidad Nacional de La Plata, La Plata, 588 pp. (unpublished).

Cione, A.L. & Azpelicueta, M.M., 2002. An oplegnathid fish from the Miocene of Patagonia. *Geobios 35*, 367–373.

Cione, A.L. & Cozzuol, M., 1990. Reidentification of *Portheus patagonicus* Ameghino, 1901, a supposed fish from the Middle Tertiary of Patagonia as a delphinoid cetacean. *Journal of Paleontology 64*, 451–453.

Cione, A.L. & Expósito, S., 1980. Chondrichthyes del "Patagoniano" s.l. de Astra, Golfo de San Jorge, provincia de Chubut, Argentina. Su significado paleoclimático y paleobiogeográfico. In *Actas del II Congreso Argentino de Paleontología y Bioestratigrafía y I Congreso Latinoamericano de Paleontología*, 2, 275–290.

Cione, A.L. & Pandolfi, A.A., 1984. A finspine of *Heterodontus* from the "Patagonian" of Trelew, Chubut, Argentina. *Tertiary Research 6*, 59–63.

Cione, A.L. & Tonni, E.P., 1995. Chronostratigraphy and "Land-mammal ages" in the Cenozoic of southern South America: principles, practices, and the "Uquian" problem. *Journal of Paleontology 69*, 135–159.

Cione, A.L. & Tonni, E.P., 2005. Bioestratigrafía basada en mamíferos del Cenozoico superior de la región pampeana. In *Geología y Recursos Minerales de la Provincia de Buenos Aires, Relatorio del XVI Congreso Geológico Argentino 11*, R. de Barrio, R. Etcheverry, M.F. Caballé & E. Llambías, eds, La Plata, 193–200.

Cortés, J.M., 1982. Estratigrafía cenozoica y estructura al oeste de la Península de Valdés, Chubut. Consideraciones tectónicas y paleogeográficas. *Revista de la Asociación Geológica Argentina 36*, 424–445.

Cozzuol, M., 1996. The record of the aquatic mammals in Southern South America. In *Contributions of southern South America to Vertebrate Paleontology*, G. Arratia, ed., *Münchner Geowissenschaftliche Abhandlungen 30*, 321–342.

Cruz, I., 1999. Pingüinos de Cabo Vírgenes (Santa Cruz). Aspectos tafonómicos e implicaciones arqueológicas. *Resúmenes de XIII Congreso Nacional de Arqueología Argentina*, Universidad Nacional de Córdoba, Córdoba, 389–391.

Cruz, I., 2003. *Paisajes tafonómicos de restos de aves en el sur de Patagonia continental. Aportes para la interpretación de conjuntos avifaunísticos en registros arqueológicos del Holoceno*. PhD Thesis, Facultad de Filosofía y Letras, UBA, 570 pp. (unpublished).

Cruz, I., 2004. Tafonomía de huesos de aves en Punta Medanosa (Depto. Puerto Deseado, Santa Cruz, Argentina). In *Contra viento y marea. Arqueología de la Patagonia*, T. Civalero, P. Fernández & G. Guraieb, eds, Instituto Nacional de Antropología y Pensamiento Latinoamericano, Buenos Aires, 455–468.

Cruz, I., 2005. La representación de partes esqueletarias de aves. Patrones naturales e interpretación arqueológica. Archaeofauna. *International Journal of Archaeozoology 14*, 69–81.

Cruz, I., 2006. Los restos de pingüinos (Spheniscidae) de los sitios de Cabo Blanco (Santa Cruz, Patagonia Argentina): Análisis tafonómico y perspectivas arqueológicas. *Intersecciones en Antropología 7*, 15–26.

Cruz, I., 2007. Avian taphonomy: observations at two Magellanic penguin (*Spheniscus magellanicus*) breeding colonies and their implications for the fossil record. *Journal of Archaeological Science 34*, 1252–1261.

Damuth, J., 1992. Taxon-free characterization of animal communities. In *Terrestrial Ecosystems Through Time*, A.K. Behrensmeyer, J.D. Damuth, J.D., W. DiMichele, R. Potts, H.D. Sues & S.L. Wing, eds, University of Chicago Press, Chicago, 183–203.

Deméré, T.A. & Cerutti, R.A., 1982. A Pliocene shark attack on a cethotheriid whale. *Journal of Paleontology 56*, 1480–1482.

Emslie, S.D., 1995. Age and taphonomy of abandoned penguin rockeries in the Antarctic Peninsula Region. *Polar Record 31*, 409–418.

Farinati, E., Spagnuolo, J.O. & Aliotta, S., 2006. Bioerosión en micromoluscos holocenos del estuario de Bahía Blanca, Argentina. *Ameghiniana 43*, 45–54.

Farinati, E., Spagnuolo, J.O. & Aliotta, S., 2007. Bioerosión en sustratos líticos de la costa sudoeste de la provincia de Buenos Aires, Argentina. In *4th European Meeting on the Palaeontology and Stratigraphy of Latin America*, E. Díaz-Martínez & I. Rábano, eds, *Cuadernos del Museo Geominero 8*, 137–142.

Fishbase, 2008. *Oplegnathus insignis*. Available online at: http://www.fishbase.de/Summary/speciesSummary.php?ID=8200&genusname=Oplegnathus&speciesname=insignis (accessed 10 September 2009).

Flynn, J.J. & Swisher, C.C., 1995. Cenozoic South American land-mammal ages: correlation to global geochronologies. In *Geochronology, Time scales, and Correlation: Framework for a Historical Geology*, W.A. Berggren, D.V. Kent & J. Handerbol, eds, *SEPM Special Publication 54*, 317–333.

Flynn, J., Novacek, M., Dodson, H.E., Frassinetti, D., McKenna, M.C., Norell, M., Sears, K., Swisher, C. & Wyss, A., 2003. A new fossil mammal assemblage from the southern Chilean Andes: implications for geology, geochronology, and tectonics. *Journal of South American Earth Sciences 15*, 285–302.

Frenguelli, J., 1928. A proposito di alcune incisioni sull' omero di uno Squalodontide. *Bollettino della Società Geologica Italiana 47*, 1–6.

Frere, E., Gandini, P. & Boersma, P.D., 1996. Aspectos particulares de la biología de reproducción y tendencia poblacional del pingüino de Magallanes (*Spheniscus magellanicus*) en la colonia de Cabo Vírgenes, Santa Cruz, Argentina. *El Hornero 14*, 50–59.

Fürsich, F.T., 1990. Fossil concentrations and life and death assemblages. In *Palaeobiology. A synthesis*, D. Briggs & P. Crowther, eds, Blackwell Scientific Publications, Oxford, 235–239.

Gandini, P., Frere, E. & Boersma, P.D., 1996. Status and conservation of Magellanic Penguins *Spheniscus magellanicus* in Patagonia, Argentina. *Bird Conservation International 6*, 307–316.

Gibert, J.M.D., Domènech, R. & Martinell, J., 2007. Bioerosion in shell beds from the Pliocene Roussillon Basin, France: Implications for the (macro) bioerosion ichnofacies model. *Acta Palaeontologica Polonica 52*, 783–798.

Goin, F., Abello, A., Bellosi, E., Kay, R., Madden, R. & Carlini, A., 2007. Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno Temprano, Edad-mamífero Colhuehuapense). Parte I: Introducción, Didelphimorphia y Sparassodonta. *Ameghiniana 44*, 29–71.

Haldemann, S.S., 1840. Supplement to number one of "*A monograph of the Limniades, and another freshwater bivalve shells of North America*," containing descriptions of apparently new animals indifferent classes, and the names and characters of the subgenera in *Paludina* and *Anculosa*. Private publication, Philadelphia, 3 pp.

Haq, B.U., Handerbol, J. & Vail, P., 1987. Chronology of fluctuating sea levels since the Triassic. *Science 235*, 1156–1167.

Jadwiszczak, P., 2009. Penguin past: the current state of knowledge. *Polish Polar Research 30*, 3–28.

Kear, B. & Godthelp, H., 2008. Inferred vertebrate bite marks on an Early Cretaceous unionoid bivalve from Lightning Ridge, New South Wales, Australia. *Alcheringa 32*, 65–71.

Kner, R., 1867. *Fische. Reise der österreichischen Fregatte "Novara" um die Erde in den Jahren 1857–1859, unter den Befehlen des Commodore B. von Wüllerstorf-Urbain. Zoologischer. Theil Fische*, Reise der öesterreichischen Fregatte "Novara" um die Erde in den Jahren 1857–59, 275–433.

Legarreta, L., Uliana, M. & Torres, M., 1990. Secuencias deposicionales cenozoicas de la Patagonia Central: sus relaciones con las asociaciones de mamíferos terrestres y episodios marinos epicontinentales. *Actas del Segundo Simposio sobre el Terciario de Chile*, Concepción, 135–176.

Leriche, M., 1907. Observations sur les Poissons du Patagonien récenment signalés par M. Fl. Ameghino. *Annales de la Societé Géologique du Nord 36*, 129–137.

Linnaeus, C., 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, Holmiae 1, 230–338.

Livingston, S.D., 1989. The taphonomic interpretation of avian skeletal part frequencies. *Journal of Archaeological Science 16*, 537–547.

Lundgreen, S.A.B., 1891. Studier öfver fossilförnader lössa block. *Geologiska Föreningens i Stockholm 13*, 111–121.

Lyman, R.R., 1994. *Vertebrate taphonomy*, Cambridge University Press, Cambridge, 524 pp.

Malacalza, V.E. & Navas, J.R., 1996. Biología y ecología reproductiva de *Phalacrocorax albiventer* (Aves: Phalacrocoracidae) en Punta León, Chubut, Argentina. *Ornitología Neotropical 7*, 53–61.

Malumián, N., 1999. La sedimentación en la Patagonia Extrandina. *Anales del Instituto de Geología y Recursos Minerales 29*, 557–577.

Malumián, N., 2002. El Terciario marino. Sus relaciones con el eustatismo. *Relatorio del XV Congreso Geológico Argentino*, Buenos Aires, 237–244.

Malumián, N. & Náñez, C., 1991. Paleogeografía del Terciario medio del cono sur: avance de aguas antárticas. *Resúmenes expandidos del VI Congreso Geológico Chileno*, Santiago de Chile, 847–851.

MARSHALL, L., HOFFSTETTER, R. & PASCUAL, R., 1983. Mammals and stratigraphy: Geochronology of the continental mammal-bearing Tertiary of South America. *Geobios, Mémoire Extraordinaire*, 1–93.

MARTIN, F.M., 2006. *Carnívoros y huesos humanos de Fuego-Patagonia*, Sociedad Argentina de Antropología. Colección Tesis de Licenciatura, Buenos Aires, 204 pp.

MENDÍA, J. & BAYARSKY, A., 1981. Estratigrafía del Terciario en el valle inferior del río Chubut. *Actas del VIII Congreso Geológico Argentino 3*, 593–606.

MIKULÁŠ, R., 2001. Modern and fossil traces in terrestrial lithic substrates. *Ichnos 8*, 177–184.

MORENO, F. & MERCERAT, A., 1891. Catálogo de los pájaros fósiles de la República Argentina. *Anales del Museo de La Plata, Paleontología Argentina 1*, 8–71.

MUÑOZ, A.S. & SAVANTI, F., 1998. Observaciones tafonómicas sobre restos avifaunísticos de la costa noreste de Tierra del Fuego. *Revista del Museo de Historia Natural de San Rafael 20*, 107–121.

NICHOLSON, H.A., 1873. Contribution to the study of the errant annelids of the older Paleozoic rocks. *Royal Society Society of London, Proceedings 21*, 288–290.

NORIEGA, J., CIONE, A.L. & ACEÑOLAZA, F.G., 2007. Shark tooth marks on Miocene balaenopterid cetacean bones from Argentina. *Neues Jahrbuch für Geologie und Paläontologie 245*, 185–192.

OGG, J., OGG, G. & GRADSTEIN, F., 2008. *The Concise Geologic Time Scale*, Cambridge University Press, 184 pp.

OSCHMANN, W., 1990. Dropstones—rocky mini islands in high-latitude pelagic soft substrate environments. *Senckenbergiana Marítima 21*, 55–75.

PASCUAL, R., ORTEGA HINOJOSA, E., GONDAR, D. & TONNI, E.P., 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atención a aquellas del Territorio Bonaerense. *Anales de la Comisión de Investigaciones Científicas de la Provincia de Buenos Aires 6*, 165–193.

PAULA COUTO, C., 1979. *Tratado de Paleomastozoologia*, Academia Brasileira de Ciencias, Rio de Janeiro, 590 pp.

PEYROT-CLAUSADE, M., 2008. *The French Polynesian Atolls: Bioerosion of the Reefs*. Available online at: http://www.com.univ-mrs.fr/IRD/atollpol/ecorecat/ukbioero.htm (accessed 10 September 2009).

PEYROT-CLAUSADE, M., CHABANET, P., CONAND, C., FONTAINE, M., LETOURNEUR, Y. & HARMELIN-VIVIEN, M., 2000. Sea urchin and fish bioerosion on La Réunion and Moorea reefs. *Bulletin of Marine Science 66*, 477–485.

REITZ, E.J. & WING, E.S., 1999. *Zooarchaeology*, Cambridge University Press, Cambridge, 455 pp.

SCASSO, R.A. & CASTRO, L.N., 1999. Cenozoic phosphatic deposits in North Patagonia, Argentina: Phosphogenesis, sequence-stratigraphy and paleoceanography. *Journal of South American Earth Sciences 12*, 471–487.

SCASSO, R.A., CASTRO, L.N., LIPPAI, H. & ALONSO, M.S., 1996. Significado estratigráfico y paleoambiental del conglomerado fosfático "Patagoniense" de Bryn Gwyn, Gaiman (Prov. del Chubut). *Actas de la VI Reunión Argentina de Sedimentología*, 117–122.

SCHULTZ, M. & VERDINELLI, M.A., 1975. Interpretación de huellas "asteriformes" en la conchilla de *Tegula orbignyana* (Pilsbry) (Gasteropoda, Trochidae). Un enfoque actuo-paleontológico. *Actas del I Congreso Argentino de Paleontología y Bioestratigrafía*, 653–660.

SCHWIMMER, D.R., STEWART, J.D. & DENT WILLIAMS, G., 1997. Scavenging by sharks of the genus *Squalicorax* in the Late Cretaceous of North America. *Palaios 12*, 71–83.

SIMPSON, G.G., 1935. Early and Middle Tertiary geology of the Gaiman region, Chubut, Argentina. *American Museum Novitates 775*, 1–29.

SIMPSON, G.G., 1970. Miocene penguins from Victoria, Australia, and Chubut, Argentina. *Memoirs of the National Museum of Victoria 31*, 17–24.

SIMPSON, G.G., 1972. Conspectus of Patagonian fossil penguins. *American Museum Novitates 2488*, 1–37.

SIMPSON, G.G., 1981. Notes on some fossil penguins including a new genus from patagonia. *Ameghiniana 18*, 266–272.

STEARLEY, R.F. & EKKDALE, E.E., 1989. Modern marine bioerosion by macroinvertebrates, northern Gulf of California. *Palaios 4*, 453–467.

STERNBERG, K.M.G. VON, 1833. *Versuch einer geognostisch-botanischen Dartsellung der Flora der Vorwelt*, Fleischer, Leipzig 5–6, 1–80.

TAYLOR, P. & WILSON, M., 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth Science Reviews 62*, 1–103.

TURNER, C.G. & TURNER, J.A., 1999. *Man Corn. Cannibalism and Violence in the Prehistoric American Southwest*, The University of Utah Press, Salt Lake City, 547 pp.

ULIANA, M.A. & BIDDLE, K.T., 1988. Mesozoic-Cenozoic paleogeographic and geodynamic evolution of southern South America. *Revista Brasileira de Geociencias 18*, 172–190.

VOIGT, E., 1977. On grazing traces produced by the radula of fossil and recent gastropods and chitons. In *Trace Fossils*, T.P. CRIMES & J.C. HARPER, eds, *Geological Journal Special Issue 9, 2*, Seel House Press, Liverpool, 335–346.

WILLIAMS, T.D., 1995. *The Penguins. Spheniscidae. Bird Families of the World*, Oxford University Press, 295 pp.

WILSON, M., 2008. *Bioerosion: Hard Work in a Hard Place*. Available online at: http://www.wooster.edu/geology/Bioerosion/Bioerosion.html (accessed 10 September 2009).

WOODBURNE, M.O., CIONE, A.L. & TONNI, E.P., 2006. Central American Provincialism and the Great American Biotic Interchange. In *Advances in late Tertiary Vertebrate Paleontology in Mexico and the Great American Biotic Interchange*, O. CARRANZA-CASTAÑEDA & E.H. LINDSAY, eds, *Publicación Especial del Instituto de Geología y Centro de Geociencias de la Universidad Nacional Autónoma de México 4*, 73–101.

Appendix 1. Specimens from the Gaiman Formation

With cracks (90 specimens: 70.30%). MLP 20-423, MLP 20-418, MLP 20-488, MLP 20-369, MLP 20-250, MLP 20-486, MLP 20-391, MLP 20-363, MLP 20-292, MLP 20-293, MLP 20-365, MLP 20-428, MLP 20-490, MLP 20-491, MLP 20-392, MLP 20-273, MLP 20-253, MLP 20-295, MLP 20-382, MLP 20-482, MLP 20-260, MLP 20-266, MLP 20-510, MLP 20-337, MLP 20-334, MLP 20-370, MLP 20-56, MLP 20-596, MLP 20-351, MLP 20-352, MLP 20-251, MLP 20-256, MLP 20-559, MLP 20-294, MLP 20-331, MLP 20-328, MLP 20-558, MLP 20-326, MLP 20-350, MLP 20-262, MLP 20-560, MLP 20-333, MLP 20-393, MLP 20-323, MLP 20-344, MLP 20-339, MLP 20-330, MLP 20-522, MLP 20-433, MLP 20-347, MLP 20-380, MLP 20-379, MLP 20-362, MLP 20-367, MLP 20-374, MLP 20-364, MLP 20-378, MLP 20-386, MLP 20-376, MLP 20-348, MLP 20-390, MLP 20-467, MLP 20-365, MLP 20-50, MLP 20-535, MLP 77-XII-22-2, MLP 77-XII-22-30/42, MLP 77-XII-22-6/15, MLP 77-XII-22-6, MLP 77-VII-14-3, MLP 71-VII-14-2, MLP 71-VII-14-1, MLP 71-VII-14-12, MLP 71-VII-14-13, MLP 77-XII-22-49/55, MLP 77-XII-22-8, MLP 77-XII-22-32, MLP 77-XII-22-11, MLP 77-XII-22-18, MLP 77-XII-22-22, MLP 77-XII-22-34, MLP 77-XII-22-23, MLP 77-XII-22-24, MLP 77-XII-22-25, MLP 77-XII-22-26, MLP 77-XII-22-27, MLP 77-XII-22/28, MLP 77-XII-22-43/47, MLP 77-XII-22-12.

Without cracks (38 specimens: 29.70%). MLP 20-368, MLP 20-349, MLP 20-329, MLP 20-383, MLP 20-529, MLP 20-393, MLP 20-429, MLP 20-372, MLP 20-258, MLP 20-342, MLP 20-353, MLP 20-325, MLP 20-336, MLP 20-332, MLP 20-324, MLP 20-346, MLP 20-343, MLP 20-340, MLP 20-332, MLP 20-338, MLP 20-327, MLP 20-341, MLP 20-335, MLP 20-389, MLP 20-380, MLP 20-385, MLP 20-377, MLP 20-373, MLP 20-381, MLP 20-387, MLP 20-390, MLP 20-384, MLP 20-371, MLP 20-366, MLP 20-345, MLP 77-XII-22-14, MLP 77-XII-22-17, MLP 77-XII-22-48.